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Centre for Fish and Fisheries Research

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Centre for Fish and Fisheries Research
Murdoch University, Western Australia

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Table of Contents

2004/045 Relationships between fish faunas and habitat type in south-western Australian estuaries

PRINCIPAL INVESTIGATOR: Dr Fiona Valesini

ADDRESS: Centre for Fish and Fisheries Research
Biological Sciences
Murdoch University
South St, Murdoch
Perth, Western Australia, 6150
Telephone: (08) 9239 8805 Fax: (08) 9239 8899

OBJECTIVES

1. Devise quantitative and readily usable approaches for classifying the local-scale nearshore habitats within a range of estuaries in south-western Australia and predicting the habitat to which any nearshore site in those systems should be assigned.

2. Determine statistically how the compositions of the fish and benthic invertebrate assemblages in selected south-western Australian estuaries are related to habitat type.

3. Formulate a readily usable and reliable method for predicting which fish and benthic invertebrate species are likely to be abundant at any particular nearshore site in one of the above estuaries.

NON-TECHNICAL SUMMARY

OUTCOMES ACHIEVED TO DATE

1. *The production of reliable tools for improving management strategies to conserve the nearshore fish faunas and their key habitats in estuaries, which have been applied to selected systems in south-western Australia.*

This outcome has been achieved through (1) the development of quantitative approaches for, firstly, classifying local-scale nearshore habitats in estuaries and, secondly, predicting the habitat of any nearshore site in those systems and (2) testing the biological validity of the habitat classification produced for each estuary, and thus the extent to which the above approaches can be used to reliably predict the fish and benthic invertebrate species likely to typify the fauna at any nearshore site at any time of year. Such outputs enable, at a spatial scale at which estuarine managers most often work, (i) production of reliable habitat and faunal inventories, against which the effects of future environmental change can be quantified, (ii) identification of those habitats that are most important to key fish and benthic invertebrate species and/or are most biodiverse and (iii) determination of those fish and benthic invertebrate species that are most likely to occur at any nearshore site in an estuary in any season.

2. *The production of a reliable framework for ecologists to investigate ecological inter-relationships among nearshore habitat types in estuaries.*

The project outputs and data collected provide a sound basis for ecologists working at local scales in south-western Australian estuaries to determine which underlying factors of particular habitats have produced the observed relationships between (i) the biota and the environment and (ii) different groups of biota. They also provide a sound framework for investigating the extent to which the fish and benthic invertebrate faunas vary between comparable habitats in different estuaries, and for forecasting the ways in which faunal assemblages and ecological interactions are likely to differ in response to projected environmental change.

The first main component of this study focused on developing fully quantitative and readily usable approaches for (i) classifying the local-scale nearshore habitats within various estuaries in south-western Australia and (ii) predicting the habitat to which any site in these systems should be assigned. The second main component concentrated on examining the extent to which the above approaches could be employed to reliably predict the fish and benthic invertebrate species likely to typify the fauna at any nearshore site in these estuaries at any time of year.

The five estuaries selected for study were the permanently-open Swan and Peel-Harvey estuaries, which are located on the lower west coast, and the seasonally-open Broke and Wilson inlets and the normally-closed Wellstead Estuary, which are situated on the south coast. A large number of environmentally-diverse sites throughout each estuary were initially selected for classification. At each of those sites, measurements for a suite of enduring environmental and biologically-relevant characteristics (*i.e.* those that remain similar over time and influence the distribution of estuarine fauna) were obtained from readily available digital maps and recorded in a Geographic Information System (GIS). These data were then subjected to a combination of multivariate statistical routines to identify those groups of sites in each estuary whose environmental characteristics were not significantly different and thus represented habitat types. Thus, of the 101, 102, 104, 60 and 34 sites chosen throughout the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary, respectively, the classification approach yielded 18, 17, 12, 15 and 6 significantly distinct habitats, respectively. The method for predicting the habitat to which any new nearshore site in each system is most appropriately assigned then involved using, in a novel way, the above classification framework and the enduring environmental data in further multivariate statistical routines. This produced a predictive decision tree for each system, containing a series of quantitative and easily interpretable thresholds for determining the habitat of any new site on the basis of measurements for its enduring environmental characteristics. Trials of this predictive approach demonstrated that new sites in each estuary were successfully allocated to their most appropriate habitat in every case.

To assess the biological applicability of the habitat classification devised for each estuary, the nearshore fish assemblages were sampled at sites representing the various habitats during each season for at least a year, and typically also during the summer and winter of the following year. In addition, the benthic macroinvertebrate, nematode and hyperbenthic faunal assemblages were sampled seasonally for a year at a subset of habitats in the Swan Estuary and, in the case of latter assemblage, also at a subset of habitats in the Peel-Harvey Estuary. These data were used to test the extent to which, in each estuary and season, (i) the composition of the faunal assemblages differed among habitats and (ii) the relative differences among habitats, as defined by their faunal composition, was correlated with that of the enduring environmental data used to classify those habitats. Various water quality measurements and, in the Swan Estuary, sediment parameters, which are often employed in studies aimed at linking the spatial distribution patterns of estuarine fish and/or benthic invertebrate fauna with the environment, were also recorded at the same sites and times at which fauna were collected.

The composition of each type of faunal assemblage differed significantly among habitats in all seasons and all estuaries. The fish and benthic invertebrate species that best characterised the faunas at each habitat in each season were then determined. In the Swan Estuary, the overall extents of the spatial differences in the compositions of the various faunal assemblages were moderate to large, and typically greatest among the fish and nematode faunas and least among the hyperbenthic fauna, the latter of which comprised a large proportion of ubiquitous planktonic taxa with poor swimming ability and thus limited capacity to actively select habitats. Although the extent of the compositional differences among the various habitats differed among faunal types and seasons, one or both habitats in the tidal stretches of the rivers generally contained the most distinct assemblages, which was mirrored by the distinctness of their enduring environmental characteristics. The faunal compositions were also distinct in the entrance channel, but not to the same degree as those in the upper estuary.

While the composition of the fish fauna in the Peel-Harvey Estuary also exhibited moderate to large overall differences among habitats in each sampling season, the extents of those differences were often less than in the nearby Swan Estuary. Moreover, the differences in hyperbenthic composition among habitats in this system were small. Although the faunal compositions at habitats in the tidal rivers and entrance channel of the Peel-Harvey Estuary were among the most distinct in several seasons, they were not as conspicuous or consistently distinct as those in the Swan Estuary. Furthermore, the most pronounced spatial differences in fish faunal composition in the Peel-Harvey Estuary almost always involved a habitat in one of the large basins. Such findings largely reflect major differences in the overall geomorphology of these two estuaries. Thus, the Swan is a drowned river valley system with an essentially linear morphology in which its two major tributaries are located at the opposite end of the system to its single entrance channel. In contrast, the Peel-Harvey is a combination of an interbarrier and basin estuary, and two of its three tributaries are located relatively close to one of its entrance channels, which is some distance from the second and artificial entrance channel.

The overall extents of the differences in fish faunal composition among the various habitats in the Broke and Wilson inlets, both of which are basin systems, and the Wellstead Estuary, a small drowned river valley system, were typically moderate to low. This largely reflected the fact that the fish faunas of these three south coast estuaries, which contained far fewer species than the two west coast estuaries (*i.e.*18-23 *vs* 60-71), were each overwhelmingly dominated by a small suite of hardyhead and/or goby species that can complete their life cycle in estuaries, *i.e. Atherinosoma elongata, Leptatherina wallacei, L. presbyteroides, Pseudogobius olorum* and/or *Afurcagobius suppositus*. The least spatial differences in fish faunal composition were often detected in Wilson Inlet, which, like the normally-closed Wellstead Estuary, either did not open to the sea for the entire 18 month period over which fish were collected for the current study, or was only open for three to four weeks. Furthermore, the geomorphology of Wilson Inlet is largely homogenous and its benthic structure, like that of Broke Inlet, is less diverse than that of the other estuaries. Moreover, the salinities at almost all habitats in Wellstead Estuary during the last sampling season reached levels that approach the tolerance of many fish species, *i.e.* 51-63‰.

The extents of the correlation in spatial pattern (*i.e.* relative spatial differences) between the faunal and enduring environmental data for the various habitats in each season and system paralleled the trends described above for differences in faunal assemblage composition. Thus, moderate to very high matches were obtained in the majority of cases in the Swan Estuary and, to a lesser extent, in the Peel-Harvey Estuary. This indicates that the extent of spatial differences in the enduring environmental measurements among habitats in these systems provide a good to excellent surrogate for identifying spatial differences in the compositions of their faunal assemblages in each season. Thus, the fish and/or benthic invertebrate species likely to typify any nearshore site in these estuaries at any time of year can be confidently predicted by simply assigning that site to its most appropriate habitat using its enduring environmental measurements and the habitat prediction tool developed for each system, and then consulting the lists of characteristic species provided. The reliability of the predictive schemes developed for the Swan and Peel-Harvey estuaries was demonstrated by the general agreement between the species that actually typified the faunal assemblages at various test sites throughout each system *vs* those that were predicted to occur by assigning those sites to their appropriate habitats on the basis of their enduring environmental measurements and then consulting the relevant species lists. In contrast, the spatial patterns among habitats in fish assemblage composition in the Broke and Wilson inlets and Wellstead Estuary exhibited moderate to low and, in several cases in the latter two systems, insignificant correlations with those of their enduring environmental characteristics. Such findings often reflected the lack of differences in fish faunal composition among many habitats in these three systems, despite notable differences in their enduring environmental characteristics. They also sometimes resulted from the effects of the pronounced schooling behaviour of the atherinid species that dominated their fish faunas. However, given the above main causes of the low spatial correlations between the faunal and enduring environmental data in these three estuaries, and that those habitats which did have relatively distinct fish compositions also had distinctive enduring environmental characteristics, it is unlikely that the results of the habitat and fish prediction procedures will produce misleading results. Nevertheless, further sampling of the fish assemblages and testing of the spatial correlations between the faunal and enduring environmental data is recommended for the Wilson Inlet and Wellstead Estuary during periods in which the mouths to those systems have been open for an appreciable time.

Importantly, in most cases in which significant spatial correlations were detected between the complementary faunal assemblage and enduring environmental data in each of the five study

estuaries, the suite of enduring criteria better explained the spatial distribution of the fauna than the complementary suite of water quality variables and, in the case of the benthic macroinvertebrate and nematode assemblages, the suite of sediment parameters. Moreover, in those cases in which the spatial correlations between faunal assemblage and enduring environmental data were not significant, neither were those between the faunal and water/sediment quality data. This implies that the enduring environmental variables are, firstly, providing suitable surrogates for a range of environmental characteristics that influence the distribution of estuarine fish and/or benthic invertebrate faunas and, secondly, capturing other influential elements of the estuarine environment that are not reflected by the water or sediment parameters measured in the field.

Finally, in order to make the current habitat and faunal prediction schemes as simple as possible for end users, an obvious future development of the current approaches is to produce a digital, spatially-continuous habitat map of each estuary in GIS, in which all nearshore waters are classified according to their most appropriate habitat and the various characteristics of the fish and/or benthic invertebrate assemblages that typify each habitat in each season are incorporated as underlying metadata. Thus, users of the scheme would then simply need the geographic coordinates of their site of interest in order to ascertain its habitat and faunal characteristics.

KEYWORDS

Estuarine habitat; habitat classification systems; habitat prediction; estuarine fauna; habitat-faunal relationships

Acknowledgements

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1. General Introduction

1.1 Background

Estuaries are transitional zones between riverine and marine waters (McLusky and Elliott 2004, 2007). These highly complex and dynamic environments, which typically exhibit pronounced physio-chemical differences over a variety of spatial and temporal scales, are crucial for a wide range of fauna, either at particular life-history stages or throughout life. This is frequently attributed to the high levels of primary and secondary productivity, diversity of habitats, calmer waters and greater protection from predation that are often found in these systems (*e.g.* Potter *et al.* 1990, Beck *et al.* 2001, McLusky and Elliott 2004). The importance of estuaries for fish and benthic invertebrates in particular, has been demonstrated and reviewed by numerous workers throughout the world (*e.g.* Levinton 1972, Haedrich 1983, Kennish 1990, Potter *et al.* 1990, Elliot and Dewailly 1995, Mees and Jones 1997, Coull 1999, Potter and Hyndes 1999, Elliott and Hemingway 2002), as has their economic value to the commercial and recreational fishing industries (*e.g.* Pollard 1981, Costa *et al.* 2002, Henry and Lyle 2003, Meynecke *et al.* 2007, Fletcher and Santoro 2008). Moreover, given their environmental and biotic attributes, estuaries and their catchments are major foci for many other types of human activity, such as shipping and boating, agriculture, industry, waste disposal and residential development. To accommodate such uses, the physical and hydrological characteristics of estuaries have often been extensively modified, such as through damming and diverting their major tributaries, dredging, construction of canals and marinas and alteration of their shorelines, and their catchments cleared of large proportions of their natural vegetation (*e.g.* Edgar *et al.* 2000, Kennish 2002, McLusky and Elliott 2004). Throughout Australia, the extent of anthropogenic modification to estuaries and their catchments was well documented in the most recent Australian Catchment, River and Estuary Assessment (Commonwealth of Australia 2002), which, through an evaluation of estuary and catchment use, hydrology and ecology, demonstrated that nearly 30% of these systems are modified or extensively modified. The multitude of environmental problems that are typically associated with anthropogenic uses of estuaries and their catchments, such as eutrophication, salinisation, pollution, anoxia and increasing sedimentation, and the resultant deleterious impacts on estuarine fauna, are now commonly reported, both in Australia (*e.g.* Johnston *et al.* 2003, Schlacher *et al.* 2007, White *et al.* 2007, Becker *et al.* 2009) and throughout the rest of the world (*e.g.* Jackson *et al.* 2001, Buzzelli *et al.* 2002, Kennish 2002, Kemp *et al.* 2005, Lim *et al.* 2006, Bustamante *et al.* 2007).

Despite the scale and intensity of the degradation of estuaries in Australia, and the fact that they are among the most vulnerable environments to the effects of climate change, estuarine conservation lags far behind terrestrial and marine conservation (Edgar *et al.* 2000). It also compares poorly to the highly integrated national initiatives in Europe and the United States to improve the ecological quality of their transitional waters, namely the Water Framework Directive and Clean Water Act, respectively (European Communities 2000, US Clean Water 2002). However, while the Australian Government has recently recognised the need to develop a national scheme for assessing the ecological integrity of estuarine and marine environments, it has also been acknowledged that development of such a scheme is hindered by the lack of reliable baseline information on the environmental and biotic characteristics of these waters (Mount 2008).

Given the environmental complexity of estuaries and the well documented spatio-temporal variability in the characteristics of their fish and benthic invertebrate faunas (*e.g.* Potter and Hyndes 1999, Elliott and Hemingway 2002, McLusky and Elliott 2004), management plans for minimising threats to the environmental health of these systems and conserving those areas that are most critical for key fish and invertebrate species must be cognisant of, firstly, the various habitats they contain and, secondly, the fauna that regularly occupy each of those habitats. Such knowledge is best derived from (i) a quantitative framework for classifying the various habitats in a system of interest based on spatial differences in a suite of environmental criteria and (ii) rigorous sampling regimes for determining the compositions of the faunal assemblages that occupy each of those habitats throughout the year. Establishing sound spatial relationships between differences in habitat type and those in the characteristics of faunal assemblages then provides a strong foundation for developing tools to predict which faunal species are likely to occur at any site on the basis of the habitat type to which it belongs, which has many important applications for estuarine management and ecology.

The importance of habitat classification schemes in providing frameworks for estuarine and coastal management is reflected by the fact that some countries have developed highly comprehensive methods for classifying all waters from a highly localised to a national scale (*e.g.* Davies *et al.* 2004, Madden *et al.* 2005) and/or legislation stating their requirement for strategies to improve the ecological quality of transitional and coastal waters (*e.g.* Ferreira *et al.* 2006). Approaches to classifying estuarine and coastal habitats vary widely, and a discussion of the range of methodologies that have been published throughout the world is provided in Chapter 3. However, as also described in that chapter, the most useful approaches are those that (i) are fully quantitative, (ii) employ a suite of environmental criteria that can be easily and accurately measured from readily available mapped sources and encompass those that are most important in influencing the distribution of biota, (iii) demonstrate statistically that the environmental characteristics of derived habitats are significantly different, (iv) can be applied at the spatial scales at which resource managers and ecologists typically operate, *i.e.* local scales and (v) are adaptable to areas beyond those for which they were initially devised. Moreover, in order to use such classification schemes as a foundation for predicting the fauna at any estuarine site of interest, the biological validity of the resultant habitat types must be verified by demonstrating statistically that spatial differences among habitats reflect those in the composition of the fauna of interest. However, many existing habitat classification and faunal prediction schemes are deficient in one or more of the above criteria.

This study is thus focused on developing approaches, that satisfy each of the criteria outlined above, for, firstly, classifying the various nearshore habitats within a range of estuaries in south-western Australia and, secondly, predicting the habitat to which any nearshore site in those systems should be assigned. The second main component of this study addresses the biological validity of the habitat types identified in each estuary by testing, on a seasonal basis, the extent to which differences among habitats mirror those in the composition of the fish and, in selected systems, benthic invertebrate assemblages. The outcomes of these analyses will thus determine whether the above habitat prediction approach can be employed to reliably predict the fish and benthic invertebrate species likely to typify the fauna at any nearshore site in these estuaries at any time of year. If the latter is confirmed, the results and implications of this project will be invaluable for estuarine management programs and ecology, both now and in the future.

1.2 Need

Since estuaries constitute such an important environment for many recreational and commercial fish species, plans for their management must be based on reliable data if they are to be useful in protecting and, if necessary, restoring crucial estuarine fish habitats. Environmental and fisheries managers and ecologists working in estuaries thus require the following.

1. Sound quantitative data on the ways in which fish species and their different life cycle stages are distributed among the different types of nearshore habitat found in selected estuaries in south-western Australia.
2. An ability to identify rapidly and reliably the particular habitat type to which any site in an estuary should be allocated and therefore be able to predict the likely composition of the fish fauna at that site.

3. Knowledge of the extent and distribution of the various habitat types within each estuary, which can serve as benchmarks against which the ecological impacts of future environmental changes can be gauged.
4. An understanding of the relationships between the benthic invertebrate components of the fauna, particularly those that make major contributions to the diets of fish, and the different types of habitat in selected estuaries. This will facilitate an assessment of the broader implications of changes in the estuarine environment on the fauna as a whole.

1.3 Objectives

4. Devise quantitative and readily usable approaches for classifying the local-scale nearshore habitats within a range of estuaries in south-western Australia and predicting the habitat to which any nearshore site in those systems should be assigned.
5. Determine statistically how the compositions of the fish and benthic invertebrate assemblages in selected south-western Australian estuaries are related to habitat type.
6. Formulate a readily usable and reliable method for predicting which fish and benthic invertebrate species are likely to be abundant at any particular nearshore site in one of the above estuaries.

2. Study Area

Five estuaries in south-western Australia, namely the Swan Estuary (32.055°S, 115.735°E), Peel-Harvey Estuary (32.526°S, 115.71°E), Broke Inlet (34.937°S, 116.373°E), Wilson Inlet (35.026°S, 117.333°E) and Wellstead Estuary (34.392°S, 119.399°E), were selected for study (Fig. 2.1). These systems vary primarily in (i) the frequency with which their mouths are open to the sea, (ii) their overall morphology and (iii) the extent to which they have been anthropogenically modified, as defined by the most recent Australian Catchment, River and Estuary Assessment (Commonwealth of Australia 2002). Thus, the Swan and Peel-Harvey estuaries, which represent a drowned river valley and a combination of an inter-barrier and basin estuary, respectively (Hodgkin and Hesp 1998), remain permanently open to the sea and are considered to be extensively modified through anthropogenic effects (Commonwealth of Australia 2002). The Broke and Wilson Inlets, both of which are basin systems, become closed off from the sea for varying periods during the year (typically from summer to winter) due to the formation of sand bars across their mouths, which are either breached naturally during periods of increased river flow or mechanically (Hodgkin and Hesp 1998, Water and Rivers Commission 2002). The Wellstead Estuary, a small drowned river valley system, can remain closed to the sea for many years and is thus classified as normally-closed (Hodgkin and Clark 1987, Young and Potter 2002). The Wilson Inlet and Wellstead Estuary are considered to be anthropogenically modified, while the Broke Inlet is the only estuary in south-western Australia to be classified as near-pristine (Commonwealth of Australia 2002). More extensive descriptions of each of the five study estuaries are provided below.

2.1 South-western Australia

The south-west coast of Australia experiences a Mediterranean climate of cool, wet winters and hot, dry summers (Gentilli 1971). The mean annual rainfall is *ca* 800 mm in the vicinity of the Swan and Peel-Harvey estuaries, *ca* 1300 and 1000 mm near the Broke and Wilson inlets, respectively, and *ca* 600 mm near the Wellstead Estuary, the latter of which can vary markedly between years. Between 60 and 80% of the rainfall in the catchments of these five estuaries occurs between May and September (www.bom.gov.au; 24/3/09).

The large-scale weather patterns of the south-west region are controlled largely by the latitudinal shift between the warmer and cooler months of a belt of anticyclonic high-pressure systems. Thus, during the warmer months of October to April, this belt is located south of the

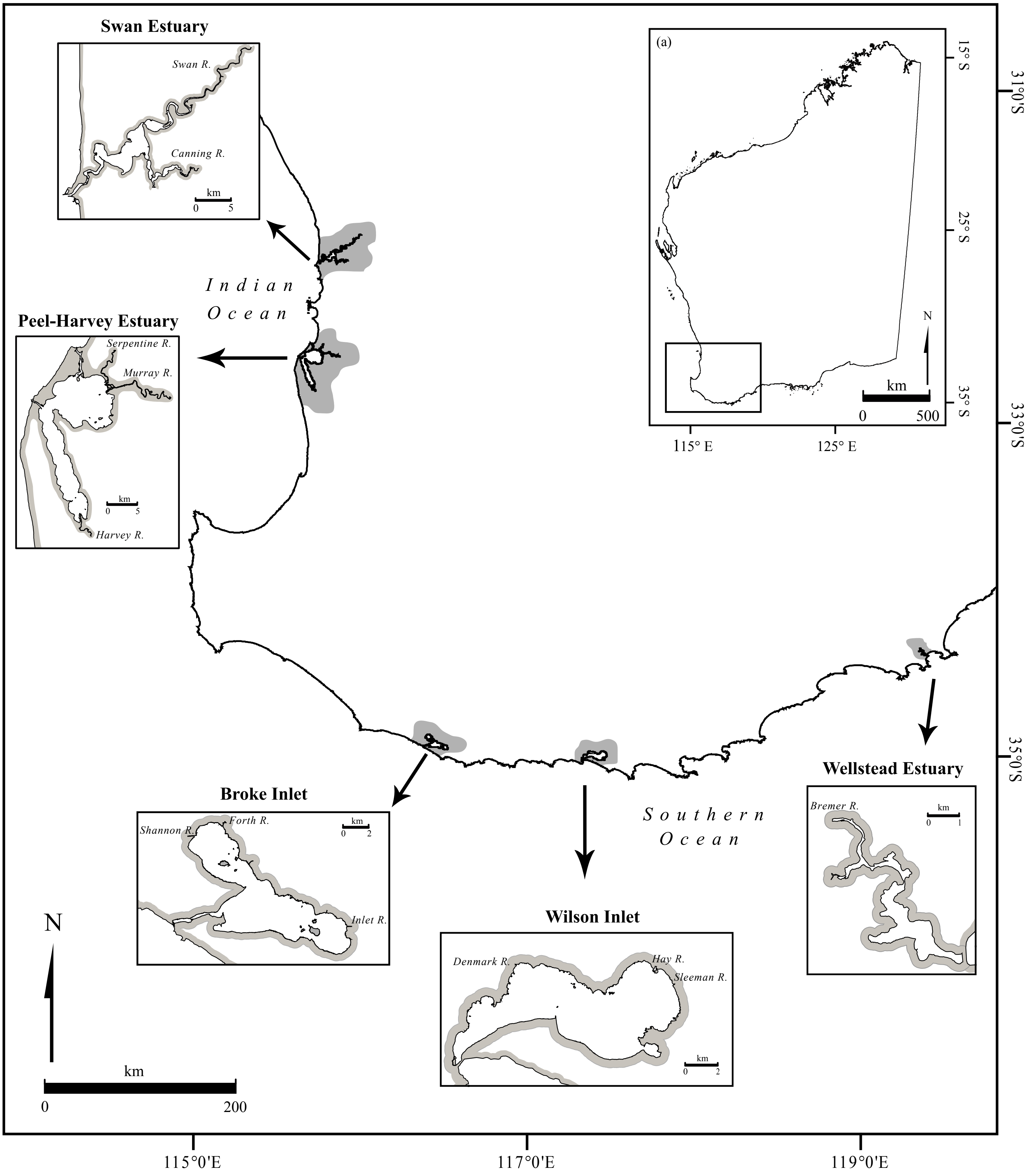

Figure 2.1: Map of south-western Australia showing the location of the five study estuaries. Inset (a) shows the location of the south-western coast in Western Australia.

state and easterly winds predominate (Gentilli 1971). However, these high-pressure systems are displaced northwards during the cooler months of May to September by the strong low-pressure mid-latitude cyclones that occur just south of Australia at this time, resulting in strong westerly and south-westerly winds, cold fronts and most of the annual rainfall (Gentilli 1971, M.P. Rogers and Associates 1995). The winds produced by these large-scale weather systems are modified locally by other wind systems, the most prominent of which is the diurnal land/sea-breeze cycle that occurs in summer. Thus, on the lower west coast, local winds switch between predominantly easterly land-breezes in the morning, to southwesterly-westerly winds during the early afternoon. This sea-breeze system is one of the most consistent and energetic in the world, occurring on *ca* 60% of summer days and frequently exceeding speeds of 15 m s^{-1} (Pattiaratchi *et al.* 1997, Masselink and Pattiaratchi 2001a). Local wind conditions during summer along the south coast of W.A. tend to be more variable, and can cycle between the eastern, northern, southern and western quadrants over a period of days, producing considerable differences in weather conditions. However, near the Broke and Wilson inlets, winds during summer mornings are predominantly easterly, and while easterly winds are still common in the afternoon, those from the south-west and south-east are more prominent. Near the Wellstead Estuary, the local winds in summer are predominantly south-easterly to southerly during both the morning and afternoon. Wind conditions during winter along the south-west coast are variable, but the strongest winds are typically from the south-west, west and/or north-west (www.bom.gov.au; 24/3/09).

The coastline of south-western Australia is classified as microtidal (Davies 1964), experiencing predominantly diurnal tides with a spring range of only *ca* 0.6 m along the lower west coast and *ca* 0.8 m along the south coast (Department of Defence 1998, Ranasinghe and Pattiaratchi 1999). However, subtidal oscillations, which may be caused by effects such as atmospheric pressure changes, gravitational circulations and alongshore wind stress, can cause comparable or larger changes in water level (*e.g.* Hamilton *et al.* 2001, O'Callaghan *et al.* 2007).

The total offshore wave climate along the coast of south-western Australia is characterised by mean significant wave heights (*i.e.* the mean height of the highest one-third of waves during a recording period) of 1.8 m in summer and 2.8 m in winter (Masselink and Pattiaratchi 2001b). These waves are a combination of swell generated by low-pressure mid-latitude cyclones in the Indian and Southern oceans, which approach the coast from a south to south-westerly direction in summer and westerly to south-westerly direction in winter, and seas that are produced from local winds (M.P. Rogers and Associates 1995, Lemm *et al.* 1999). The energy of offshore waves approaching the lower west coast is substantially attenuated by the extensive limestone reef chains that run parallel to the shoreline, and by other nearshore features such as sand banks, islands and headlands (Sanderson and Eliot 1996). Thus, waves reaching the shore in this region are, on average, *ca* 60% of the height of those offshore (Masselink and Pattiaratchi 2001b), and can be far smaller in more sheltered locations (Department of Environmental Protection 1996). Although localised aspects of the nearshore bathymetry and coastal morphology partially attenuate offshore waves approaching the south coast of W.A., they are typically attenuated to a notably lesser extent than along the lower west coast.

2.1.1 Swan Estuary

The Swan Estuary is a drowned river valley system that remains permanently-open to the sea (Hodgkin and Hesp 1998). The estuary is approximately 50 km long and covers a surface area of *ca* 55 km^2 (Swan River Trust 2000). It comprises a narrow winding entrance channel that is about 8 km long and 400 m wide and which has been modified to accommodate a major international shipping port (Fremantle) at its mouth, a central lagoonal basin that is *ca* 13 km long and up to 4 km wide, a much smaller second basin (*ca* 2.5 km long and 1.5 km wide) and the tidal portions of two main tributaries, the Swan and Canning rivers (Fig. 2.1; Thomson *et al.* 2001). These rivers are estuarine for *ca* 25 and 11 km upstream from their mouths, respectively, the latter of which is demarcated by a weir. Water depth varies considerably throughout the system. Thus, Fremantle port has been dredged to a depth 13 m, while the remaining waters in the channel are generally less than 5 m deep. The main basin reaches depths of 21 m in its lower reaches, but the rest of this region of the estuary is typically less than 9 m deep, except for dredged boat channels, and contains extensive areas that are particularly shallow on its southern and eastern shores, *i.e. ca* 0.5 m deep or less. The smaller second basin, which is connected to the main basin by a narrow opening, is also shallow, with water depths of only 1 m in most parts. The tidal portions of the two tributaries of the Swan Estuary are typically between 2 and 3 m in depth, but are up to *ca* 5 m deep in some locations (Thomson *et al.* 2001).

The 121 000 km^2 catchment for this system comprises the relatively small Swan-Canning catchment (*ca* 2 120 km^2) and the much larger Swan and Avon catchments. The former drains the Swan Coastal Plain and houses the city of Perth, which contains *ca* 75% of Western Australia's population (*i.e.* 2 million people; www.abs.gov.au; 27/3/09), while the latter two drain extensive areas of the Darling Plateau (Peters and Donohue 2001, Brearley 2005). Catchment land use is mixed, comprising extensive urban (residential and industrial) zones on the Swan Coastal Plain and agricultural and rural areas on the Darling Scarp (Peters and Donohue 2001). The Swan Estuary has thus been modified extensively by anthropogenic activity (Commonwealth of Australia 2002), including widening and deepening of parts of the system, construction of dams, weirs and diversions on its major tributaries, extensive modification of its shoreline, the development of major drainage networks for stormwater and wastewater discharge and the construction of numerous marinas and jetties. Furthermore, the majority of natural vegetation in its catchment has been cleared and surrounding wetlands reclaimed (*e.g.* Seddon 1972, Riggert 1978, Chan *et al.* 2002).

Tidal height within the estuary is attenuated approximately 1% per kilometre moving upstream from the mouth, and is thus *ca* 85% of that along the coast in the middle reaches of the system (Lewis and Pattiaratchi 1989). River flow is highly seasonal, reflecting the pronounced seasonality of rainfall in this region. The average annual freshwater discharge from the Swan Estuary and its tributaries is *ca* 440 GL (Swan River Trust 2009). However, nearly 60% of that flow is derived from the riverine reaches of the Swan River, which is dammed. Of the remaining discharge, *ca* 60 and 40% is derived from the estuarine reaches of the Swan and Canning rivers, respectively, but only *ca* 17% of the latter flows from areas downstream of the weir that has been constructed on the Canning River (Swan River Trust 2009). The estuary is considered to be partially-mixed and exhibits pronounced differences throughout the year in the extent of vertical salinity stratification, particularly in its upper reaches. This region of the estuary is thus typically highly stratified in spring due to the upstream intrusion of a salt wedge after winter river flows decrease, and only weakly stratified in summer and autumn (Stephens and Imberger 1996).

The substrate of the entrance channel is generally comprised of sand of differing grain sizes and shell fragments and, in some parts, limestone outcrops. These rocky outcrops also extend into the lower reaches of the main basin. Sand comprises the rest of the substrate in both basins, with that in deeper waters containing finer grain sizes. Finer sands, silts and, in some parts, river gravels, are found in the upper reaches, with fine black muds comprising most of the substrate in the deeper waters. The seagrasses *Zostera* sp., *Heterozostera* sp. and *Halophila ovalis* occur in the channel, as do the most diverse macroalgal assemblages in the estuary, comprising rhodophytes (*e.g. Gracilaria comosa*), phaeophytes (*e.g. Cystoseira trinodis*) and chlorophytes (*e.g. Chaetomorpha linum, Enteromorpha prolifera* and *Ulva* sp.; Astill and Lavery 2004). Both *H. ovalis* and *Ruppia megacarpa* are found in the shallow waters of the main basin, but the former dominates, covering about 25% of the surface area of that region of the estuary in the early 1980s (Hillman *et al.* 1995). The macroalgae *G. comosa* and *C. linum* are also common throughout the basins, as is the former species in the upper reaches. However, the above macroalgal assemblages are subject to considerable seasonal variability (Astill and Lavery 2004). Emergent macrophytes, such as bulrushes (*Typha* sp.), also grow along the littoral waters of the upper reaches of the system (Swan River Trust 2001).

2.1.2 Peel-Harvey Estuary

The Peel-Harvey Estuary is a combination of an inter-barrier and basin estuary (Hodgkin and Hesp 1998), and comprises the elongate Harvey Estuary, which lies parallel to the coast, and the connected Peel Inlet, which is roughly circular in shape (Fig. 2.1). The short narrow entrance channel connecting the Peel Inlet to the sea (Mandurah Channel) is natural, while that connected to the Harvey Estuary (Dawesville Channel) was constructed artificially in 1994 to improve flushing of the system and thus alleviate a multitude of environmental problems associated with its highly eutrophic state, including massive blooms of macro- and micro-alage (McComb and Lukatelich 1995, Young and Potter 2003a). The Murray and Serpentine rivers flow into Peel Inlet, while the Harvey River flows into the southern end of Harvey Estuary (Fig. 2.1). This large estuary covers an area of *ca* 130 km^2 (Hodgkin and Hesp 1998), and is the largest inland water body in south-western Australia (Brearley 2005). The Peel Inlet is *ca* 10 km in diameter, while the Harvey Estuary is *ca* 20 km long and up to 3 km wide (Hale and Butcher 2007). Both of these basins contain extensive shallow areas that are <1 m deep and have central waters that reach *ca* 2 m. The 5 km long and 200 m wide Mandurah Channel, which is dredged to maintain its opening to the sea, reaches depths of about 4 m, while the Dawesville Channel, which is *ca* 2.5 km long and 200 m wide, is between 4 and 6 m deep (Hale and Butcher 2007). The tidal portion of the Murray River is approximately 20 km long and reaches depths of *ca* 8 m, while that of the Serpentine River is *ca* 8 km long and up to 5 m deep.

The catchment of the Peel-Harvey Estuary covers about 11 000 km^2 (www.ozcoasts.org.au; 27/3/09), and has been cleared extensively for agriculture, horticulture and, on the low-lying Swan Coastal Plain, for urban development. The latter is reflected by the growing city of Mandurah and its surrounding suburbs, which house approximately 56 000 people (www.abs.gov.au; 27/3/09).

The average annual river discharge into the Peel-Harvey Estuary is *ca* 620 000 ML, 45, 35 and 20% of which is derived from the Murray, Harvey and Serpentine rivers, respectively (McComb and Humphries 1992). Each of these three rivers and/or their major tributaries are dammed, and have been modified extensively through desnagging, diversion and shoreline modification. The most prominent of these modifications is the Harvey River diversion, which drains the majority of the flow from that river to the sea, rather than into the estuary (Brearley 2005, Hale and Butcher 2007). Given the wide and shallow nature of the basins and the local climate, annual evaporation from the system is high, and is estimated to be, on average, approximately 30% of the annual river flow (Hodgkin *et al.* 1981). Construction of the Dawesville Channel increased the tidal range within the Peel-Harvey Estuary from <0.1 m to *ca* 0.3 m (Brearley 2005, Hale and Butcher 2007). It has also affected the hydrological mixing of the system. Thus, vertical salinity stratification of the water column in the deeper waters of the basins has been reduced and, while stratification still occurs, it generally persists for only a few months over the winter period. However, such stratification is now more prominent in the estuarine portion of the rivers during spring, as the salt-wedge is able to move further upstream (Brearley 2005, Hale and Butcher 2007).

The substrate of the basins is comprised predominantly of sands of various grain sizes and silts, while that of the rivers comprises mainly soft muds. The main aquatic macrophytes in the basins include the seagrass *H. ovalis* and, to a lesser extent, *R. megacarpa*. *Heterozostera* sp. is also found growing on the sandy substrates of the Mandurah Channel. Macroalgae in the basins, and particularly in the shallows of Peel Inlet where the largest accumulations are found, are dominated by green algae, the majority of which is *Chaetomorpha* sp (Wilson *et al.* 1999). Samphire (*Sarcocornia* sp. and *Halosarcia* sp.) and the sea rush (*Juncus kraussii*) are also present along the littoral margins of parts of the basins and tidal portions of the rivers (Brearley 2005, Hale and Butcher 2007).

2.1.3 Broke Inlet

Broke Inlet is a large basin estuary that is 15 km long, up to 4 km wide and has a surface area of *ca* 48 km^2. It has a small entrance channel, *ca* 3.5 km long and up to 250 m wide, which connects to the basin approximately half way along its southern shore (Hodgkin and Clark 1989; Fig. 2.1). The mouth of this channel, which is fully exposed to south-westerly seas and swell, becomes blocked off from the sea by a marine sand bar that typically forms during summer and may be up to 500 m long and 1.8 m above mean sea level. However, due to the high wave energy along the coast, waves sometimes break over this bar. The bar is either broken naturally or artificially during winter/early spring when seasonal river flow causes water levels inside the estuary to rise. The bar has been opened every year between 1964 and 1989 except 1969 and 1986, but records of bar openings since then are more sporadic (Hodgkin and Clark 1989, Brearley 2005). The bar may remain open for anywhere between one and six months, depending on climatic and oceanographic conditions (Hodgkin and Clark 1989). Throughout the period in which fish were sampled in Broke Inlet during the current study (*i.e.* spring 2007 to winter 2008), the bar opened in early September 2007 and closed in mid January 2008, then reopened at the start of August 2008.

Broke Inlet is fed by three rivers, namely the Shannon, Forth and Inlet rivers, which enter the system on the western, north-western and eastern sides of the basin, respectively. They are estuarine for approximately 3 km, 300 m and 2 km, respectively, upstream from their mouths. Shallow and dynamic sand banks (*i.e. ca* 0.5 m deep) broadly separate the main basin into three smaller basins, one of which is located in the middle and the others to the west and east, and which reach depths of *ca* 4, 3 and 2 m, respectively. Shallow banks also form around the periphery of the main basin, but are particularly extensive on the eastern side and middle part of the northern shore. Water depths in the entrance channel are *ca* 5-6 m, while those in the basin vary considerably depending on river flow and bar state, but typically reach 2-3 m. The Shannon River is typically *ca* 3 m deep, but can reach 10 m in depth (Hodgkin and Clark 1989). However, there is little water depth information for the other two tributaries.

The 928 km^2 catchment for Broke Inlet is located entirely within the D'Entrecasteaux and Shannon national parks, approximately 95% of which is forested and thus subject to minimal human impact. The former park, which surrounds the estuary, contains dune systems, endemic coastal flora and fauna and nationally-significant wetlands, while the latter, which houses the middle and upper reaches of the Shannon River, contains extensive old and new-growth karri forest (Department of Conservation and Land Management 2005). While the shoreline of Broke Inlet and its islands are included in the management plan for the D'Entrecasteaux National Park, its waters are not. However, it has been recommended for marine reserve status (Conservation and Land Management Act 1984).

Riverine water entering Broke Inlet is highly tannin-stained and, on average, comprises *ca* 160 GL per year (Hodgkin and Clark 1989). The Shannon, which is *ca* 47 km long, is the largest of the three rivers and is four to five times longer than either the Inlet or Forth River (Brearley 2005). During those periods when the mouth of the estuary is open, the influence of oceanic tides on water levels in the estuary is minimal (*i.e.* <0.1 m), due to the large degree of attenuation by the narrow entrance channel. Changes in barometric pressure thus cause more notable changes in water level within the estuary, both when the bar is open and closed. Data on the water mixing patterns within Broke Inlet is limited, but available information indicates that the extent of vertical salinity stratification is highly dependent on the bar state, extent of river flow and wind conditions. Thus, when the bar is closed, salinity is generally uniform throughout much of the system. Some stratification may occur during periods of high river flow, but is likely to be eliminated relatively quickly in the wide basin by wind mixing. When the bar is open and river flow is high, pronounced stratification of the water column has been recorded throughout the estuary, as marine waters penetrate upstream beneath the fresh riverine waters. This stratification may persist for some time after bar closure in the narrow reaches of the channel (Hodgkin and Clark 1989).

The substrate of the entrance channel is comprised predominantly of marine sands, though some patches of limestone are also present. The basin also has a largely sandy substrate, though contains a number of granite outcrops, the most pronounced of which are Shannon and Clarke islands, located in the middle of the western and eastern basins, respectively. Other granite outcrops occur along the north-eastern shore of the basin. Some clay substrates are also found in this area, and along the banks of the Shannon River (Hodgkin and Clark 1989). The deeper waters of the basin contain fine sands and muds (J. Tweedley, pers. obs.). Beds of the seagrass *R. megacarpa* are present in the middle to upper reaches of the channel and in some areas of the basin. Macroalgal and seagrass wrack from nearby marine waters also wash into the estuary when the bar is open (Brearley 2005).

2.1.4 Wilson Inlet

Wilson Inlet is a basin system that has very similar dimensions to the nearby Broke Inlet. Thus, it is about 14 km long, up to 4 km wide and has a surface area of *ca* 48 km^2, making these two estuaries the largest on the south coast (Brearley 2005). However, unlike the latter system, Wilson Inlet has a poorly-defined entrance channel (Fig. 2.1). The entrance, which is located at the western end of the basin, is *ca* 300-900 m wide and becomes seasonally blocked off from the sea by a sand bar that is about 500 m wide, 150 m long and 1.8 m above mean sea level (Water and Rivers Commission 2002). This dynamic sand bar, which forms as a result of the onshore transport of sediment by persistent swell waves (Ranasinghe and Pattiaratchi 1999), typically accretes during summer and persists throughout autumn. It has been opened mechanically each winter since the 1920s when waters inside the estuary exceed 1 m above sea level, in order to prevent flooding of surrounding land (Ranasinghe and Pattiaratchi 1999, Water and Rivers Commission 2002, Brearley 2005). Over the period in which the fish assemblages were sampled in Wilson Inlet during the current study (*i.e.* winter 2006 to summer 2008), the bar was only open for approximately one month between early October and November 2006. The basin reaches depths of 4-6 m in its middle region, and the shallow banks along the shores (<1 m deep) often dry out during summer. A shallow and unstable sand delta (<0.5 m deep) extends throughout the entrance to the estuary. The system is fed by three main rivers, the Denmark River, which enters the basin on the north-western side, and the Hay and Sleeman rivers, whose mouths are located on the north-eastern side of the basin. The estuarine portions of the Denmark and Hay rivers reach *ca* 4 m in depth, and frequently have steep banks up to 3 m high (Brearley 2005).

The catchment of Wilson Inlet covers *ca* 2 300 km^2 (Water and Rivers Commission 2002). Approximately 70 and 30% of the catchments for the Hay and Denmark rivers, respectively, have been cleared for farming and horticulture (Brearley 2005), while a considerable portion of the remaining land is still forested. The catchment contains the town and shire of Denmark, which houses a growing residential population of *ca* 4 500 people (www.abs.gov.au; 27/3/09) and is a popular tourist destination.

The mean annual river flow entering Wilson Inlet is *ca* 200 GL. The Hay River carries about 65% of this water, while the Denmark and Sleeman rivers, the former of which is dammed, contribute about 25 and 10%, respectively (Hodgkin and Clark 1988, Water and Rivers Commission 2002). Like Broke Inlet, river water flowing into Wilson Inlet is highly stained with tannins. Also like the former system, changes in water level associated with oceanic tide (*i.e.* when the entrance is open) are very small (<0.1 m), and the influence of changes in barometric pressure is typically greater, *i.e. ca* 30 cm (Water and Rivers Commission 2002). The level of vertical salinity stratification in the deeper waters of the basin of Wilson Inlet depends on the degree of intrusion of marine waters, the salinity of basin waters when marine exchange occurs and the degree of wind mixing. Thus, about one month after the entrance is opened during winter or spring, denser marine waters penetrate the basin, lying below the fresh waters derived from seasonal river flow. This stratification persists unless wind conditions are sufficient to continually mix the water column. However, any such mixing is generally temporary, as the halocline is quickly reestablished by successive tidal inflows. Vertical stratification is least pronounced after the mouth of the estuary has closed, in which conditions throughout the water column are predominantly marine or relatively fresh in periods of low and high river flow, respectively. The lack of vertical stratification under these conditions is also assisted considerably by wind mixing, which can be extensive, as reflected by the fact that local winds can generate waves of up to 1.2 m high in the basin of Wilson Inlet (Water and Rivers Commission 2002).

The substrate in the entrance of Wilson Inlet comprises mainly marine sands and shell fragments, while that in the nearshore waters of the basin contains predominantly sands of varying grain sizes and that in the deeper waters of this region are mainly silt. The western and northern shores of the basin also contain extensive granite outcrops (Brearley 2005). The seagrass *R. megacarpa*, along with associated epiphytic algae, grows extensively throughout Wilson Inlet, which has increased considerably since the 1970s. The prolific growth of this macrophyte has caused problems for boat operation and led to extensive beach fouling throughout the system (Department of Environment 2003). The biomass of *R. megacarpa* in

Wilson Inlet undergoes pronounced variability throughout the year, with that in summer estimated to be twice that in winter, and also among years. Furthermore, this highly adaptable seagrass exhibits different life history strategies in different parts of the estuary depending on local environmental conditions, and thus spatial variability in its characteristics is also considerable (Department of Environment 2003).

2.1.5 Wellstead Estuary

Wellstead Estuary is a small drowned river valley system that is about 13 km long and has a surface area of only *ca* 2.5 km^2. It has a very short entrance channel that broadens into a lagoonal basin up to 600 m wide, and single tributary, the Bremer River, which is about 70 km long (Fig. 2.1; Hodgkin and Clark 1987). The basin and channel are generally less than 1 m in depth, while water depths reach 5 m on bends in the upper estuary. The mouth of the entrance channel, which is sheltered from south-westerly seas and swell by a granite coastal headland, is normally blocked off from the sea by a marine sand bar that is *ca* 300 m wide, up to 2 m above mean sea level and forms an extensive tidal delta extending *ca* 1 km upstream of the mouth (Hodgkin and Clark 1987). For example, Wellstead Estuary was closed between 1972 and 1977 (Hodgkin and Clark 1987) and other records show it was closed between October 1993 and September 1997, after which it opened for approximately one month, then remained closed for the next six months (Young and Potter 2002). The bar was closed for the duration of the faunal sampling undertaken in the current study (*i.e.* winter 2006 to summer 2008), but it had been open between early June 2005 and late April 2006.

The catchment of the Wellstead Estuary is small, covering only 716 km^2. Approximately 80% of this catchment has been cleared for pasture, and the remaining land near the upper reaches of the estuary comprises Shire Reserve that is surrounded by the Fitzgerald River National Park (Hodgkin and Clark 1987, Brearley 2005).

Hydrological data for Wellstead Estuary is limited. The mean annual river flow into the system is estimated to be *ca* 2.64 GL and, when the bar is open, marine waters penetrate *ca* 2 km upstream from the mouth (Hodgkin and Clark 1987). Salinities throughout this system become extremely hypersaline during periods of mouth closure, low river flow and high temperatures (Young and Potter 2002, Brearley 2005). Vertical stratification of the water column in deeper areas of the estuary would thus be likely following periods of river flow, particularly in the narrower middle to upper reaches of the system that would be less likely to experience wind mixing.

The substrate of the middle to upper reaches in the Wellstead Estuary is dominated by grey to black mud, while that of the lowermost reaches is dominated by marine sands. Rocky banks are also prevalent on the eastern shore of the middle reaches. The seagrass *R. megacarpa* is prolific throughout the shallows of the system, particularly in the lower and middle reaches, and samphire (mainly *Sarcocornia blackiana*) grows extensively along the littoral margins of the middle to upper estuary. The sea rush *J. kraussii* is also present along the banks in some reaches of the system (Hodgkin and Clark 1987). Marine macrophyte wracks are also washed into the system when the bar is open, or when particularly heavy seas wash over the bar.

3. Quantitative approaches for classifying and predicting local-scale habitats in estuaries

3.1 Introduction

The ecological, commercial and recreational importance of estuaries, and the range of anthropogenic pressures that threaten their condition and function, are well documented by a multitude of studies throughout the world (*e.g.* Potter and Hyndes 1999, Edgar *et al.* 2000, Jackson *et al.* 2001, McLusky and Elliot 2004, Kemp *et al.* 2005). Those studies emphasise that estuarine ecologists and resource managers need to possess (i) sound knowledge of the environmental characteristics of the systems under their jurisdiction or study, (ii) quantitative data on the faunal assemblages of those systems at appropriate spatial and temporal scales and, often most importantly, (iii) an ability to reliably predict the types of biota likely to occur at any estuarine site and (iv) an understanding of the ecological consequences of environmental change.

During the last few decades, many efforts at managing environmental resources in coastal waters have shifted from attempts to conserve species to those aimed at preserving the structure and processes of habitats and, at larger scales, ecosystems (*e.g.* Allee *et al.* 2000, Zacharias and Roff 2000, Diaz *et al.* 2004, Gregr and Bodtker 2007). It is now commonly acknowledged that this requires protection of both distinctive and representative habitats and different habitat mosaics (Roff and Taylor 2000, Banks and Skilleter 2002, Roff and Evans 2002, Skilleter and Loneragan 2003). It thus follows that an essential prerequisite for achieving this level of environmental management is a reliable classification framework for characterising habitats within an area of interest (Roff and Taylor 2000, Diaz *et al.* 2004, Kurtz *et al.* 2006, Hume *et al.* 2007, Mount *et al.* 2007, Snelder *et al.* 2007). This classification then provides a reliable foundation for investigating the biota that occupy those habitats, ascertaining the ecological processes that occur within them and developing tools to predict which species are likely to occur at any site on the basis of its assigned habitat type (Roff and Taylor 2000, Diaz *et al.* 2004, Kurtz *et al.* 2006, Hume *et al.* 2007, Snelder *et al.* 2007). The latter has countless applications for environmental planning, monitoring and ecology and is now often considered to be the main objective of many species-environment studies (*e.g.* Schoch and Dethier 1996, Zacharias *et al.* 1999, De'ath 2002, Valesini *et al.* 2004). The extent to which habitat classification schemes underpin sound environmental management is reflected by the fact that several countries have developed legislation stating their requirement for coastal and transitional waters, *e.g.* the

European Water Framework Directive and the United States Clean Water Act (European Communities 2000, Ferreira *et al.* 2006).

It is important to distinguish between habitat maps derived from a classification scheme and those created from seabed mapping techniques that delineate geomorphological features associated with the substrate. The former are produced from a framework that collates information on spatial differences in the environment and can systematically assign sites to a group using specified differences in a suite of criteria (Diaz *et al.* 2004, Valentine *et al.* 2005, Snelder *et al.* 2007). However, in several cases, the latter do not employ such decision rules and represent only benthic features, such as seabed topography and texture, different substrates or broad groups of sessile biota (Diaz *et al.* 2004, Valentine *et al.* 2005). Advances over recent decades in the ability and availability of remote sensing and acoustic methods for determining seabed features and Geographic Information Systems (GIS) for spatially representing such data, have led to a proliferation of the latter type of benthic habitat maps. While such information commonly provides an important component of coastal habitat classification schemes (*e.g.* Kenny *et al.* 2003), it provides no systematic framework for defining and, more importantly, predicting habitat types, and has no relevance beyond the area for which it was created. Furthermore, as they rely largely on benthic features, seabed mapping techniques fail to capture the full variety of other attributes that typically comprise a biologically-relevant habitat, such as differences in wave exposure or water quality.

Numerous habitat classification schemes for coastal and/or estuarine waters have been published in the scientific and grey literature or are available as web-based information systems (*e.g.* European Nature Information System, Digby *et al.* 1998, Interim Marine and Coastal Regionalisation for Australia Technical Group 1998, Roff and Taylor 2000, Roy *et al.* 2001, Banks and Skilleter 2002, Pihl *et al.* 2002, Connor *et al.* 2004, Madden *et al.* 2005, Ball *et al.* 2006, Hume *et al.* 2007, Mount *et al.* 2007, Snelder *et al.* 2007). They can be broadly categorised by whether they are based on a hierarchical (nested) series of decision rules or are non-hierarchical, employ largely abiotic or biotic criteria and the spatial and/or temporal scales they encompass. However, the most useful schemes are those that (1) are based on fully quantitative data and decision rules, (2) employ a suite of enduring environmental criteria that can be easily and accurately measured from readily available mapped data and encompasses those that either directly influence the distribution of biota or provide good surrogates for influential variables, (3) are flexible in their ability to incorporate new data and be applied to areas beyond those for which they were developed, (4) are applicable at the spatial scales at which most resource managers and ecologists operate, *i.e.* local to regional scales, (5) are easy to use and (6) can be used to reliably predict the habitat of any new site (*e.g.* Zacharias *et al.* 1999, Roff and Taylor 2000, Banks and Skilleter 2002, Roff *et al.* 2003, Valesini *et al.* 2003, Madden *et al.* 2005, Hume *et al.* 2007, Snelder *et al.* 2007). However, many existing habitat classification schemes are deficient in one or more of the above criteria. Another important criterion, which is surprisingly lacking in almost all existing coastal and/or estuarine habitat classification schemes, is a statistical demonstration that the environmental characteristics of the derived habitats differ significantly, rather than assumed to be so. An exception is provided by Valesini *et al.* (2003).

In order to improve strategies to address the numerous anthropogenic and environmental pressures threatening the ecological health of estuaries in south-western Australia (*e.g.* Commonwealth of Australia 2002), resource managers and ecologists require a reliable and rigorous scheme for classifying the various local-scale habitat types found within those systems. Although a hierarchical scheme for classifying the intertidal and subtidal habitats in Australian estuarine and coastal waters is being developed (Mount *et al.* 2007), this classification is based largely on substrate and benthic "structural macrobiota" (*e.g.* seagrass), is not fully quantitative and does provide a statistical demonstration that the characteristics of derived habitats differ significantly. Furthermore, most of the schemes available for identifying local habitats within estuaries in other parts of the world do not satisfy at least one of the criteria outlined above. The main aims of this component of the current study were thus as follows.

(1) Devise an approach for classifying nearshore habitats within a range of estuaries in south-western Australia which has the following characteristics; (i) fully quantitative, (ii) ascertains statistically that derived habitat types are significantly different, (iii) based on measurements of a suite of enduring, biologically-relevant and easily obtainable environmental criteria, (iv) able to accommodate new environmental criteria and (v) directly pertinent to managers and ecologists working at local scales.

(2) Develop a quantitative and readily usable method for predicting the habitat type to which any new nearshore site in a study estuary should be assigned.

The south-western Australian estuaries selected for study include the permanently-open Swan and Peel-Harvey estuaries, the seasonally-open Broke and Wilson inlets and the normally-closed Wellstead Estuary. Extensive descriptions of the geomorphological and hydrological features of each of the above estuaries, and the extent to which they have been anthropogenically modified, are provided in Chapter 2.

3.2 Materials and Methods

3.2.1 Data sources and preliminary data processing

The main data sources employed for identifying the various habitat types in nearshore shallow waters (< 2 m deep) of each estuary, ranging from the mouth to the extent of tidal influence, were (i) a high resolution and digitally georeferenced remotely sensed image, *i.e.* the red, green and blue bands of digital aerial photos (1 pixel=40 cm) or Quickbird satellite images (1 pixel=2.4 m) and (ii) high resolution bathymetric data (one depth sounding per 10-50 m). All preliminary processing of these mapped data and the subsequent measurement of the suite of enduring environmental variables employed in the habitat classification and prediction approaches for each estuary (see subsection 3.2.2) were carried out using GIS software Idrisi Kilimanjaro v14 or ArcGIS v9.1.

The above data for each system were prepared for measuring the suite of enduring variables by (i) tracing the shoreline, including the outline of any islands or larger structures such as marinas, from the remotely sensed image and (ii) constructing a digital elevation model (DEM) by subjecting the bathymetric data to triangular irregular network (TIN) interpolation. The outline and DEM of each estuary were then used in combination to mask out all unwanted areas for each band of the remotely sensed images, namely all waters greater than 2 m deep and land. The masked bands for each image were then further prepared for measuring the areas of the various substrate/submerged vegetation types they contained (see subsection 3.2.2) by enhancing differences in the spectral reflectance of pixels belonging to different benthic categories. Thus, spectral “noise” resulting from the misreading of light characteristics on the day the image was taken was removed by subjecting the data for each of the three colour bands to an unstandardised Principle Components Analysis (PCA). The principal component (PC) that accounted for the least variation was considered to represent mainly noise, and the eigenvector values from the remaining PCs were then used to produce data for three new noiseless bands. The influence of water depth on the level of light reaching the benthos was then reduced for each noiseless band by employing a water correction equation based on that devised by Lyzenga (1978).

3.2.2 Measurement of enduring environmental variables

A large number of environmentally diverse nearshore sites were initially selected throughout each estuary, which were considered likely to capture the full extent of their nearshore habitat diversity. Thus, 101, 102, 104, 60 and 34 sites were selected throughout the

Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary, respectively (Figs 3.2.2.1-3.2.2.5). These sites were chosen on the basis of visual assessment of the high resolution images of each system and several reconnaissance trips in the field. Each site was defined as all waters within a 100 m radius of a central point on the shoreline.

The following three broad categories of enduring environmental variables were measured at each site in each estuary, thus providing the data required to allocate those sites to their respective habitat types. These variables are summarised in Table 3.2.2.1.

(1) Location with respect to marine and riverine water sources

This group of variables was intended mainly as a surrogate for the range of water quality parameters that typically vary spatially throughout an estuary due to differences in the extent of mixing between tidal and riverine waters, such as salinity, water temperature, dissolved oxygen concentration, water colour, turbidity and ion composition. Note that, while these water quality variables are not necessarily expected to vary in accordance with a simple gradient from estuary mouth to the riverine extent of tidal influence, they are likely to exhibit spatial differences throughout those systems.

In those estuaries whose overall morphology (i) was predominantly linear with respect to the locations of the major sources of tidal *vs* riverine waters and (ii) exhibited pronounced "S-shaped" formations somewhere along its length, *e.g.* the Swan Estuary (Fig. 3.2.2.1), the location of each nearshore site was quantified by measuring its distance from the estuary mouth along a line drawn down the middle longitudinal axis of the estuary (Fig. 3.2.2.6). This "midline" was constructed by calculating the midpoint between opposing banks at regular intervals along the estuary and then joining those points. In those estuaries whose overall morphology was essentially non-linear, *e.g.* the Peel-Harvey Estuary (Fig. 3.2.2.2), the location of each site with respect to its vicinity to marine and freshwater sources was quantified by determining their latitude and longitude.

(2) Exposure to wave activity

This group of variables reflected the exposure of each site to waves generated by local winds (*i.e.* fetch in each cardinal direction and that along the bearing perpendicular to the aspect of each site) and the impact of local bathymetry on waves as they approach the shoreline (*i.e.* average slope of the substrate and distance to the wave shoaling margin).

Table 3.2.2.1: Suite of enduring environmental variables employed in the habitat classification schemes for the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary, including the broad category to which they were assigned, their unit of measurement and the data transformation (Tr.) and weighting (Wt) applied prior to analysis. L= location; E=exposure; S=substrate/submerged vegetation type.

			Swan Estuary		**Peel-Harvey Estuary**		**Broke Inlet**		**Wilson Inlet**		**Wellstead Estuary**	
Broad category	Enduring environmental variable	Unit	Tr.	Wt	Tr.	Wt	Tr.	Wt	Tr.	Wt	Tr.	Wt
L	Distance from estuary mouth	m	√	100	-	-	-	-	-	-	√	100
L	Latitude	°	-	-	none	50	none	50	none	50	-	-
L	Longitude	°	-	-	none	50	none	50	none	50	-	-
E	Direct fetch	m	√	14.28	√	14.28	√	14.28	none	14.28	√	14.28
E	N fetch	m	√√	14.28	√√	14.28	√√	14.28	√√	14.28	√√	14.28
E	E fetch	m	√√	14.28	√√	14.28	√√	14.28	√√	14.28	√√	14.28
E	S fetch	m	√√	14.28	√√	14.28	√√	14.28	√√	14.28	√√	14.28
E	W fetch	m	√√	14.28	√√	14.28	√√	14.28	√√	14.28	√√	14.28
E	Distance to 1-2 m depth*	m	√√	14.28	√√	14.28	√√	14.28	√	14.28	√	14.28
E	Slope	°	√√	14.28	√√	14.28	√√	14.28	√	14.28	√	14.28
S	% Submerged aquatic vegetation	%	√	20	√	16.67	√√	100	none	50	√	20
S	% Rock	%	√	20	√	16.67	-	-	none	50	√	20
S	% Snags	%	√	20	√	16.67	-	-	-	-	√	20
S	% Reeds	%	√	20	√	16.67	-	-	-	-	√	20
S	% Bivalve beds	%	√	20	-	-	-	-	-	-	-	-
S	% Jetty	%	-	-	√	16.67	-	-	-	-	-	-
S	% Samphire	%	-	-	√	16.67	-	-	-	-	√	20

* wave shoaling margin located at a water depth of 1 m in Broke Inlet and 2 m in all other systems.

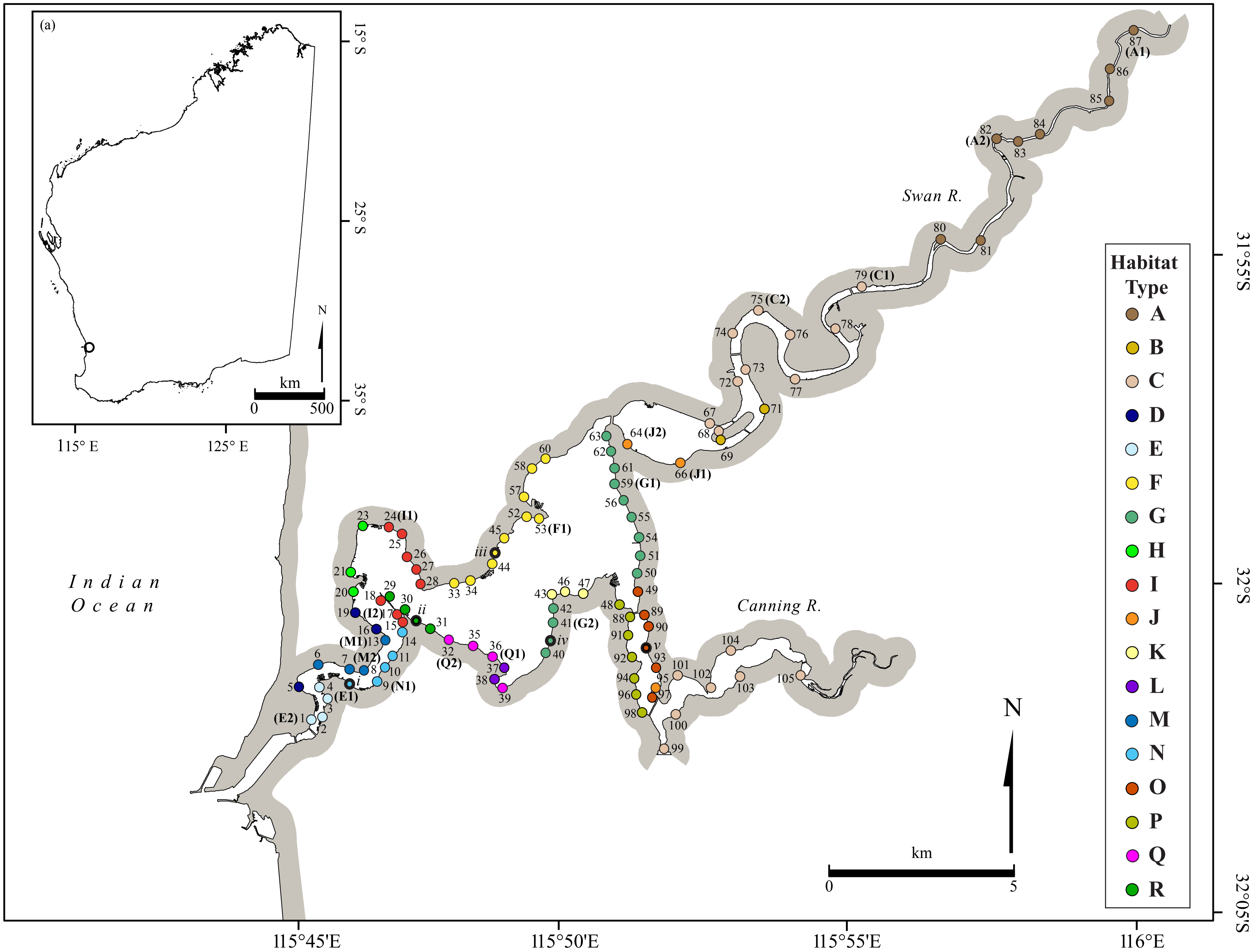

Figure 3.2.2.1: Map of the Swan Estuary showing the location of the 101 nearshore study sites and the habitat type to which each site was assigned by the CLUSTER and SIMPROF procedures (○), sites at which faunal and water quality measurements were collected (bold text in brackets) and the location, number and habitat of new nearshore sites chosen to demonstrate the use of the habitat prediction procedure (◉). Inset (a) shows the location of the Swan Estuary in Western Australia.

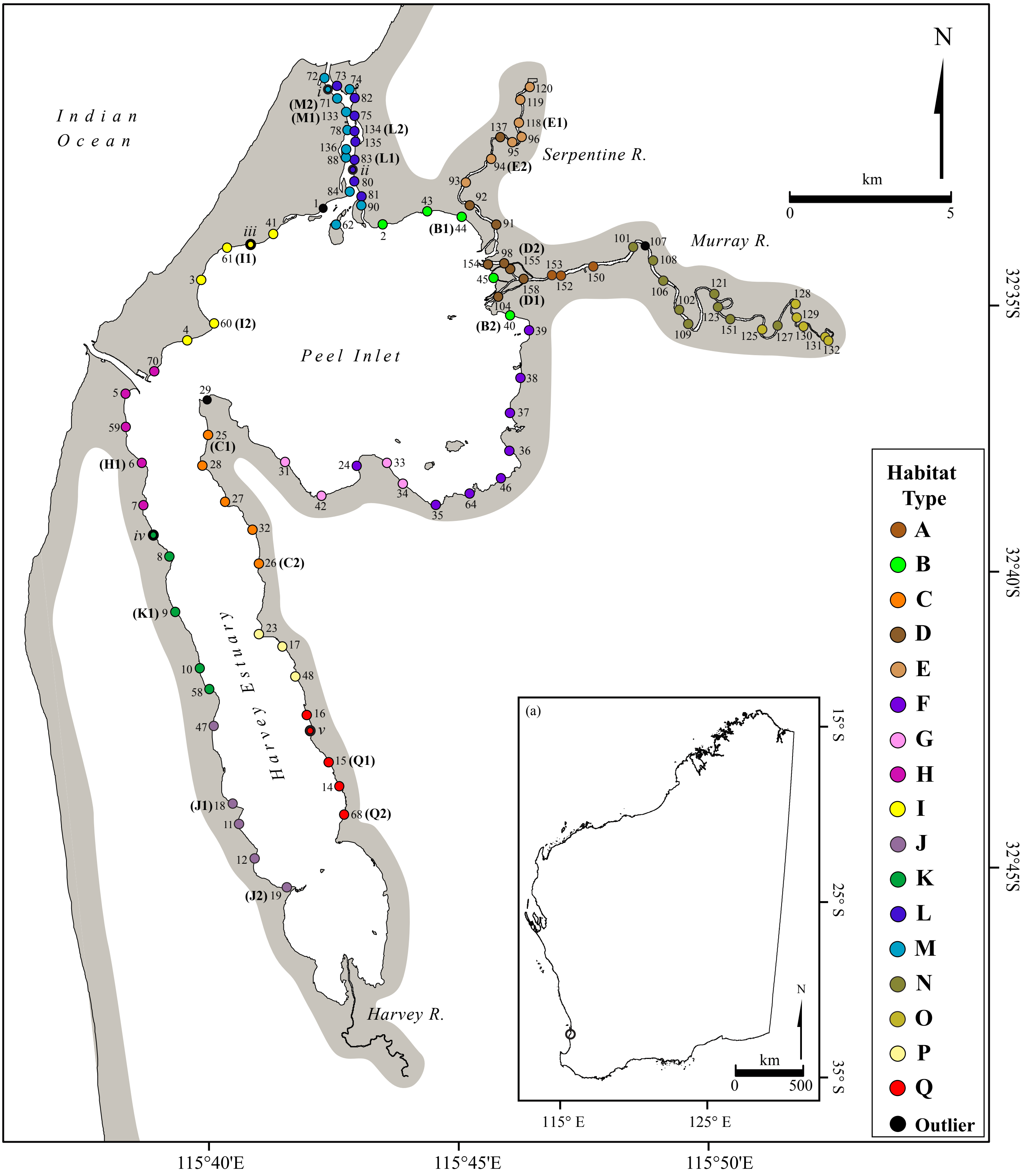

Figure 3.2.2.2: Map of the Peel-Harvey Estuary showing the location of the 102 nearshore study sites and the habitat type to which each site was assigned by the CLUSTER and SIMPROF procedures (●), sites at which fauna and water quality measurements were collected (bold text in brackets) and the location, number and habitat of new nearshore sites chosen to demonstrate the use of the habitat prediction procedure (◉). Inset (a) shows the location of the Peel-Harvey Estuary in Western Australia.

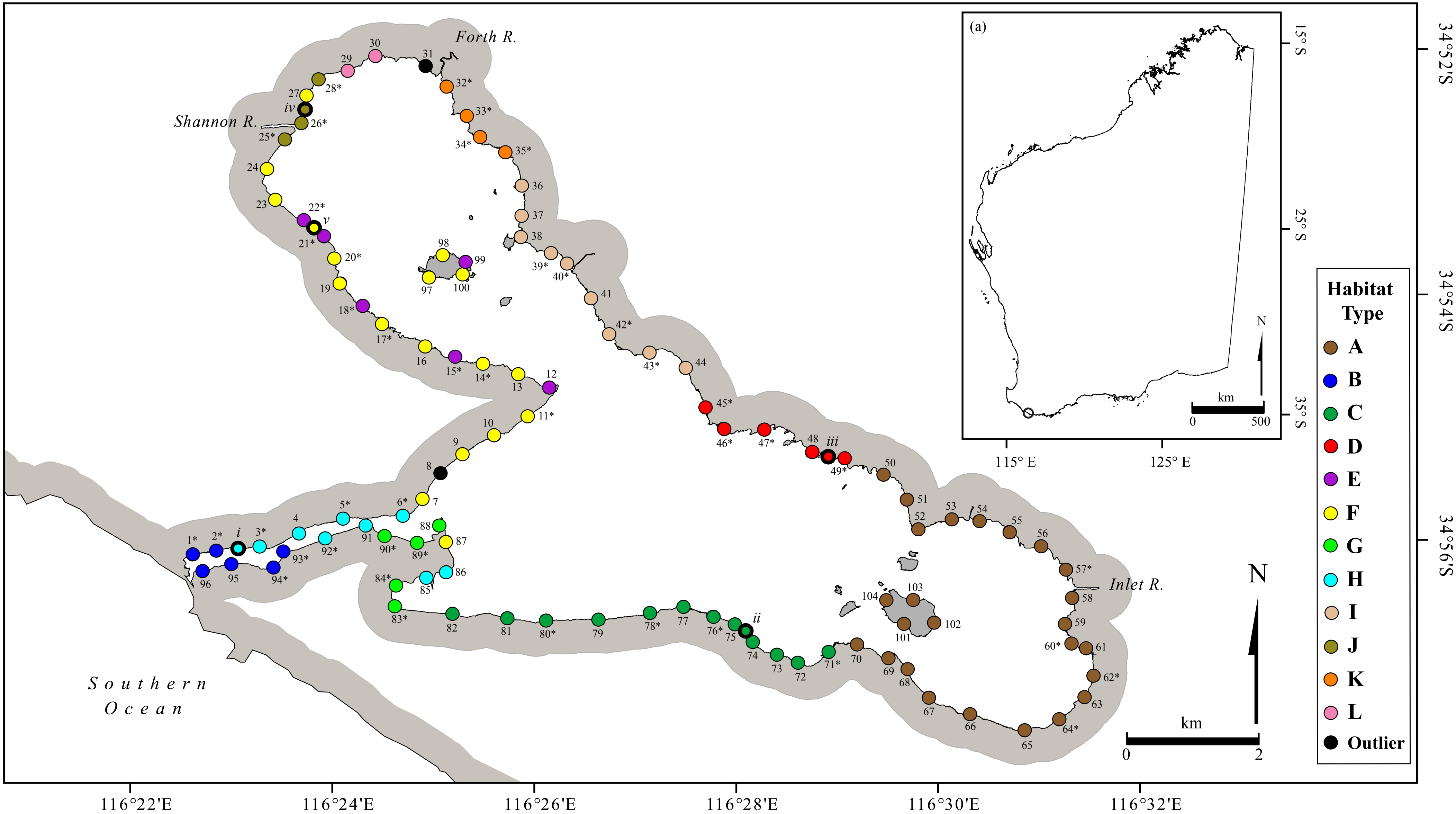

Figure 3.2.2.3: Map of the Broke Inlet showing the location of the 104 nearshore study sites and the habitat type to which each site was assigned by the CLUSTER and SIMPROF procedures (●), sites at which faunal and water quality measurements were collected (*) and the location, number and habitat of new nearshore sites chosen to demonstrate the use of the habitat prediction procedure (◉). Inset (a) shows the location of the Broke Inlet in Western Australia.

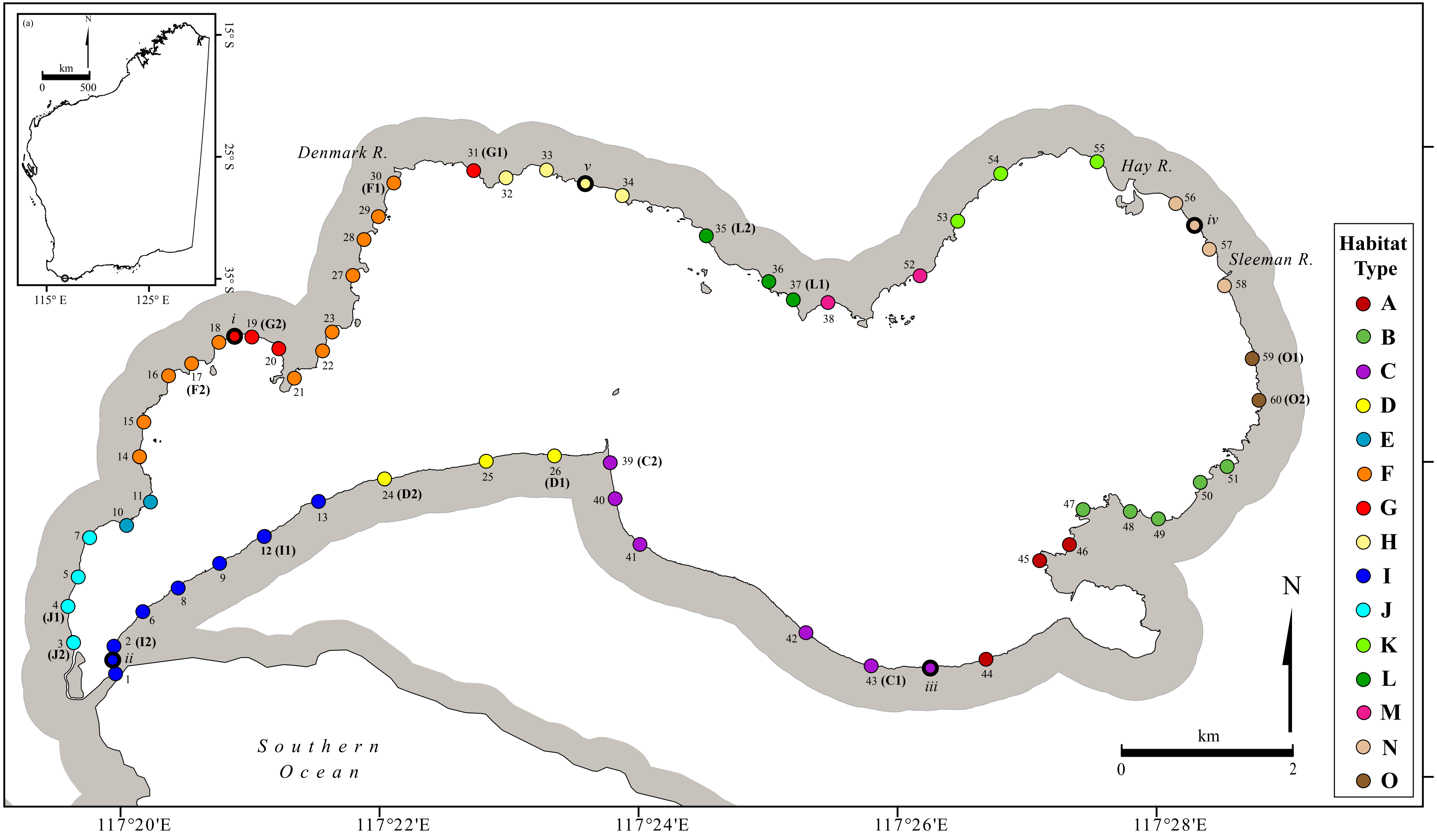

Figure 3.2.2.4: Map of the Wilson Inlet showing the location of the 60 nearshore study sites and the habitat type to which each site was assigned by the CLUSTER and SIMPROF procedures (●), sites at which fauna and water quality measurements were collected (bold text in brackets) and the location, number and habitat of new nearshore sites chosen to demonstrate the use of the habitat prediction procedure (◉). Inset (a) shows the location of the Wilson Inlet in Western Australia.

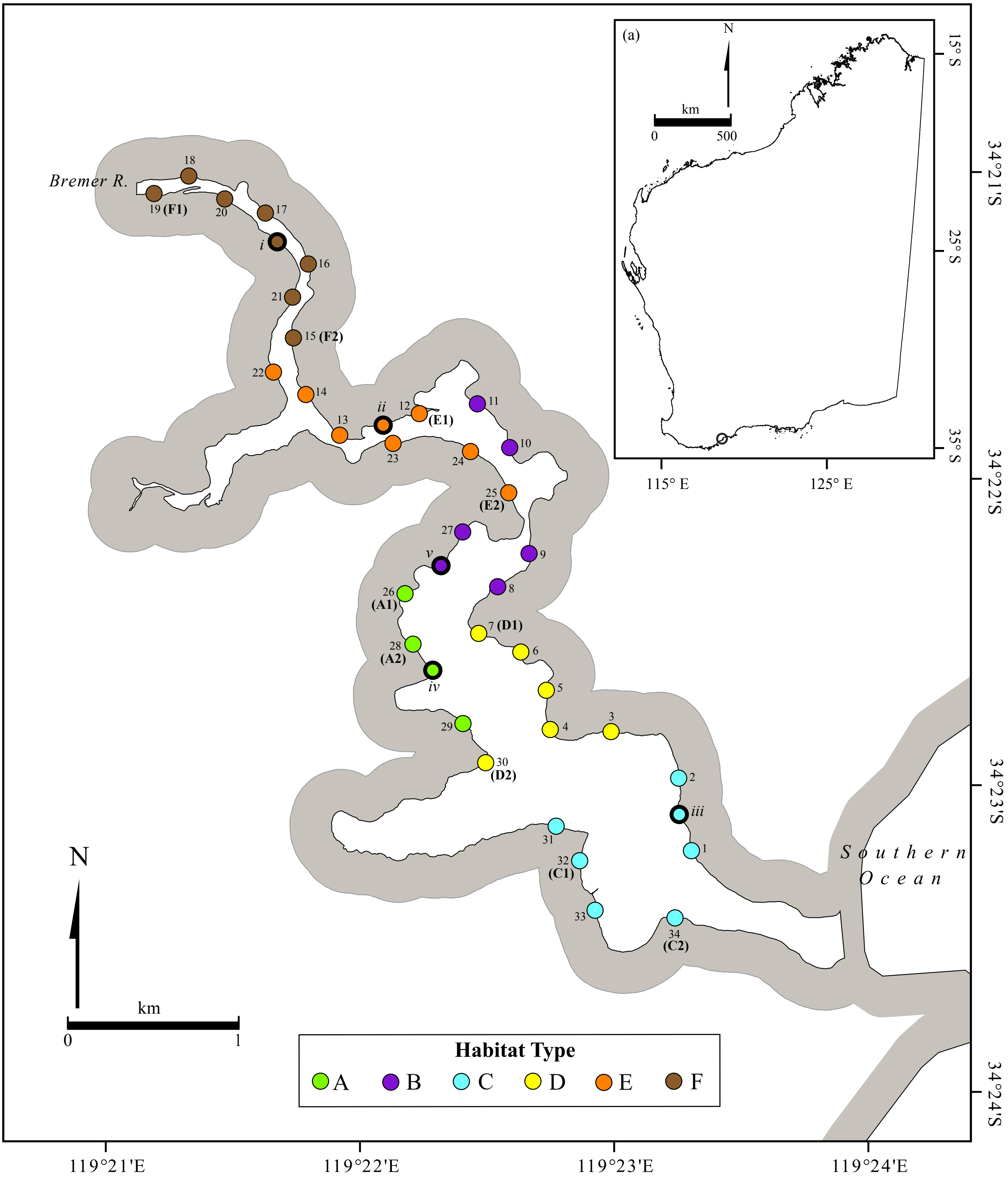

Figure 3.2.2.5: Map of the Wellstead Estuary showing the location of the 34 nearshore study sites and the habitat type to which each site was assigned by the CLUSTER and SIMPROF procedures (●), sites at which fauna and water quality measurements were collected (bold text in brackets) and the location, number and habitat of new nearshore sites chosen to demonstrate the use of the habitat prediction procedure (◉). Inset (a) shows the location of the Wellstead Estuary in Western Australia.

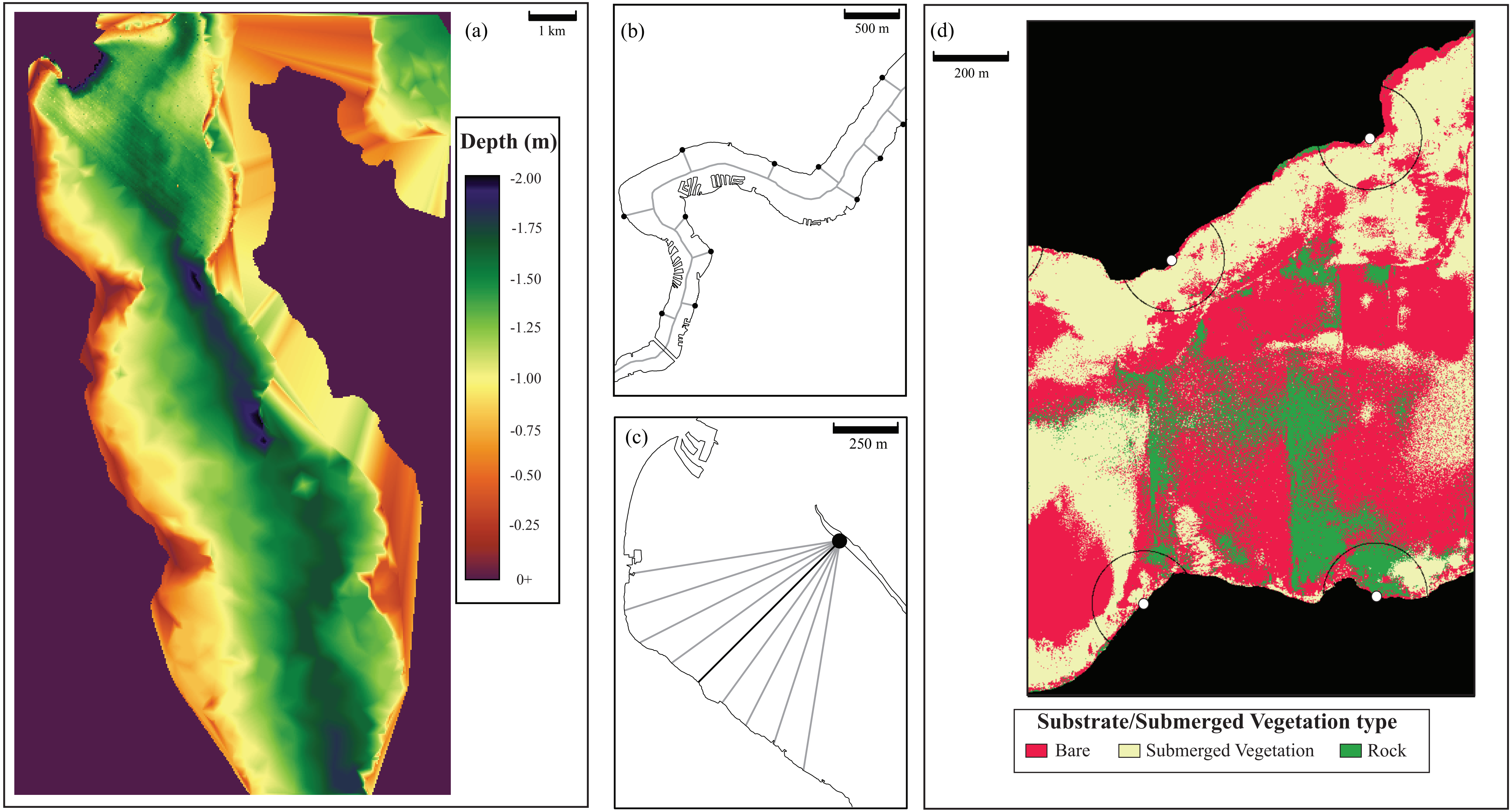

Figure 3.2.2.6: Examples of the ways in which particular enduring environmental characteristics were measured in GIS at each site in the various study estuaries. (a) Digital Elevation Model of the substrate, from which variables such as slope were measured and the location of the 1-2 m depth contour identified. (b) The midline used to measure site distance from the estuary mouth. (c) The component fetch lines used to measure modified effective fetch along a given bearing at each site. (d) The percentage contribution of the various substrate/submerged vegetation types at each site.

Northerly, southerly, easterly, westerly and direct fetch were measured at each site using the formula below for modified effective fetch (MEF; Coastal Engineering Research Centre 1977). This method encompasses a range of fetches within a limited arc of a given bearing, and thus provides a robust reflection of wave exposure, *i.e.* by moderating the influence that any fine scale coastal indentations or emergent features such as rocky outcrops may have on fetches measured along a single bearing. Four component fetch lines orientated at 9° increments on both sides of each true bearing were used to calculate the MEFs at each site (Fig. 3.2.2.6). The length of any lines that lay entirely over land were recorded as zero.

$$MEF = \frac{\sum (X_i . Cos\gamma_i)}{\sum Cos\gamma}$$

where X_i is the length (m) of fetch *i* and γ_i is the angle of deviation from fetch *i*.

The distance of each nearshore site to the wave shoaling margin, which was considered to be adequately reflected by the 2 m depth contour, was determined by trimming the MEF lines for direct fetch at the point at which they intersected that depth contour. In those cases where a fetch line did not extend over waters greater than 2 m in depth, it was terminated at the opposite shoreline.

The slope of the substrate at each site was determined by averaging the slopes of every plane surface within the site area.

(3) Substrate and submerged vegetation types

The pretreated images for each estuary were subjected to a non-hierarchical unsupervised CLUSTER analysis to assign each pixel to one of ten nominal benthic classes on the basis of differences in their spectral signatures. However, as comparison of the images and results from the CLUSTER analysis indicated that several of the derived classes reflected the same benthic category under different light or water conditions, they were then assigned to one of three broad and more distinct groups, *i.e.* bare unconsolidated substrate, rock or submerged aquatic vegetation. The last group represented both seagrass and macroalgae, which could not be reliably discriminated from each other on the images, due either to the fact that they grew in close association with each other and/or their spectral signatures were not sufficiently different. The accuracy of the resultant benthic classifications were determined by firstly nominating a subplot of 5 m radius around a pixel in each benthic class at all sites on the classified map, visiting each of those subplots in the field and then calculating the number of times the substrate/submerged vegetation type derived from the classified map matched that observed in the field. The overall accuracies of the benthic classification maps for the Swan and Peel-Harvey estuaries and Broke and Wilson inlets were 74, 76, 85 and 68%, respectively. The area (m^2) occupied by each substrate/submerged vegetation type within the boundary of each site was then calculated and converted to a percentage of the total site area.

Tannin stained and/or turbid waters in the upper reaches of the Swan and Peel-Harvey estuaries, and throughout the entire Wellstead Estuary, precluded classification of their substrate/submerged vegetation types from the remotely sensed image. In those circumstances, the contributions of the various benthic classes were quantified entirely from data collected in the field. Thus, at each of those sites, linear transects that extended from the shore to the 2 m depth contour were spaced at 20 m intervals along the shoreline. The contribution of each benthic class within a 2 m swath either side of each of the eight transects was visually estimated, and those data were then averaged to provide an overall estimate for each site.

3.2.3 Statistical Analyses

Each of the following data analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke and Gorley 2006) with the PERMANOVA+ for PRIMER add-on module (Anderson *et al.* 2008).

3.2.3.1 Pretreatment of enduring environmental data

Prior to multivariate analysis, the data for each of the enduring environmental variables recorded at each site in a particular estuary were firstly used to construct scatterplots between each pair of variables, *i.e.* Draftsman plots. These plots allowed (i) visual detection of whether the distribution of the data for any variable was notably skewed, and thus provided a basis for selecting an appropriate transformation to ameliorate any such effect and (ii) calculation of the extent to which each pair of variables were correlated. The data transformations applied to the values for each environmental variable in each estuary are given in Table 3.2.2.1. For all estuaries, percentage cover of unconsolidated bare substrate was the only variable that was highly correlated with several others, *i.e.* the remaining substrate/submerged vegetation variables, and was thus excluded from subsequent analyses.

Secondly, to overcome the fact that several of the enduring environmental variables were not directly comparable due to their different units of measurement, the transformed data were then normalised (*i.e.* for each variable, the mean was subtracted from each data value and the result divided by the standard deviation) to place each variable on the same (dimensionless) scale. Finally, to ensure that each of the three broad categories of enduring variables, *i.e.* location, exposure to wave activity and substrate/submerged vegetation type, contributed equally to the habitat classification procedure, each variable was then weighted on the basis of the total number of variables that comprised the broad category to which it had been assigned. Thus, each of the three categories was assumed to contribute an equal and arbitrary proportion of 100% to the overall data matrix, *i.e.* a total of 300% for all categories. The weight assigned to each variable was then calculated by dividing 100 by the total number of variables in its broad category. For example, as five variables comprised the substrate/submerged vegetation type category in the Swan Estuary, each of those variables was assigned a weight of 100/5=20. The weights applied to each variable in each estuary are provided in Table 3.2.2.1.

For each estuary, the pretreated enduring environmental data were then used to construct a Manhattan distance matrix containing the resemblances between each pair of sites.

3.2.3.2 Habitat classification

To identify those groups of sites within each estuary that did not differ significantly in their suite of enduring environmental characteristics and thus represented distinct habitat types, the Manhattan distance matrix was subjected to hierarchical agglomerative clustering with group-average linking (CLUSTER) and an associated Similarity Profiles (SIMPROF) test (Clarke *et al.* 2008). The latter routine is a permutation test that determines whether any significant group structure exists within a set of samples for which there is no *a priori* grouping hypothesis. When used in conjunction with CLUSTER, a SIMPROF test is performed at each node of the dendogram to ascertain whether the particular group of samples being subdivided contains significant internal structure, except in those cases when a test carried out at a broader division returned a non-significant result. This routine thus provides a sound basis for identifying those points in the clustering procedure at which further subdivision of samples is unwarranted. The null hypothesis that there were no significant environmental differences among sites was rejected if the significance level (p) associated with the test statistic (π) was <1%. Habitat types represented by only one site were considered to be outliers and were thus removed from further analyses.

3.2.3.3 Habitat prediction

For each estuary, any new nearshore site (*i.e.* one not used in the habitat classification procedure) could be quantitatively assigned to its appropriate habitat type using the following novel application of the Linkage Tree (LINKTREE) routine. Broadly, this approach was used to ascertain which enduring environmental variables, and their true quantitative thresholds, were most tightly linked with the separation of sites into the habitats identified by the above classification procedure. These environmental variables and their thresholds were then used as the quantitative criteria to predict the habitat of any new site.

LINKTREE (Clarke *et al.* 2008) is a non-metric modification of the multivariate regression tree technique published by De'ath (2002). Thus, a binary "linkage tree" is constructed that reflects how samples from an underlying (fixed) resemblance matrix are most naturally split into successively smaller groups, based on maximising the R-statistic (Clarke 1993). At each branching node of the tree, the quantitative thresholds of the variable(s) from a complementary sample x variable data matrix that best mirror those divisions are also provided. The notation associated with the variable thresholds (*e.g.* variable A $< x$ [$> y$], where x and y are quantitative values of variable A), indicates whether a left ($< x$) or right path ([$> y$]), should be followed at each branching node. The terminal group to which any new multivariate sample should be assigned can thus be determined by ascertaining whether its values for the variables specified at each successive node of the tree are less or greater than the given thresholds.

The fixed resemblance matrix employed in this procedure was a "model" matrix constructed by (i) averaging the pretreated data for each enduring environmental variable across the various sites representing each individual habitat type, (ii) replicating those average values for all sites representing any given habitat type and (iii) employing these data to produce a Manhattan distance matrix containing all pairs of sites. This distance matrix thus reflected the average pattern of environmental differences among habitats identified by the above classification procedure, but without any environmental heterogeneity between sites representing the same habitat type, *i.e.* pairs of sites belonging to the same habitat type had a distance of zero, while those belonging to different habitats had a distance that reflected their average dissimilarity. The complementary sample x variable data matrix employed in the routine was that containing the untreated (true) measurements for the suite of enduring environmental variables recorded at each site. A SIMPROF test was also used in conjunction with LINKTREE to terminate construction of the tree at those nodes at which there was no significant structure among the remaining samples. The associated null hypothesis and criteria for rejecting it were the same as those described above. The LINKTREE and SIMPROF routines thus produced a linkage tree with terminal nodes comprising groups of sites that precisely represented the habitat types identified by the classification procedure, along with the environmental variables, and their true quantitative thresholds, that were most tightly linked with the separation of those habitats.

To assign any new site to its appropriate habitat type, each of the enduring environmental variables in the defined suite were firstly measured at that site using the techniques described in subsection 3.2.2. The untreated site measurements were then compared with the thresholds for the environmental variable(s) specified at each successive branching node of the linkage tree, and the directed path followed until a terminal node (habitat type) was reached.

3.3 Results

3.3.1 Habitat classification

The CLUSTER and SIMPROF procedures performed on the data for the suite of enduring environmental variables recorded at the various nearshore study sites throughout the Swan and Peel-Harvey estuaries (101 and 102 sites, respectively), Broke and Wilson inlets (104 and 60 sites, respectively) and Wellstead Estuary (34 sites) yielded, in that order, 18, 17, 12, 15 and six habitat types (Figs 3.3.1.1-3.3.1.3). Outliers comprised of only one site were detected in three cases in the Peel-Harvey Estuary and two cases in the Broke Inlet, all of which were removed prior to further analyses. The locations of the sites assigned to each habitat type in each estuary are shown in Figs 3.2.2.1-3.2.2.5. The letter notation of each habitat reflects the level of resemblance at which it separated from the remaining habitat types, *i.e.* habitat type A separated from the remainder at the greatest level of dissimilarity and is thus the most environmentally distinct. The particular enduring environmental characteristics of each habitat in each estuary are provided below.

3.3.1.1 Swan Estuary

Within the Swan Estuary, habitat type A represented a group of eight sites in the uppermost reaches of the tidal portion of the Swan River, while the next most distinct habitat, B, comprised just two sites in the lowermost reaches of this river (Figs 3.2.2.1, 3.3.1.1a). The distinctiveness of the former habitat was clearly attributable to it being located the greatest distance from the estuary mouth, containing the greatest proportion of snags on the substrate and reeds along the banks and having very limited fetches in all directions, the latter of which makes it highly sheltered from wave activity (Fig. 3.3.1.4). Habitat B, which was also located relatively far from the estuary mouth and had small fetches, was the only one in which the substrate contained substantial quantities of large empty bivalve shells. No submerged aquatic vegetation was recorded at either of these habitats and both had particularly shallow slopes and narrow wave shoaling margins (Fig. 3.3.1.4).

The remaining sites in this system then separated into two broad groups, one of which contained habitats in the middle to lower reaches of the Swan and Canning rivers and the basins, while the second contained those in the lowermost reaches of the main basin and the entrance channel (Figs 3.2.2.1, 3.3.1.1a). The first of the above groups contained the expansive habitat C, which comprised 17 sites in the middle to lower reaches of both rivers. Like A and/or B, this

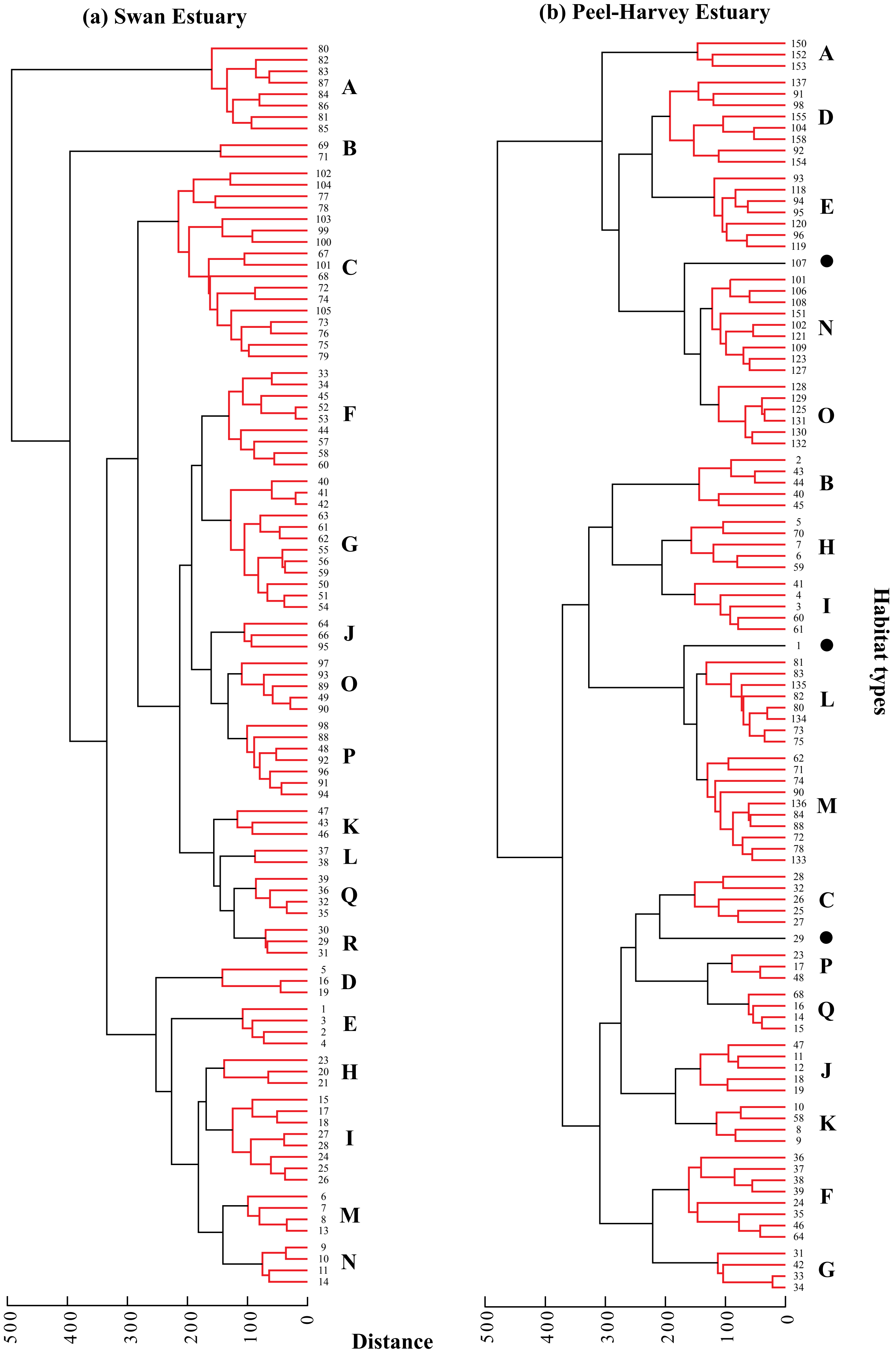

Figure 3.3.1.1: Dendograms derived from subjecting the data for the enduring environmental variables measured at each study site in the (a) Swan Estuary and (b) Peel-Harvey Estuary to CLUSTER and SIMPROF. Groups of sites marked by red lines are those which do not contain significant environmental differences and thus represent habitat types. ● denotes single sites considered to be outliers.

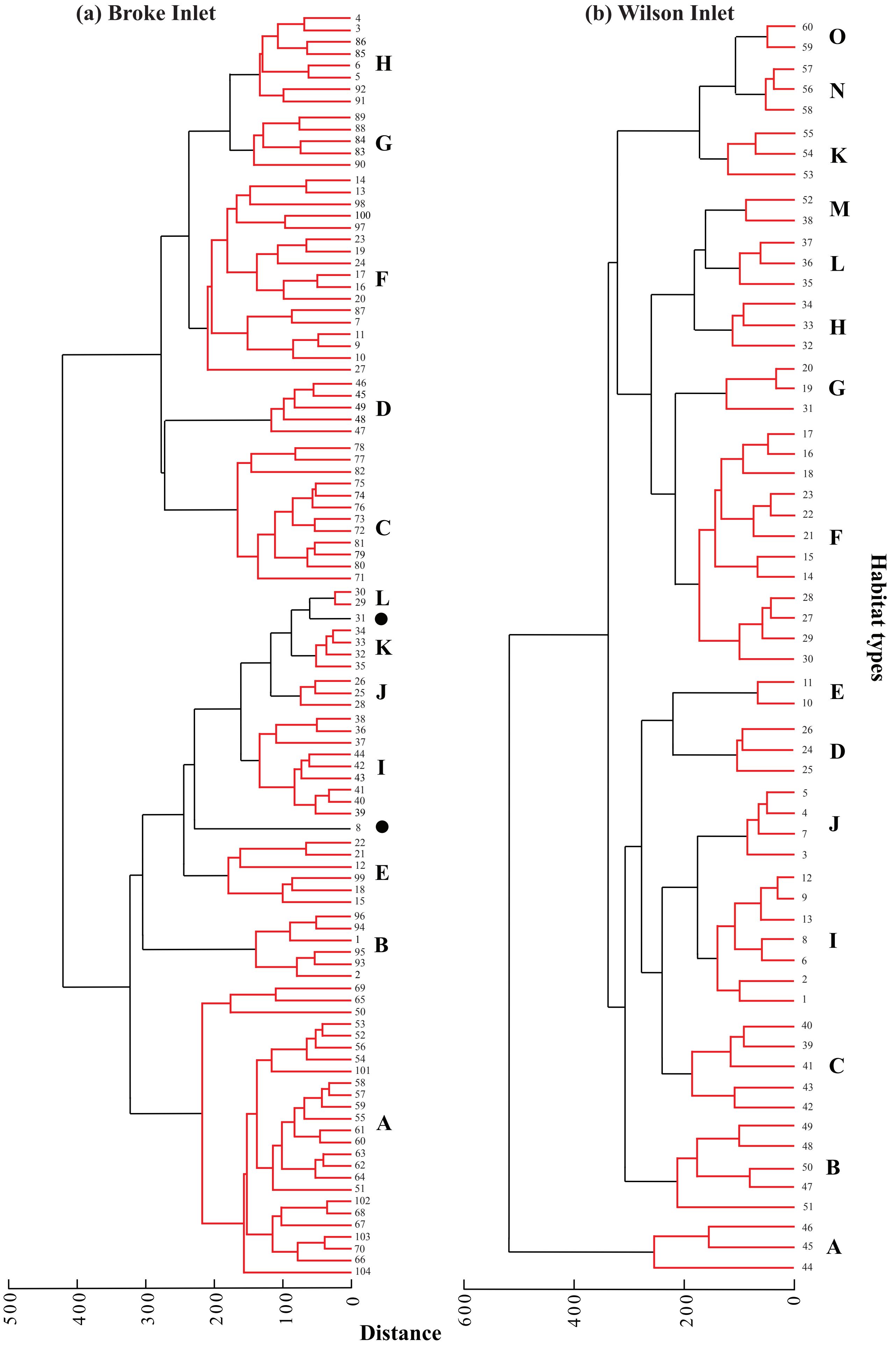

Figure 3.3.1.2: Dendograms derived from subjecting the data for the enduring environmental variables measured at each study site in the (a) Broke Inlet and (b) Wilson Inlet to CLUSTER and SIMPROF. Groups of sites marked by red lines are those which do not contain significant environmental differences and thus represent habitat types. ● denotes single sites considered to be outliers.

Wellstead Estuary

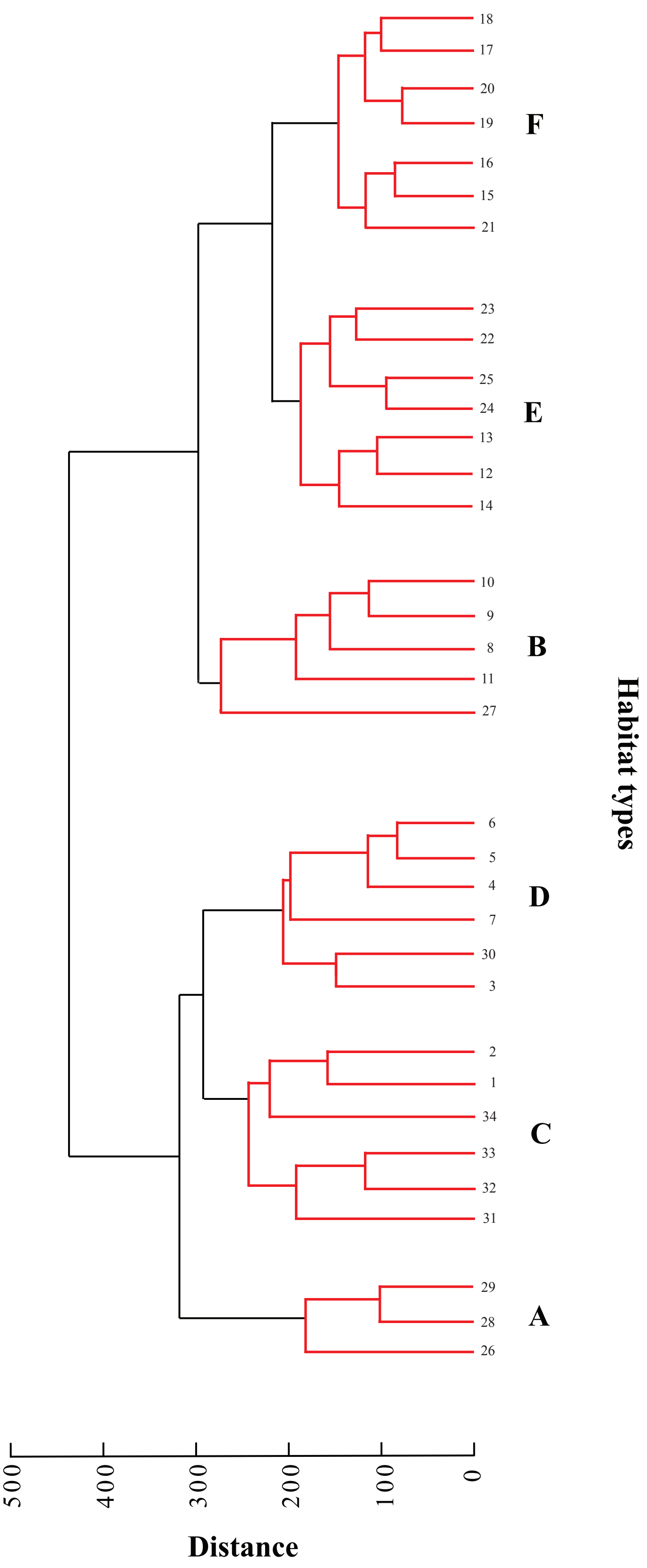

Figure 3.3.1.3: Dendogram derived from subjecting the data for the enduring environmental variables measured at each study site in the Wellstead Estuary to CLUSTER and SIMPROF. Groups of sites marked by red lines are those which do not contain significant environmental differences and thus represent habitat types.

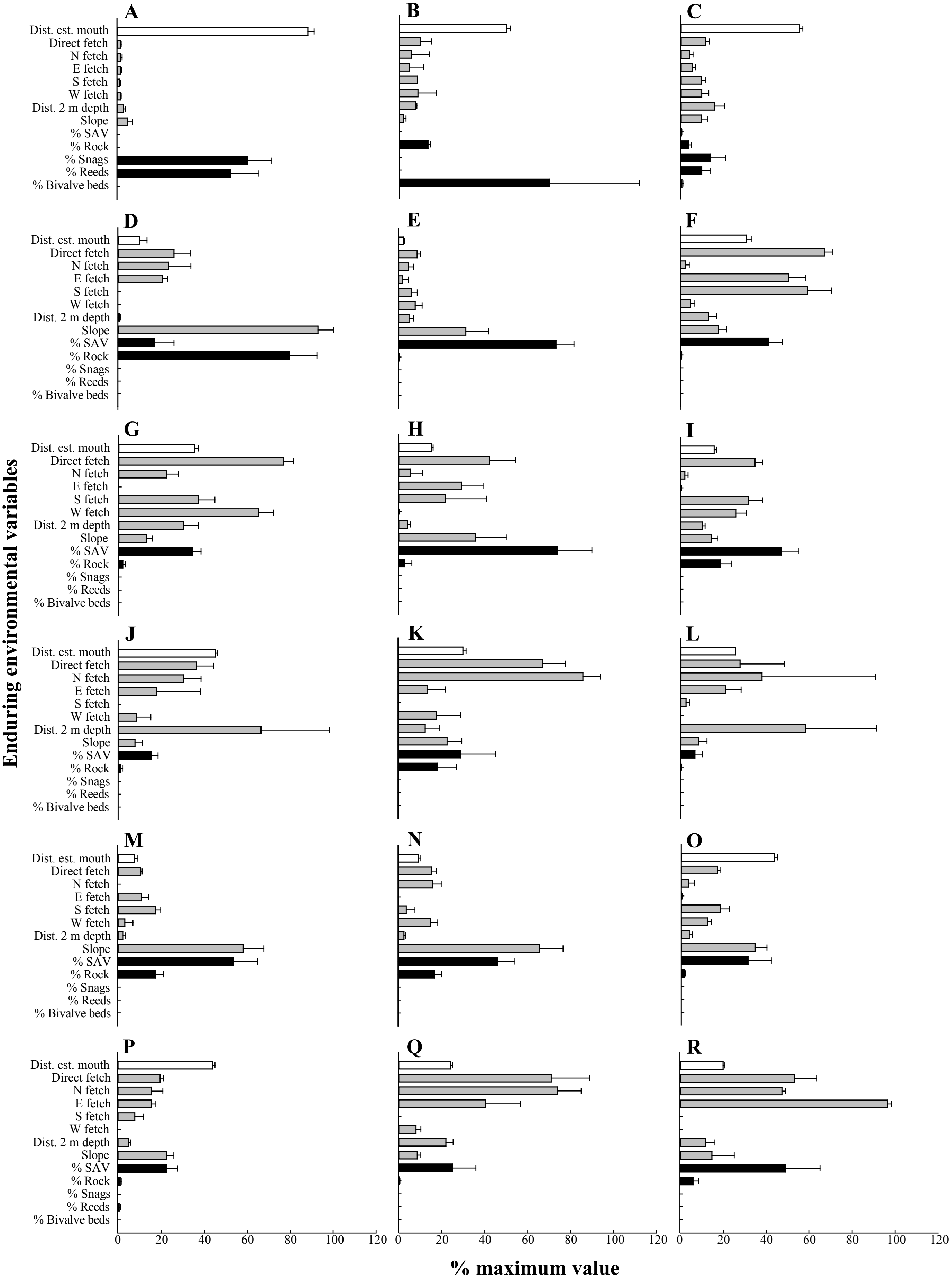

Figure 3.3.1.4: Mean (+SD) values of each enduring environmental variable at each habitat type in the Swan Estuary, expressed as a percentage of the maximum value recorded at any site throughout the system. Histogram bars are shaded according to the main category of enduring characteristics they represent, *i.e.* ☐=location, ▨=exposure to wave activity and ■=substrate/submerged vegetation type. Full names for each variable are provided in Table 3.2.2.1.

upper estuary habitat had relatively small fetches in all directions and was the only one to contain reasonable proportions of snags and reeds and at least some bivalve beds as part of the substrate. However, it had a wider wave shoaling margin and a steeper slope than either of those other upper estuary habitats (Fig. 3.3.1.4). The remaining sites in this group separated into three smaller groups, all at a similar level of resemblance. The first group comprised habitats located on the northern and eastern banks of the main basin (F and G, respectively), the second represented those in the lower reaches of the Canning River and in the small basin at the foot of the Swan River (J, O and P), while the third contained four habitats located on the southern bank of the main basin (K, L, Q and R; Figs 3.2.2.1, 3.3.1.1a). These middle estuary habitats were distinguished from each other mainly on the basis of pronounced dissimilarities in their exposure to winds from different directions, the widths of their wave shoaling margins and the proportions of submerged vegetation and rock comprising the substrate (Fig. 3.3.1.4).

Within the second of the above broad groups, the most distinct habitat, D, was represented by sites in the entrance channel that had the steepest slope and largest proportion of rock of any others throughout the estuary. The next most distinct habitat, E, was positioned closest to the estuary mouth and contained among the greatest areas of submerged vegetation (Figs 3.2.2.1, 3.3.1.4). Both of these habitats had small to moderate fetches and, in the case of D, were entirely fetch-limited in some directions. Habitat types H and I, located in the upper channel and lowermost reaches of the main basin, and M and N, located in the middle channel, were distinguished largely by differences in their exposure to prevailing winds, quantities of rock and submerged vegetation and the slope of their substrates (Figs 3.2.2.1, 3.3.1.4).

3.3.1.2 Peel-Harvey Estuary

Habitat types identified throughout the Peel-Harvey Estuary initially formed two main groups, the first comprising those in the Murray and Serpentine rivers and the second containing those throughout the two large basins and natural entrance channel (Figs 3.2.2.2, 3.3.1.1.b). Habitat type A in the lower reaches of the Murray River was distinct largely because it was the only one that contained substantial jetty constructions. However, like all other riverine habitats in this system (*i.e.* D, E, N and O), it had very limited fetches due to the narrow banks of that part of the estuary, contained snags, lacked submerged vegetation, had a very narrow wave shoaling margin and a moderately to steeply sloping substrate (Fig. 3.3.1.5). Habitat types D and E, located in the Serpentine River and/or at the mouth of the Murray River, were separated from N and O in the middle to upper reaches of the Murray River, due largely to the fact that the former two were the only ones that contained samphire in their shallowest waters and had

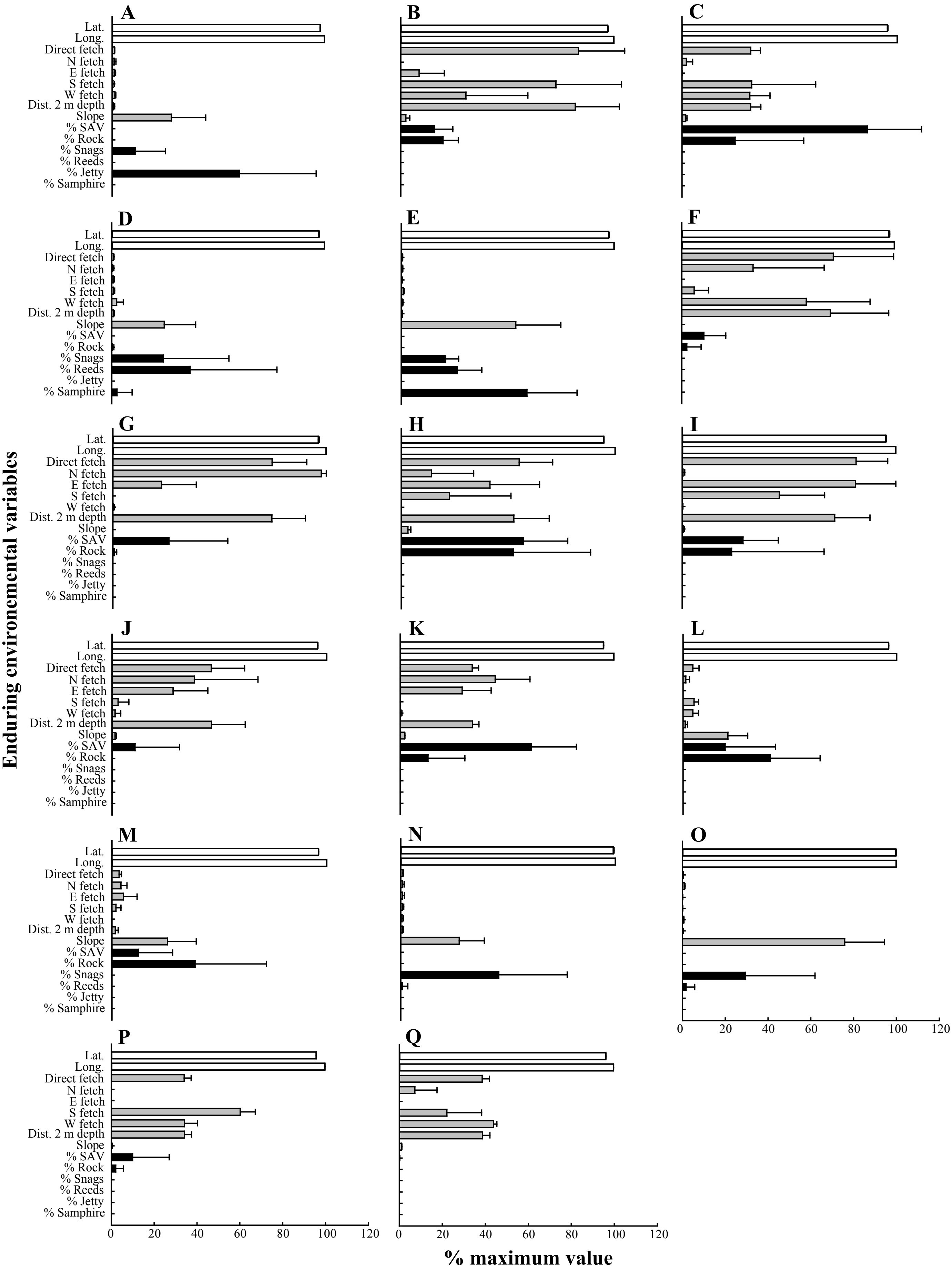

Figure 3.3.1.5: Mean (+SD) values of each enduring environmental variable at each habitat type in the Peel-Harvey Estuary, expressed as a percentage of the maximum value recorded at any site throughout the system. Histogram bars are shaded according to the main category of enduring characteristics they represent, *i.e.* ☐=location, ▨=exposure to wave activity and ■=substrate/submerged vegetation type. Full names for each variable are provided in Table 3.2.2.1.

substantially greater proportions of riparian reeds, while the latter two had greater proportions of snags (Figs 3.2.2.2, 3.3.1.5).

The second broad group of habitats split into two other groups at a relatively high level of dissimilarity. The first contained habitats located in the natural entrance channel (L and M), on the north-eastern to north-western shores of the large circular Peel Inlet (B and I) and on the north-western shore of the elongate Harvey Estuary, adjacent to the artificial entrance channel (H; Figs 3.2.2.2, 3.3.1.1b). These habitat types could easily be distinguished by differences in their exposure to wave activity, proportion of submerged vegetation and/or substrate type. Thus, L and M had small to non-existent fetches in all directions, but had very narrow wave shoaling margins and moderately sloping substrates. They also both comprised small to moderate areas of submerged vegetation and rock. However, B and I had very large direct fetches and the largest southerly or easterly fetches of any habitat, wide wave shoaling margins and very shallow sloping substrates. Like L and M however, B and I also comprised small to moderate areas of submerged vegetation and rock. In contrast, habitat H had small to moderate fetches in all directions except west, from which it was completely sheltered, a moderate wave shoaling margin, shallow slope and large areas of submerged vegetation and rock (Fig. 3.3.1.5).

The second of the above groups contained all habitats in the southern waters of the Peel Inlet (F and G) and most of those throughout the Harvey Estuary (C, J, K, P and Q; Figs 3.2.2.2, 3.3.1.1b). Apart from the first two of these habitat types, which had large direct and westerly or northerly fetches, those remaining in this group had only small to moderate fetches. Furthermore, F and G had large wave shoaling margins and virtually flat substrates, whereas the wave shoaling margins of habitats in the Harvey Estuary were of only a moderate width (Fig. 3.3.1.5). The latter group of habitats were easily distinguishable by differences in their exposure to particular prevailing winds and areas of submerged aquatic vegetation. For example, J and K were almost entirely sheltered from westerly and southerly winds but had moderate easterly and northerly fetches, while the opposite was true for C, P and Q. Furthermore, C and K had relatively large proportions of submerged vegetation, whereas the remaining Harvey Estuary habitats had either small proportions or were completely lacking vegetation (Fig. 3.3.1.5).

3.3.1.3 Broke Inlet

Nearshore habitats in Broke Inlet split into two broad groups at a high level of dissimilarity. The first of these, which contained habitats from various locations throughout the estuary (*i.e.* A, B, E, I, J, K and L), was characterised by sites that either lacked or contained very small amounts of submerged vegetation, while the opposite was true for those in the second group, *i.e.* C, D, F, G and H (Figs 3.3.1.2a, 3.3.1.6). The most distinct habitat within the first broad group, *i.e.* A, was represented by 25 sites that were all located at the eastern end of the large basin and within the vicinity of the mouth of the Inlet River (Fig. 3.2.2.3). This habitat had moderate direct and westerly fetches but was relatively sheltered from other prevailing winds, a shallow sloping substrate and the widest wave shoaling margin of any other habitat throughout the estuary. Conversely, habitat type B, located in the narrow entrance channel and closest to the estuary mouth, was characterised by small fetches in all directions and had the second steepest slope and second narrowest wave shoaling margin of any other habitat in this system (Figs 3.2.2.3, 3.3.1.6). The remaining habitats in the first broad group were all located at the western end of the large basin. The most distinct of these, E, which was represented by sites that typically lay on the south-western shore, was distinguished largely by the fact that it was not exposed at all to southerly winds but was moderately exposed to those from the north, while the opposite was true for the other four of the above habitats, which were situated on the western to north-western shore. In fact, habitat L had the largest southerly fetch of any habitat in the estuary. Habitat I was further distinguished from the others in this group by its relatively wide wave shoaling margin, particularly when compared to that at E, while the small habitats J and K, which were located near the mouths of the Shannon and Forth rivers, respectively, were distinguished by differences in their exposure to winds from various directions (Figs 3.2.2.3, 3.3.1.6).

The most distinct habitat type in the second of the above broad groups, *i.e.* C, was located along the southern shore of the middle reaches of the basin and had the largest northerly fetch of any habitat in Broke Inlet and among the largest of direct fetches. It also had the smallest contribution, by far, of submerged vegetation covering the substrate compared to other habitats in this broad group (Figs 3.2.2.3, 3.3.1.6). Habitat D, which essentially lay on the bank directly opposite that of C, was almost completely sheltered from both northerly and easterly winds but had the largest direct and westerly fetches of any habitat throughout the estuary and a large southerly fetch. It also contained among the greatest quantities of submerged vegetation. Sites representing habitat F, which were scattered mainly along the south-western shore of the estuary from the lower reaches of the basin to the mouth of the Shannon River, were partly distinguished from those representing G and H, which were located either in the lowermost reaches of the basin or in the upper half of the entrance channel, by their markedly greater exposure to prevailing winds. Moreover, habitat H had a particularly narrow wave shoaling margin and by far the steepest slope of any habitat throughout Broke Inlet, while G contained the greatest quantities of submerged vegetation (Figs 3.2.2.3, 3.3.1.6).

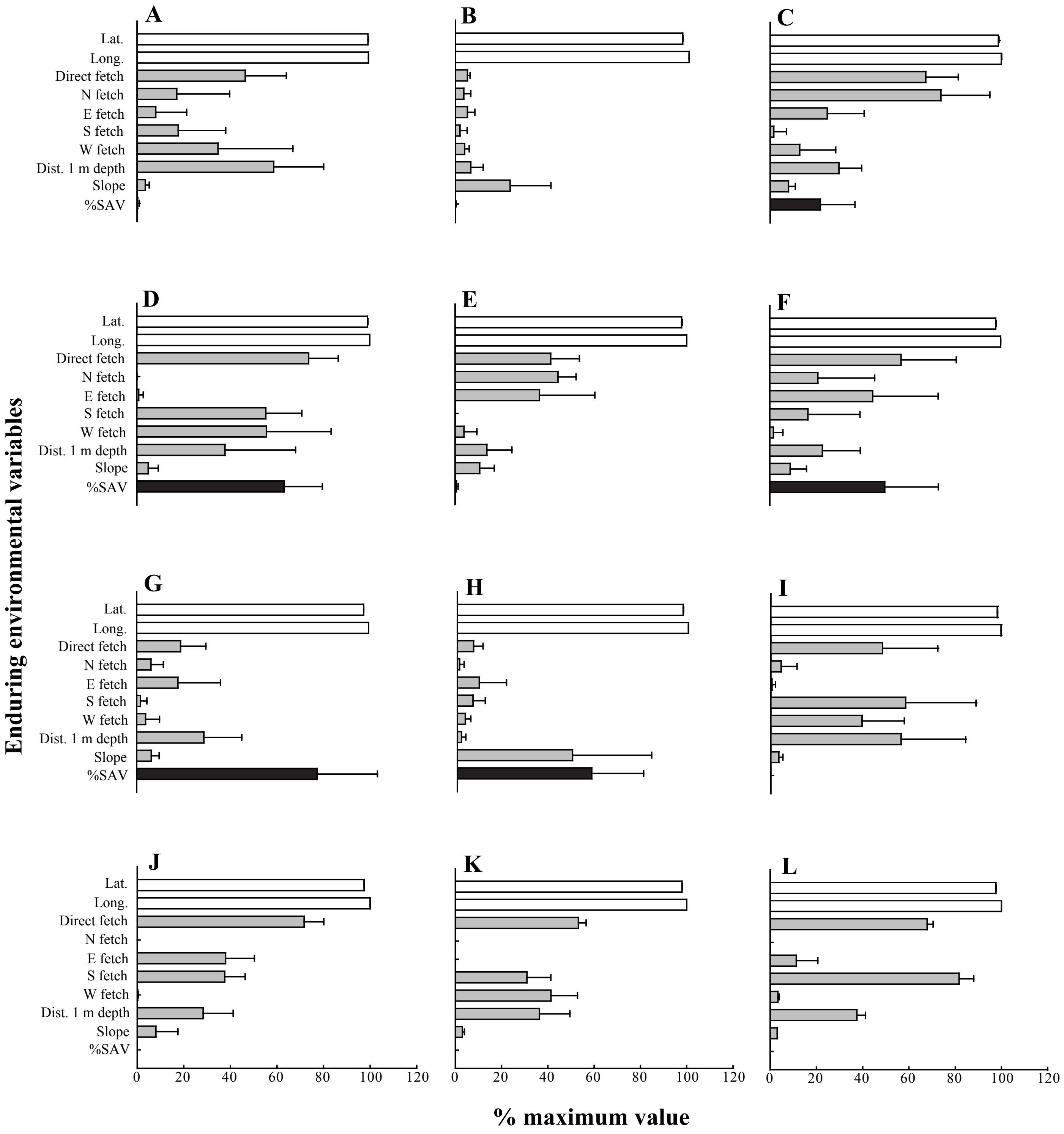

Figure 3.3.1.6: Mean (+SD) values of each enduring environmental variable at each habitat type in the Broke Inlet, expressed as a percentage of the maximum value recorded at any site throughout the system. Histogram bars are shaded according to the main category of enduring characteristics they represent, *i.e.* □=location, ▒=exposure to wave activity and ■=substrate/submerged vegetation type. Full names for each variable are provided in Table 3.2.2.1.

3.3.1.4 Wilson Inlet

Habitat type A in the seasonally-open Wilson Inlet, which separated from the others at the highest level of dissimilarity, represented a group of three sites in the south-eastern corner of the wide lagoonal basin that had by far the largest quantities of rock comprising the substrate. It also had the second largest direct and westerly fetch of any habitat type and was completely sheltered from easterly winds (Figs 3.2.2.4, 3.3.1.2b, 3.3.1.7). The remaining habitat types split into two broad groups, one of which comprised all other habitats located in the southern half of the basin and in the short entrance channel (*i.e.* B, C, I, J, D and E), and the other of which represented all habitat types in the northern half of the main basin (*i.e.* F, G, H, K, L, M, N and O; Figs 3.2.2.4, 3.3.1.2b). Within the first of these broad groups, habitat B, which was located adjacent to A, separated from the others at a relatively high level of dissimilarity due, firstly, to the fact that it was only one which contained patches of rock and, secondly, to its particular combination of fetches from various directions, *i.e.* minimal to no easterly and southerly fetches yet a moderate direct fetch. Habitats D and E, located on opposite banks in the upper channel or lower basin, separated from C, I and J, located in a wide embayment along the southern shore of the basin and opposite shores of the channel, respectively, due mainly to the fact that the first two of these habitats contained far greater areas of submerged vegetation and, particularly in the case of E, had far steeper substrates. The distinctness of habitat C relative to I and J was due not only to the differences in their locations, but also because the former had far greater direct, northerly and easterly fetches than the latter two (Figs 3.2.2.4, 3.3.1.7).

Within the second of the above broad groups of habitat types, K, N and O, which all lay in the north-eastern corner of the basin and, in the case of the former two, also near the mouths of the Hay and/or Sleeman rivers, separated from the others at a relatively high level of dissimilarity (Figs 3.2.2.4, 3.3.1.2b). Aside from their similar locations, the distinctiveness of these three habitats was also attributable to their notably wider wave shoaling margins and mainly or entirely bare substrates (Fig. 3.3.1.7). Of the remaining habitats in this broad group, H, L and M, positioned on the northern shore of the basin, were distinguished from F and G on the north-western shore near the mouth of the Denmark River, largely by the considerably greater areas of submerged vegetation in the former three habitats. Differentiation among individual habitats at lower levels of dissimilarity in this broad group was generally attributable to differences in their magnitude of particular fetches, slope of their substrate and quantities of submerged vegetation (Figs 3.2.2.4, 3.3.1.7).

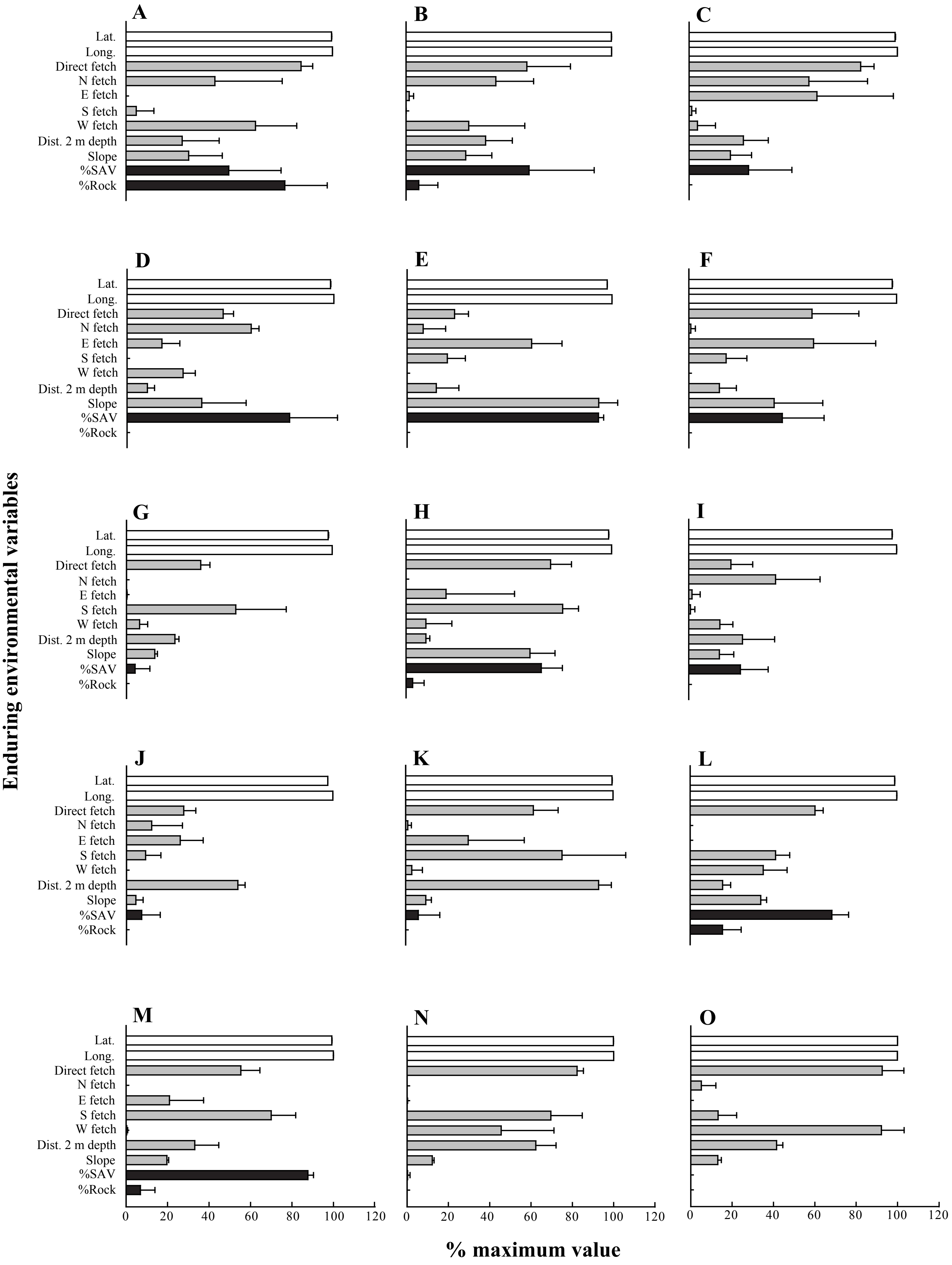

Figure 3.3.1.7: Mean (+SD) values of each enduring environmental variable at each habitat type in the Wilson Inlet, expressed as a percentage of the maximum value recorded at any site throughout the system. Histogram bars are shaded according to the main category of enduring characteristics they represent, *i.e.* □=location, ▨=exposure to wave activity and ■=substrate/submerged vegetation type. Full names for each variable are provided in Table 3.2.2.1.

3.3.1.5 Wellstead Estuary

The six habitat types identified throughout the small and normally-closed Wellstead Estuary initially split into two groups at a relatively high level of dissimilarity. The first of these contained habitats A, C and D, all of which were located in the lower half of the estuary, while the second group contained habitats B, E and F found in the upper half of the system, including those in the tidal portion of Bremer River (Figs 3.2.2.5, 3.3.1.3). Furthermore, unlike habitats in the first of these groups, those in the second group all lacked submerged vegetation and had relatively narrow wave shoaling margins (Fig. 3.3.1.8).

Habitat A, located on the western shore of the middle reaches of the estuary, was distinct from all others due mainly to the fact that it contained by far the greatest proportion of reeds in its shallowest waters and snags. In comparison to the other two habitats in its broad group, A also had lower proportions of rock comprising the substrate, particularly when compared to D, a far greater easterly fetch and an almost non-existent westerly fetch (Figs 3.2.2.5, 3.3.1.8). Habitats C and D were distinguishable not only by their differences in location, *i.e.* with the former being located closest to the estuary mouth, but also by differences in their fetch characteristics and proportions of different substrate/aquatic vegetation types. For example, whereas C contained the greatest areas of submerged vegetation of any habitat in the Wellstead Estuary, the same was also true of rock at D, and the former habitat also contained greater areas of snags (Figs 3.2.2.5, 3.3.1.8).

In the second of the above broad groups of habitats, B, located mainly on the eastern bank of the middle reaches, was particularly distinct from E and F further upstream due not only to its difference in location, but also to its far lower proportion of fringing samphire and greater quantities of rock and reeds, and greater direct, westerly and southerly fetches. The uppermost habitat F was distinguishable from E mainly by its particularly steeply sloping substrate, which was the steepest by far of any habitat, greater proportion of snags and smaller areas of samphire (Figs 3.2.2.5, 3.3.1.8).

3.3.2 Habitat type prediction

The linkage trees representing the separation of study sites in each estuary into the habitat types identified by the above CLUSTER and SIMPROF procedures, as well as the quantitative thresholds of the enduring environmental variable(s) that best reflect the division at each node of those trees, are provided in Figs 3.3.2.1-3.3.2.5 for the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary, respectively. These trees thus provide a set of quantitative decision rules for assigning any new nearshore site in these systems (*i.e.* one outside

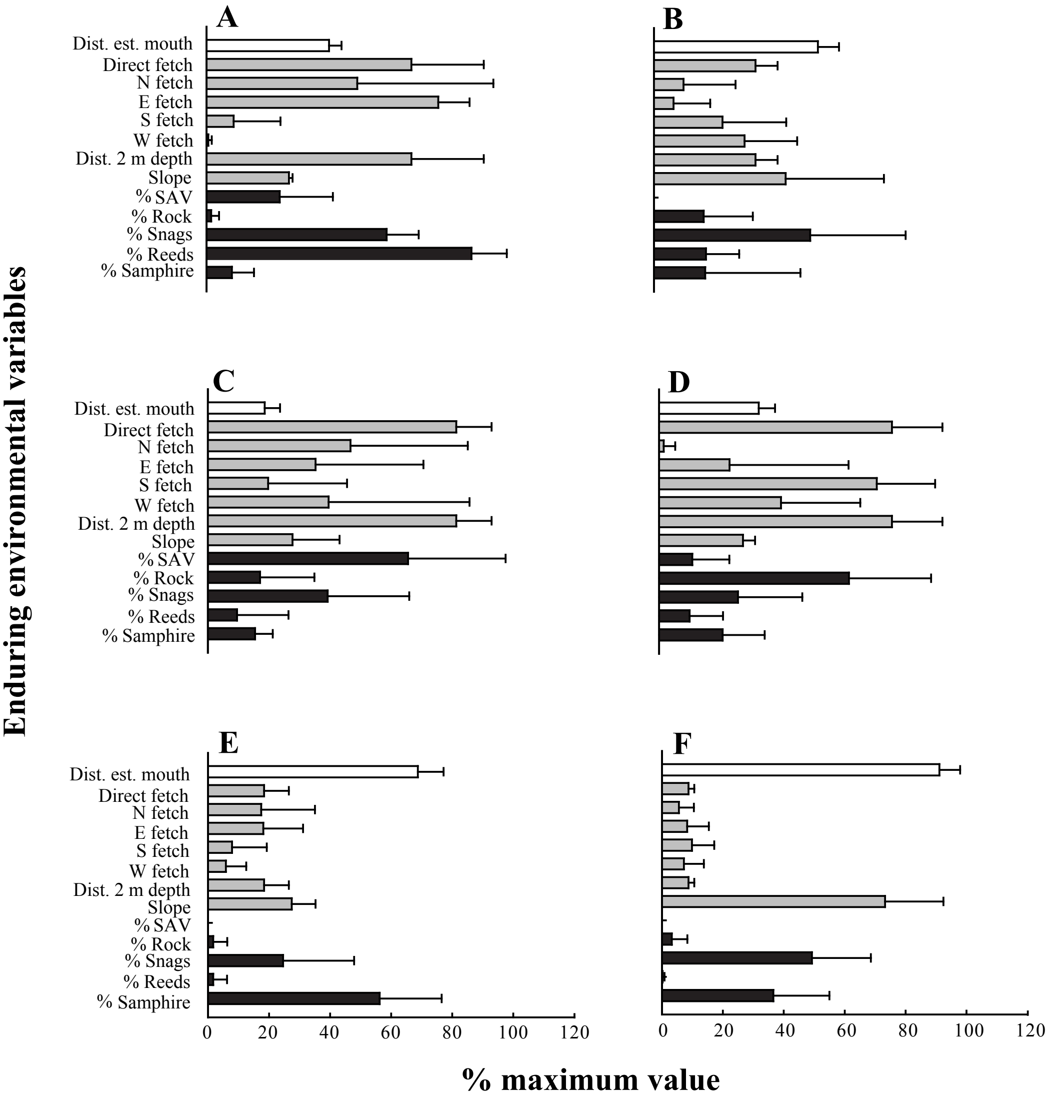

Figure 3.3.1.8: Mean (+SD) values of each enduring environmental variable at each habitat type in the Wellstead Estuary, expressed as a percentage of the maximum value recorded at any site throughout the system. Histogram bars are shaded according to the main category of enduring characteristics they represent, *i.e.*□=location, ▨=exposure to wave activity and ■=substrate/submerged vegetation type. Full names for each variable are provided in Table 3.2.2.1.

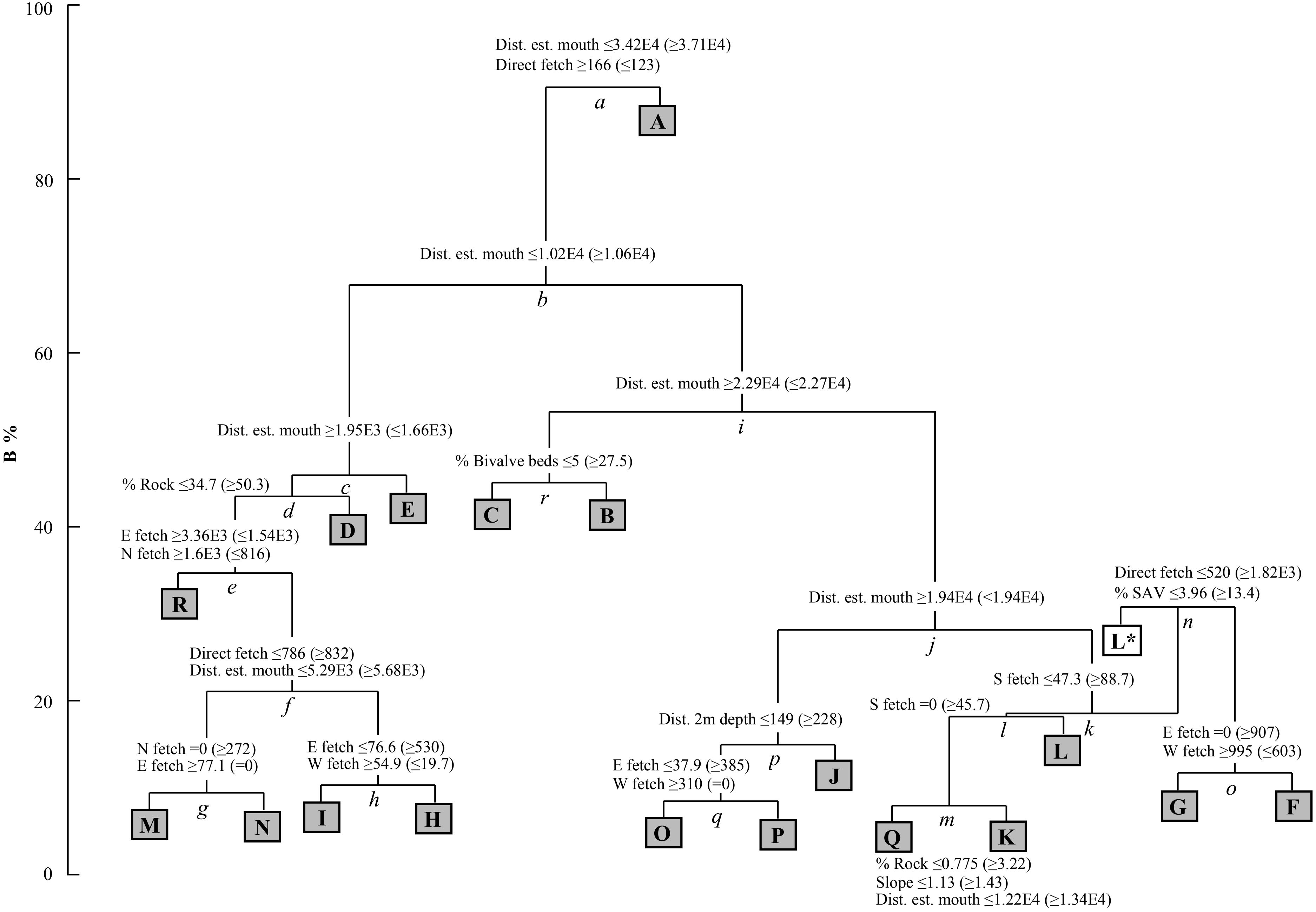

Figure 3.3.2.1: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites in the Swan Estuary to their appropriate habitat type (terminal nodes in grey boxes). Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. The units of measurement and full names for each variable are provided in Table 3.2.2.1. Note that threshold values have not been subjected to any data pretreatment. The terminal node represented by a white box with a habitat type marked by an asterisk denotes an alternative path for assigning sites to that habitat (n=1). The main path is provided elsewhere in the linkage tree. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitats.

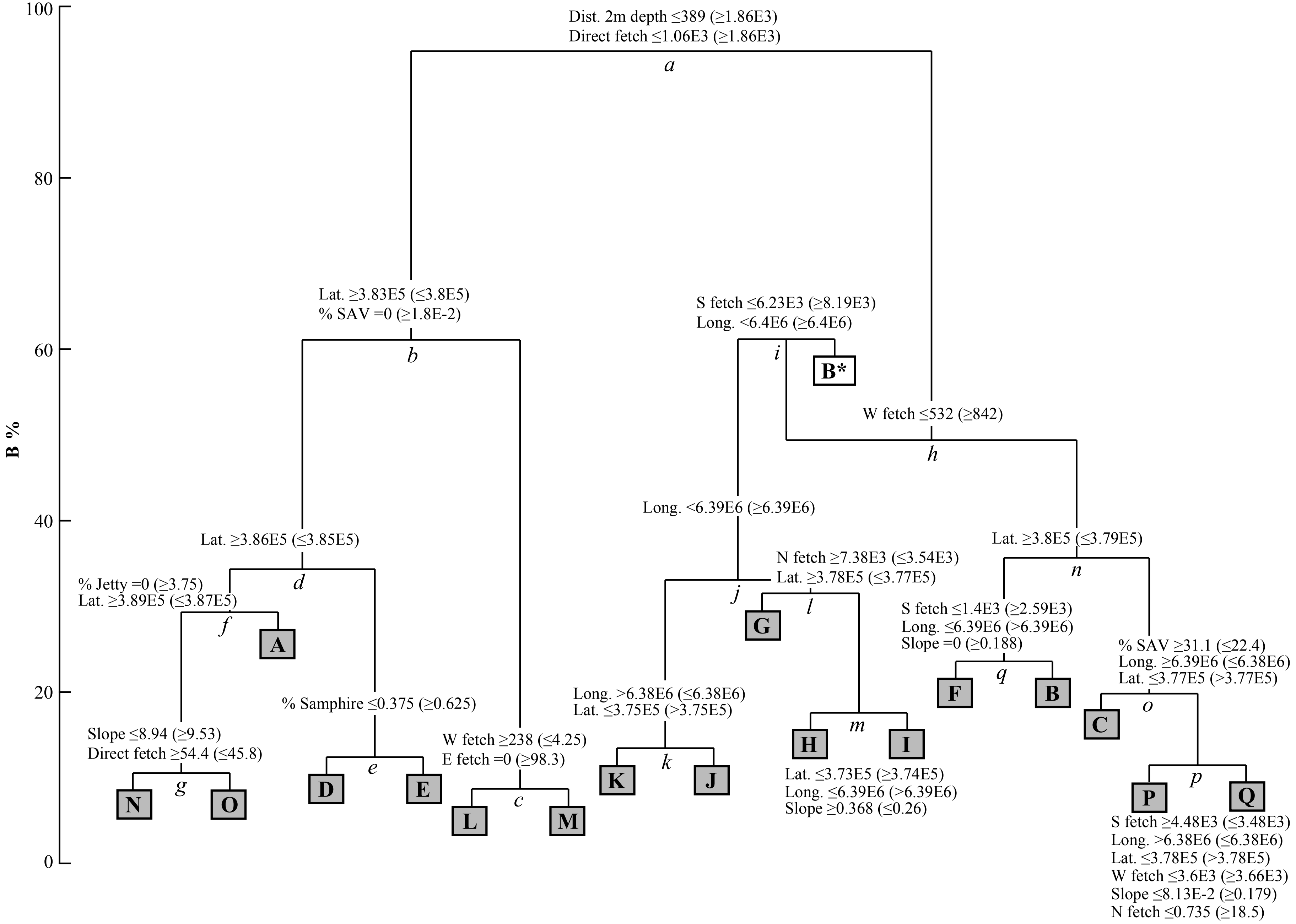

Figure 3.3.2.2: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites in the Peel-Harvey Estuary to their appropriate habitat type (terminal nodes in grey boxes). Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. The units of measurement and full names for each variable are provided in Table 3.2.2.1. Note that threshold values have not been subjected to any data pretreatment. The terminal node represented by a white box with a habitat type marked by an asterisk denotes an alternative path for assigning sites to that habitat (n=1). The main path is provided elsewhere in the linkage tree. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitats.

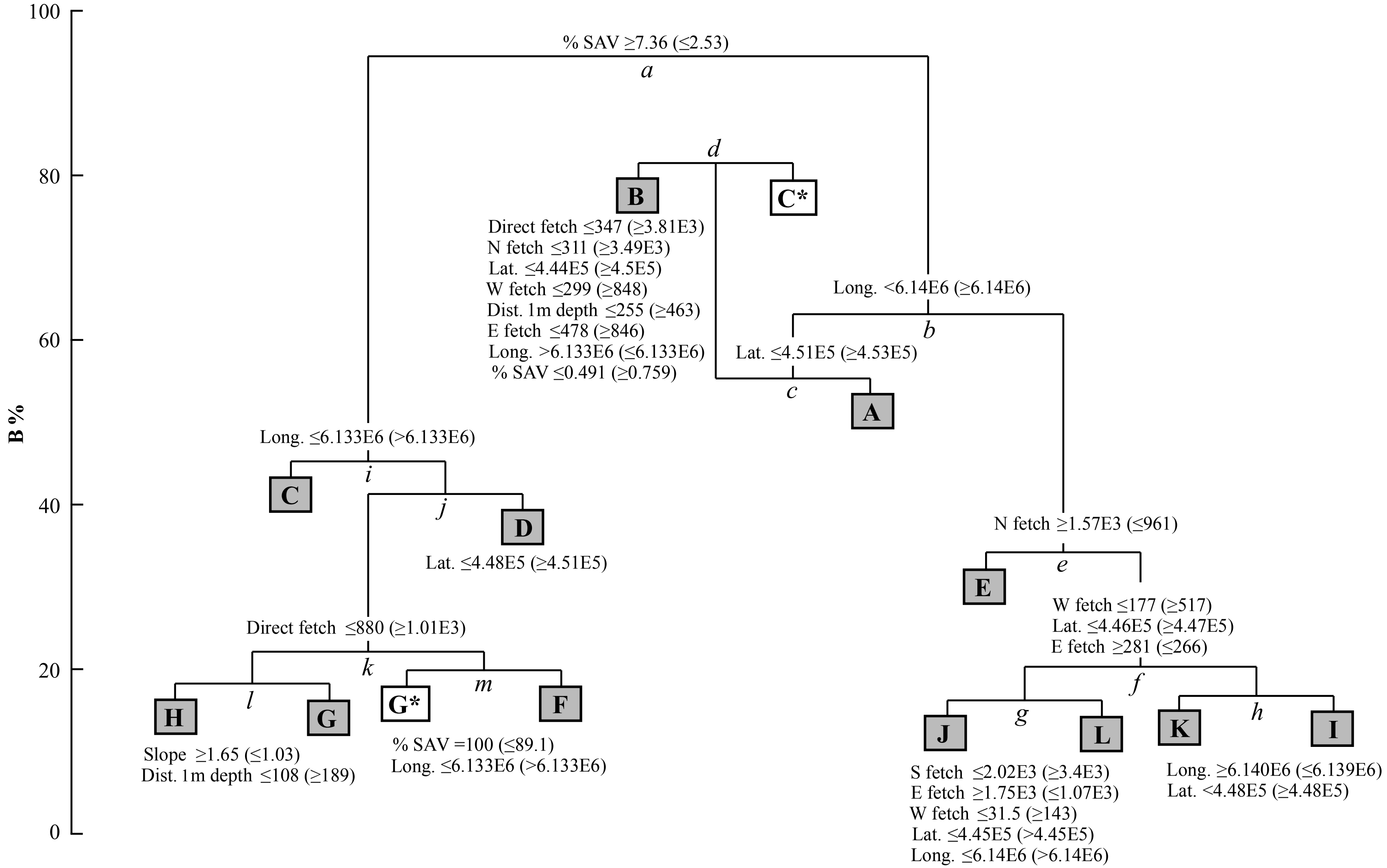

Figure 3.3.2.3: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites in the Broke Inlet to their appropriate habitat type (terminal nodes in grey boxes). Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. The units of measurement and full names for each variable are provided in Table 3.2.2.1. Note that threshold values have not been subjected to any data pretreatment. The terminal node represented by a white box with a habitat type marked by an asterisk denotes an alternative path for assigning sites to that habitat (n=1). The main path is provided elsewhere in the linkage tree. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitats.

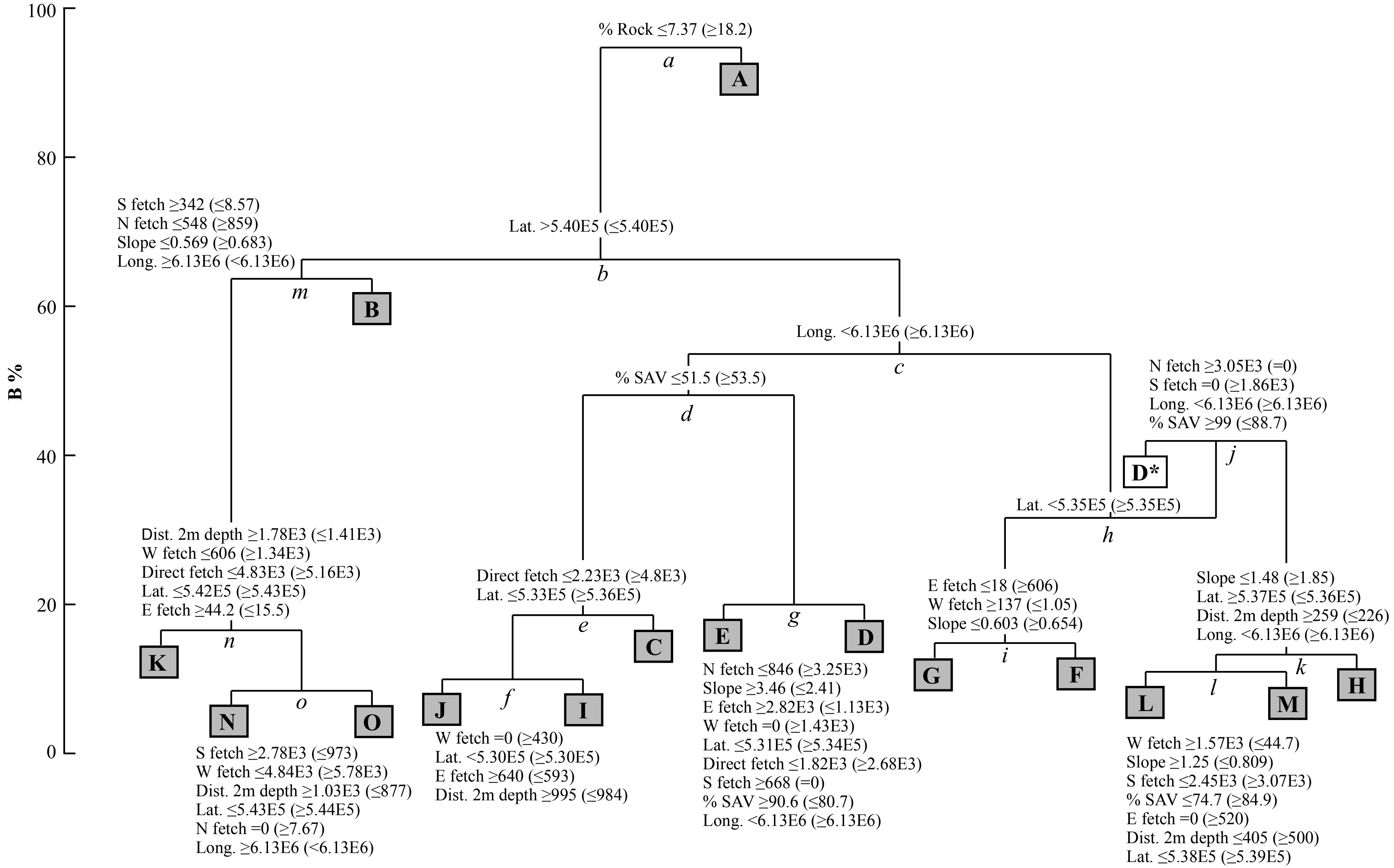

Figure 3.3.2.4: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites in the Wilson Inlet to their appropriate habitat type (terminal nodes in grey boxes). Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. The units of measurement and full names for each variable are provided in Table 3.2.2.1. Note that threshold values have not been subjected to any data pretreatment. The terminal node represented by a white box with a habitat type marked by an asterisk denotes an alternative path for assigning sites to that habitat (n=1). The main path is provided elsewhere in the linkage tree. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitats.

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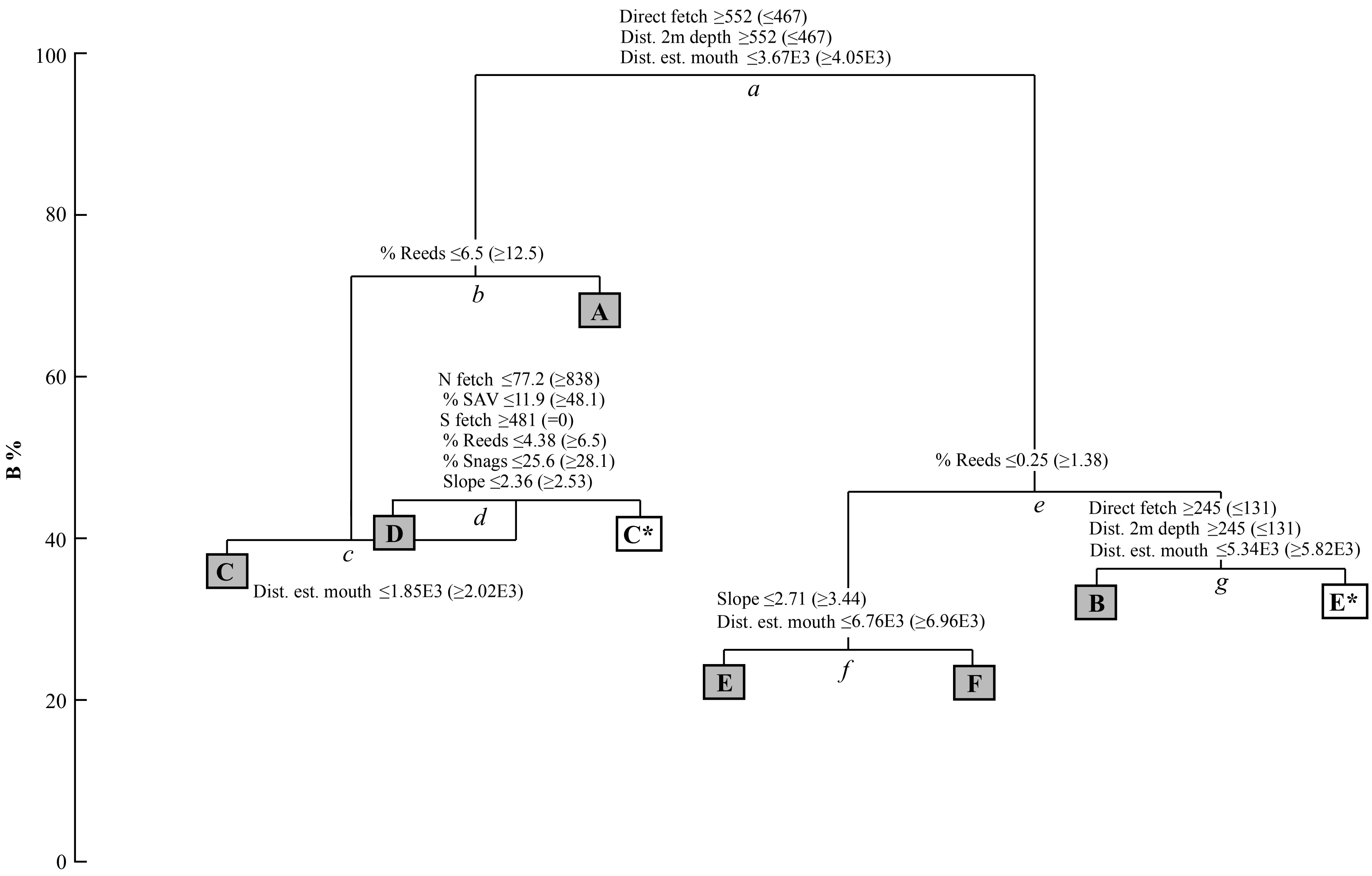


Figure 3.3.2.5: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites in the Wellstead Estuary to their appropriate habitat type (terminal nodes in grey boxes). Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. The units of measurement and full names for each variable are provided in Table 3.2.2.1. Note that threshold values have not been subjected to any data pretreatment. The terminal node represented by a white box with a habitat type marked by an asterisk denotes an alternative path for assigning sites to that habitat (n=1). The main path is provided elsewhere in the linkage tree. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitats.

of those used in the habitat classification procedure) to the appropriate habitat type on the basis of measurements for its enduring environmental characteristics. They also provide a way of detecting which particular enduring environmental variables from the full suite employed in the classification procedure are most important for defining the habitat types in any given system.

The paths at several nodes in each linkage tree were defined by thresholds for only one environmental variable. For the Swan Estuary, these singular decision rules represented either distance from the estuary mouth, southerly fetch, width of the wave shoaling margin or the percentage contribution of rock or large bivalve shells comprising the substrate, while for the Peel-Harvey Estuary, they included latitude or longitude, westerly fetch or the percentage contribution of fringing samphire (Figs 3.3.2.1, 3.3.2.2). Singular decision rules nominated at particular nodes of the linkage tree for Broke Inlet included latitude or longitude, the percentage contribution of submerged vegetation or direct or northerly fetch, while those for Wilson Inlet were represented by the first three of the above variables or percentage contribution of rock, and those for Wellstead Estuary comprised distance from the estuary mouth or percentage contribution of fringing reeds (Figs 3.3.2.3-3.3.2.5). All of the remaining enduring environmental variables recorded in each study estuary were selected in combination with others at other nodes of their respective linkage trees. The only exceptions were the contributions of reeds and snags to the substrate in both the Swan and Peel-Harvey estuaries and also of rock in the latter, and easterly and westerly fetches and the contributions of rock and samphire in the Wellstead Estuary.

To demonstrate the use of the linkage trees, five additional nearshore sites were nominated in each system (see Figs 3.2.2.1-3.2.2.5) and their suite of enduring environmental criteria measured from the appropriate maps in GIS (see subsection 3.2.2 and Table 3.3.2.1). The measurements for each site were then compared with the thresholds given at each node of the appropriate linkage tree, and the directed path followed until a terminal node (habitat type) was reached. For each new site in each system, comparison of their derived habitat with their location in that system, and thus their proximity to established habitat types, strongly indicates that the habitat predictions in each case are appropriate (see Figs 3.2.2.1-3.2.2.5).

For each estuary, there were some very minor inconsistencies between the habitat classifications derived from the CLUSTER and SIMPROF procedures and the habitats produced at the terminal nodes of their respective linkage trees. Thus, for the Swan, one of the sites representing the small habitat L (left branch of node *n*) separated from the only other representative (right branch of node *l*) within a localized area of the linkage tree, while for the Peel-Harvey, one of the sites representing habitat B (right branch of node *i*) separated from the

Table 3.3.2.1: Measurements for the suite of enduring environmental variables at each of the five additional nearshore sites selected in the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary that were used to trial the habitat prediction tool developed for each system. Full variable names are given in Table 3.2.2.1. See Figs 3.2.2.1-3.2.2.5 for the location and predicted habitat type of each site.

	Site	Dist. est. mouth (m)	Latitude (°)	Longitude (°)	Direct fetch (m)	N fetch (m)	E fetch (m)	S fetch (m)	W fetch (m)	Dist. 1-2 m depth (m)*	Slope (°)	SAV (%)	Rock (%)	Snags (%)	Reeds (%)	Bivalve beds (%)	Jetty (%)	Samphire (%)
Swan Estuary	*i*	3416	-	-	750	374	775	0	3	3	5.74	0	0	0	0	0	-	-
	ii	9910	-	-	1543	1763	2949	0	70	289	2.81	77.22	0	0	0	0	-	-
	iii	13891	-	-	3098	44	3057	1809	0	44	3.83	32.85	0.1	0	0	0	-	-
	iv	12565	-	-	3026	1953	0	271	2769	907	1.8	58.78	5.49	0	0	0	-	-
	v	21050	-	-	505	184	0	681	529	33	2.66	23.13	0.02	0	0	0	-	-
Peel-Harvey Estuary	*i*	-	378827	6400466	293	234	434	52	0	80	6.05	0	0.01	0	0	-	0	0
	ii	-	379717	6397820	331	119	0	273	331	186	1.45	4.17	9.29	0	0	-	0	0
	iii	-	376385	6395415	6134	0	4337	6483	463	5248	0.05	13.4	1.17	0	0	-	0	0
	iv	-	373379	6386348	2975	2695	3241	22	0	2975	0.6	30.18	2.79	0	0	-	0	0
	v	-	378597	6379553	3520	0	0	3014	2275	3520	0	0	0	0	0	-	0	0
Broke Inlet	*i*	-	443829	6134133	280	0	113	252	333	77	1.94	29.54	-	-	-	-	-	-
	ii	-	451473	6132876	1228	2247	1974	38	0	900	0.25	34.57	-	-	-	-	-	-
	iii	-	452747	6135491	4481	0	256	2518	0	1907	0.10	76.00	-	-	-	-	-	-
	iv	-	444800	6140766	2788	84	2698	721	0	115	0.76	0	-	-	-	-	-	-
	v	-	444963	6138979	2949	1838	3740	0	91	162	0.65	14.04	-	-	-	-	-	-
Wilson Inlet	*i*	-	531680	6128311	1757	0	265	1798	69	428	0.55	7.18	0	-	-	-	-	-
	ii	-	530303	6124519	509	643	0	142	478	509	0.92	34.57	0	-	-	-	-	-
	iii	-	539911	6124422	4618	4900	356	0	2040	633	0.55	24.34	0	-	-	-	-	-
	iv	-	543391	6129990	5491	0	0	3804	2247	1179	0.47	0.00	0	-	-	-	-	-
	v	-	535795	6130139	3351	0	11	3909	991	178	2.83	61.15	1.45	-	-	-	-	-
Wellstead Estuary	*i*	7680	-	-	87	78	135	84	18	87	5.36	0	0	23.75	0	-	-	9.94
	ii	5816	-	-	103	0	200	132	108	103	2.08	0	0	1.56	0	-	-	14.69
	iii	1529	-	-	856	71	0	523	1059	856	1.21	16.25	7.50	14.06	0	-	-	3.38
	iv	3353	-	-	575	620	669	0	10	575	1.83	16.56	0.94	22.81	14.06	-	-	1.25
	v	3901	-	-	330	2	550	385	0	330	4.19	0	0	18.44	3.25	-	-	16.50

* wave shoaling margin located at a water depth of 1 m in Broke Inlet, but 2 m in all other systems.

other four members of its group (right branch of node *q*), also within a relatively localized area of the tree (Figs 3.3.2.1 and 3.3.2.2, respectively). Similarly, two sites representing the large habitat C in Broke Inlet (right branch of node *d*) and one site representing habitat G (left branch of node *m*), separated from the other members of their groups (left branch of node *i* and right branch of node *l*, respectively), and in the Wilson Inlet, one member of the small habitat D (left branch of node *j*) separated from the remaining two sites in that habitat (right branch of node *g*; Figs 3.3.2.3 and 3.3.2.4, respectively). Lastly, one site from habitat C in the Wellstead Estuary (right branch of node *d*) split from its counterparts found at the left branch of node *c*, and one of the sites representing habitat E (right branch of node *g*) separated from the remainder located at the left branch of node *f* (Fig. 3.3.2.5). Despite the slight inconsistencies in the location of these individual sites within their respective linkage trees, the decision rules that lead to them provide clear demarcation from all other habitats in all cases. They can thus still be considered representative of the habitat type to which they were originally assigned, should future users of these predictive linkage trees find that the enduring environmental characteristics of their nearshore site of interest matches those of these particular terminal groups.

3.4 Discussion

3.4.1 Current approaches to habitat classification and prediction

The current approach to classifying nearshore habitat types within estuaries, which was developed for a range of systems in south-western Australia, produced a logical and intuitive separation of an environmentally diverse range of sites throughout the permanently-open Swan and Peel-Harvey estuaries, the seasonally-open Broke and Wilson inlets and the normally-closed Wellstead Estuary. As discussed below, this approach also satisfies each of the criteria outlined in the first aim of this component of the study. Furthermore, a quantitative method has also been developed for subsequently predicting the habitat type to which any new nearshore site in each of these systems should be assigned. To our knowledge, these approaches to estuarine habitat classification and prediction represent the first of their kind to be developed in Australia and, with respect to some of their characteristics, anywhere in the world.

(i) Quantitative approaches and significantly different habitat types

The quantitative nature of the current habitat classification and prediction approaches is two-fold. Firstly, they are based on fully quantitative measurements for each of the enduring environmental criteria employed in the scheme (see below) and, secondly, the decision rules for assigning sites to habitat types are entirely quantitative and derived from rigorous statistical tests. These features are considered crucial, as they remove any ambiguity in the use of the schemes, ensure that the results are both reliable and repeatable and provide a sound foundation for ascertaining statistically the extent to which the spatial differences among habitats are reflected by those of various faunal assemblages. With respect to the classification approach, the use of the SIMPROF test in conjunction with CLUSTER to ascertain those groups of sites within any particular estuary that did not differ significantly in their suite of enduring characteristics and thus represented habitat types, provided, firstly, a completely objective method for classifying sites into their most appropriate habitats and, secondly, ensured that each habitat type was significantly distinct from all others within the system, *i.e.* there were no redundant classes. Furthermore, the habitat prediction approach, which employed a novel application of the LINKTREE and SIMPROF routines, provided, at each node of the resultant linkage trees, quantitatively-defined thresholds for those environmental variables that were most important in separating sites into their respective habitats. These thresholds thus provide sound and easily interpretable decision rules for assigning any new nearshore site to its most appropriate habitat on the basis of measurements for its enduring environmental characteristics.

The above approaches represent considerable advances on several other published methods for classifying and/or predicting habitats in estuarine or coastal waters. Firstly, several schemes contain, at least in part, descriptive or subjective decision rules, and thus the resultant categorisation of a given site to a habitat type can vary among users, depending on their interpretation of those criteria (*e.g.* Dethier 1992, Allee *et al.* 2000, Pihl *et al.* 2002). Furthermore, the capacity of these schemes to be used as a basis for statistically predicting faunal composition is, at best, limited. Secondly, while other and particularly more recent habitat classification schemes commonly nominate numerical decision rules for assigning sites to a particular habitat, those rules are often derived subjectively and/or are categorical in nature (*e.g.* Madden *et al.* 2005, Hume *et al.* 2007, Mount *et al.* 2007). Thirdly, while several other habitat classification approaches have also adopted a hierarchical clustering technique to determine the patterns of environmental similarity among sites, they have typically chosen an arbitrary resemblance level as a “cut-off point”, below which those groups of sites that have formed in the clustering process are considered to represent different habitats (*e.g.* Edgar *et al.* 2000, Connor *et al.* 2004, Snelder *et al.* 2007). However, such approaches do not demonstrate statistically that the resultant groups actually represent distinct habitat types, or whether any such group may contain more than one habitat. Fourthly, given more recent advancements in the accessibility, quality and capability of satellite-derived environmental data and GIS techniques, many habitat classification studies have employed non-hierarchical clustering techniques (*e.g.* K-means clustering) to partition large numbers of spatially defined units into one of a series of classes based on differences in their optima of particular characteristics, *e.g.* satellite image pixels based on differences in their spectra (*e.g.* Engle *et al.* 2007, Gregr and Bodtker 2007). However, these clustering methods require an arbitrary pre-specification of the number of classes to which those spatial units can be assigned, and the number of “true” classes within the data is not known. Workers such as Zharikov *et al.* (2005) have attempted to circumvent this issue by subsequently employing other techniques such as Classification and Regression Tree approaches (De’ath and Fabricus 2000) to identify the optimal number of habitat classes, but they still lack a statistical demonstration that those classes are significantly distinct. The lack of rigorous testing of whether the resultant classes within habitat classification schemes are distinct and homogeneous has led to a proliferation of “theoretical habitat types” (Kurtz *et al.* 2006), particularly within nested classification schemes that encompass wide spatial and/or temporal scales (see below). Lastly, although the habitat classification approach developed by Valesini *et* *al.* (2003) for nearshore marine waters along the lower west coast of Australia employed quantitative measurements for a range of enduring environmental criteria and demonstrated statistically that the resultant habitats were significantly different, the initial stages of that approach depended on an *a priori* and partly subjective categorisation of habitat types based on a visual assessment of wave exposure and the dominant substrate/submerged vegetation types. Furthermore, this approach did not demonstrate whether the resultant classification was optimal, or whether particular sites may have been more appropriately assigned to another group.

(ii) Enduring, biologically-relevant and easily obtainable environmental criteria

The environmental criteria employed in the current approaches to habitat classification and prediction were enduring and considered to make an important contribution to broader groups of variables (*i.e.* site location with respect to its vicinity to marine and freshwater sources, level of exposure to wave activity and substrate/submerged vegetation type) that are known to influence, either directly or indirectly, the spatial distribution of estuarine fish and benthic invertebrate fauna.

The use of environmental rather than biological criteria in habitat classification schemes, and particularly those that are enduring, has several advantages which have been recognised by numerous workers (*e.g.* Roff and Taylor 2000, Banks and Skilleter 2002, Roff *et al.* 2003, Valesini *et al.* 2003, Hume *et al.* 2007, Snelder *et al.* 2007). Firstly, the resultant habitats are applicable to a range of fauna, while the "biotopes" (*i.e.* community and their habitats; Connor *et al.* 2004, Olenin and Ducrotoy 2006) that are often derived from biological schemes are applicable only to the biota on which they are based and the area for which they were devised (*e.g.* Zacharias *et al.* 1999, Connor *et al.* 2004, Stevens and Connolly 2005). Secondly, enduring environmental criteria are easy to measure directly from mapped sources, whereas the costs of acquiring quantitative biotic data over appropriate spatio-temporal scales and levels of replication are often prohibitive (*e.g.* Edgar *et al.* 2000, Roff and Taylor 2000, Banks and Skilleter 2002). Thirdly, enduring criteria often represent good surrogates for complex suites of non-enduring environmental variables that may be difficult and/or costly to measure.

The magnitude of non-enduring environmental characteristics (*e.g.* salinity, wave height etc) at each habitat will of course vary over a range of temporal scales in response to climatic changes, particularly in dynamic environments such as estuaries. However, habitats defined on the basis of enduring characteristics are still expected to remain distinct and display largely similar spatial patterns over time due to (i) temporal shifts in the importance of different non-enduring environmental variables and (ii) the persistent influence of directly influential (*i.e.* nonsurrogate) enduring variables. For example, while two habitats located on opposing banks of an estuary may be best distinguished by differences in wave height generated by prevailing north-westerly winds in winter, they will be equally well distinguished by waves from south-westerly winds that prevail in summer.

(iii) Flexible

The enduring environmental criteria employed in this study are also likely to be useful for classifying nearshore habitats within other estuaries, both throughout south-western Australia and in other areas of the world. However, the current approaches to habitat classification and subsequently prediction are entirely flexible in that the particular enduring criteria they employ can be easily tailored to suit the local conditions in any estuary, or indeed, any other type of environment, so long as they can be easily measured from available mapped sources.

(iv) Applicable at local scales

The local-scale habitats derived from the classification and prediction approaches developed in this study are at a spatial resolution that is highly appropriate for undertaking rigorous studies of the extent to which spatial differences in the characteristics of particular faunal assemblages (*i.e.* fish and benthic invertebrates) are associated with those in the environment (*e.g.* Valesini *et al.* 2004, Hourston *et al.* 2005, Stevens and Connolly 2005, Wildsmith *et al.* 2005). As estuarine ecologists and managers often work at local scales, the results of the current approaches, in combination with associated faunal studies (see subsection 3.4.3), will provide them with highly useful tools to obtain habitat and faunal inventories of a given system, reliably predict the fauna at any nearshore site and prioritise research and management questions. On this point, numerous classification schemes for estuaries have focused on categorising whole systems and/or their catchments, or making very broad distinctions among environmental zones within estuaries (*e.g.* Digby *et al.* 1998, Edgar *et al.* 2000, Roy *et al.* 2001, Engle *et al.* 2007, Hume *et al.* 2007). While these classifications are often useful at a national level for summarising broad differences in estuarine function, identifying their susceptibility to particular environmental impacts and/or qualifying their overall environmental or cultural value, they are of limited or no use to local resource managers and do not provide a reliable basis for predicting the distribution of biota at finer taxonomic levels, particularly for small benthic fauna (*e.g.* Dye 2006).

3.4.2 Some comparisons with nested habitat classification schemes

Many habitat classification schemes developed for coastal waters have adopted a hierarchical approach, in which finer spatial units of the classification are nested within successively broader groups. These classifications are inherently predictive, in that the user is guided through a series of interconnected decision rules to reach a final classification unit. In several cases, the broadest level of these schemes incorporates all marine and/or estuarine waters with a national Economic Exclusion Zone, and the finest levels represent highly localised habitats at the scale of metres (*e.g.* Allee *et al.* 2000, Connor *et al.* 2004, Madden *et al.* 2005). Necessarily, the finest levels of these hierarchies must be tailored by the individual user to accommodate the particular features of their local environment. This approach facilitates the growing trend towards the development of standardised habitat classification systems at national and continental scales, which has been motivated by the proliferation of different schemes at local and regional levels and subsequently a requirement for parity in habitat definition between one part of a country and another (*e.g.* Diaz *et al.* 2004, Madden *et al.* 2005, Mount *et al.* 2007).

Given that ecological studies and resource management of coastal waters typically occur at regional to local scales, the finer levels of large hierarchical classification schemes are usually the most critical. However, while several of these schemes provide clear decision rules at the broader levels of the hierarchy, those at finer levels (*e.g.* the local habitat, biotope or ecounit levels) are often less clear, either because they are more qualitative, copious and/or, when used in conjunction with the additional suite of "descriptors", "classifiers" or "modifiers" (*e.g.* salinity, water temperature, sediment grain size) that can be applied at various levels, present individual users with a myriad of ways of ultimately defining their local unit of interest. Consequently, choices made by one user at the finer levels of such schemes may differ from those of another, which, to some extent, contradicts the very purpose of these standardised hierarchical methods. Furthermore, the number of potential habitats/biotopes/ecounits that can be derived from such schemes is often extraordinarily large, particularly when several are designed to be adaptable at any temporal scale and to different sized biota and each of their activities, *e.g.* feeding, spawning etc.

Some of the above problems were exemplified by Keefer *et al.* (2008) when they applied the Madden *et al.* (2005) classification scheme, which encompasses all North American marine and estuarine waters, to the Columbia River Estuary. While this impressive six tiered scheme has, in many cases, provided numerical decision rules to minimize ambiguity, Keefer *et al.* (2008) found they could not make a clear choice at the second level, since several options were applicable. These workers, who had to collect measurements for a range of non-enduring physico-chemical characteristics throughout the estuary in order to use the classification (*e.g.* water velocity, conductivity, temperature, depth and sediment composition), also experienced difficulty at finer levels of the scheme due to indecision about which spatial resolution was most applicable to their data, and the fact that their study was not focused *a priori* on a particular type of biota or ecological question. They also found some qualitative decision rules to be insufficient. These issues highlight the fact that the outcomes of such classification schemes depend heavily on the objectives of the study, and may differ among users due to differences in interpretation. They also demonstrate that a substantial amount of quantitative data for a suite of abiotic characteristics at a diversity of spatio-temporal scales needs to be acquired in the field before such schemes can be used with confidence.

3.4.3 Future Developments

The next and most critical step in developing the current approaches to habitat classification and prediction is to test their ability to reliably reflect spatial differences in fish and benthic invertebrate assemblages at appropriate temporal scales. Thus, samples of the nearshore fish and/or benthic macroinvertebrate, nematode and/or hyperbenthic assemblages have been collected seasonally for at least one year at representatives of the various habitats in each of the study estuaries, and the extent to which their pattern of spatial distribution in each season matches that of the enduring features of the habitats is examined in Chapters 5-9. If these studies demonstrate that, for any given estuary, (i) the characteristics of the faunal assemblages differ significantly among habitats and (ii) the spatial pattern of those differences is significantly correlated with that of the enduring environmental criteria used to classify habitats, then the current habitat prediction approach, in combination with the above faunal data, can be used to reliably predict a range of faunal characteristics for any nearshore site. Examples of the type of faunal information that could be provided for each habitat in each season include the species most likely to occur at that site, average abundance, species diversity and species size ranges, which would thus provide a comprehensive tool for a host of ecological and management applications. If, on the other hand, the associated faunal studies show that the composition of those assemblages does not differ significantly between particular habitats in any season, then the habitat prediction approach can be modified to combine those habitats, and the revised scheme subsequently used as described above.

In order to make the habitat prediction process as simple as possible for end users, another obvious development of the current approaches is to produce a digital, spatially-continuous habitat map of each estuary in a GIS, in which all nearshore waters are classified according to their most appropriate habitat type. This could be achieved by automating the habitat prediction technique for every unclassified site along the coastline. Thus, users of the scheme would simply need the geographic coordinates of their site of interest in order to ascertain its habitat type, without the need to undertake any measurements of its enduring environmental characteristics.

Finally, the current approaches to local habitat classification and prediction in estuaries, or indeed, other coastal waters, could complement the finer levels of a nested habitat classification scheme developed for Australian marine and estuarine waters, such as that of Mount *et al.* 2007.

4. Relationships between habitat types and faunal assemblages in south-western Australian estuaries

4.1 Introduction

Estuaries represent crucial environments for numerous fish species (*e.g.* Haedrich 1983, Potter *et al.* 1990, Elliot and Dewailly 1995, Meynecke *et al.* 2007). Several of these species are important for commercial and/or recreational fishers, which, in south-western Australia, include Black Bream *Acanthopagrus butcheri*, Sea Mullet *Mugil cephalus*, Yellow-eye Mullet *Aldrichetta forsteri* and Cobbler *Cnidoglanis macrocephalus*. The value of estuaries to fisheries in this region can be gauged by the fact that, during 2007, the economic value to commercial fishers of their catch in south-western Australian estuaries was *ca* \$2.85 million, and the catch by recreational fishers in these waters was estimated to be 30-75% of the combined commercial and recreational catch (Smith and Brown 2008a, b).

Some marine fish species use estuaries either as a nursery area or for more protracted periods, while other species employ these environments as a migratory route between their spawning and main feeding grounds, and several species spend the whole of their life cycle in these systems (*e.g.* Lenanton and Hodgkin 1985, Kennish 1990, Potter and Hyndes 1999). Aside from the relatively calm waters and greater protection from predation that are typically found in estuaries (*e.g.* Potter *et al.* 1990), one of the main reasons for the importance of these environments to a wide range of fish is that they contain an abundance of benthic invertebrates, which are a main food source for many species (*e.g.* Coull 1999, Humphries and Potter 1993, Mees and Jones 1997, Mouny *et al.* 1998, Sarre *et al.* 2000, Platell *et al.* 2006). These typically comprise benthic macroinvertebrates (*i.e.* those invertebrates which inhabit aquatic substrate and are retained by a 500 μm sieve; Howard *et al.* 1989, Bennett 1992), free-living nematodes, which typically form the largest component of the meiofauna (*i.e.* those benthic invertebrates that pass through a 500 μm sieve but are retained on meshes of 40-63 μm; Coull 1999) and the hyperbenthic fauna (*i.e.* swimming bottom-dependent fauna which perform, with varying amplitude, intensity and regularity, vertical migrations above the substrate; Friedrich 1969, Mees and Jones 1997). These benthic invertebrate assemblages play a crucial role in estuarine food webs, not only by providing a highly important food source for secondary consumers, but also by consuming large amounts of detritus and primary food sources such as benthic and pelagic microphytes and facilitating the remineralisation of organic matter (*e.g.* Levinton 1972, Gee 1989, Edgar and Shaw 1995, Mees and Jones 1997, Coull 1999, Pennifold and Davis 2001, Smith and Parrish 2002, Riera and Hubas 2003).

Given the extreme physico-chemical gradients and diversity of benthic environments that are often found naturally within estuaries (*e.g.* Day *et al.* 1989, McLusky and Elliott 2004) and the vulnerability of these systems to environmental decline from a wide range of anthropogenic activities (*e.g.* Edgar *et al.* 2000, Jackson *et al.* 2001, Kennish 2002, Kemp *et al.* 2005), many studies throughout the world have examined spatial differences in the characteristics of estuarine fish and benthic invertebrate assemblages and attempted to identify their relationships with particular environmental criteria. Reliably establishing such relationships provides the foundation for developing tools to predict the characteristics of estuarine fauna on the basis of differences in particular environmental attributes, which has numerous highly important applications for estuarine conservation, resource management and ecology. However, many of these studies have (i) been undertaken at relatively broad spatial scales, such as between main regions within a system (*e.g.* Loneragan *et al.* 1989, Moreira *et al.* 1993, Potter *et al.* 1993, Platell and Potter 1996, Tararam *et al.* 1996, Valesini *et al.* 1997, Young *et al.* 1997, Mouny *et al.* 2000, Abookire *et al.* 2000, Castro *et al.* 2009) or among different estuaries, in which a small number of sites have been studied in each (*e.g.* Mees *et al.* 1995, Edgar *et al.* 2000, Thrush *et al.* 2003, Dye and Barros 2005), (ii) examined only a small number of environmental variables, and often on an individual basis, when attempting to identify the environmental drivers of spatial differences in faunal assemblages (*e.g.* Loneragan *et al.* 1987, Austen and Warwick 1989, Mees and Hamerlynck 1992, Soetaert *et al.*, 1995, Thrush *et al.* 2003, Shervette and Gelwick 2008, Castro *et al.* 2009) and (iii) made only descriptive, and not statistical, links between spatial differences in faunal characteristics and those of the environment. However, differences in a small number of environmental characteristics, particularly when examined individually and at relatively broad scales, do not encapsulate the complexity of the estuarine environment. Thus, a wide range of attributes must be considered in combination in order to adequately characterise the variety of habitats that are invariably present in these systems (*e.g.* Pihl *et al.* 2002, Madden *et al.* 2005, Dye 2006). This was clearly demonstrated in Chapter 3 of the current study for various estuaries in south-western Australia, in which the differences throughout each system in a suite of environmental criteria that broadly encompassed (i) the relative influences of marine and riverine water sources, (ii) exposure to wave activity and (iii) the type and extent of substrate and submerged vegetation, were shown to reflect a wide range of significantly different habitats at a much finer spatial scale than has traditionally been examined in many studies of estuarine faunal-environment relationships. Moreover, workers such as Dye (2006) have shown that, for particular estuaries in south-eastern Australia, their separation into broad geomorphological zones on the basis of differences in a small number of environmental criteria was a poor predictor of spatial patterns in various benthic invertebrate assemblages, which was partly reflected by the marked differences in the characteristics of these fauna within each zone. Lastly, although several other workers in estuaries have investigated spatial differences in moderate to large numbers of environmental variables and related them to the distribution of faunal species, they have not attempted to (i) use the collective differences in those environmental variables to identify significantly different habitat types and (ii) test whether faunal composition varies significantly among those habitats (*e.g.* Akin *et al.* 2005, Granados-Dieseldorff and Baltz 2008, Selleslagh *et al.* 2009).

Accurately predicting the fish or benthic invertebrate species that are likely to characterise a particular estuarine site by employing data for its environmental characteristics thus requires, firstly, a rigorous classification of the local-scale habitats found throughout a system that have been identified statistically on the basis of measurements for a suite of environmental criteria, secondly, quantitative data on the species composition of faunal assemblages at each of those habitats that has been collected at a temporal scale that is reflective of marked changes in the estuarine environment and the life-history patterns of the fauna of interest (*e.g.* seasonally) and, thirdly, statistical demonstration of significant relationships between spatial differences in habitat type and those of faunal composition.

Although estuaries in south-western Australia are displaying increasing signs of environmental decline (*e.g.* Potter *et al.* 1983, Steckis *et al.* 1995, Commonwealth of Australia 2002, Swan River Trust 2009), managers of these systems do not currently have a quantitative method for undertaking the following at appropriate spatial and temporal scales. (i) Establishing reliable habitat and faunal benchmarks, against which the effects of future environmental change can be determined, (ii) identifying those habitats that are most important for key fish and benthic invertebrate species and/or are most biodiverse, and thus are priority candidates for inclusion within conservation areas and (iii) predicting the fish and benthic invertebrate species that are most likely to occur at any nearshore site in an estuary at any time of year, and thus, for example, those that are most likely to be impacted by proposed anthropogenic modifications. The need by local managers for such methods was stated clearly by the Western Australian Department of Fisheries in their most recent report on the State of the Fisheries in estuaries in south-western Australia, *i.e. "West coast estuaries are highly modified, and often degraded, environments. In these estuaries, the impacts of environmental factors on stock abundances are likely to be at least as important as fishing pressure. Hence, the sustainable management of the fish communities in west coast estuaries requires a collaborative effort between fishery and habitat* *managers."* (Smith and Brown 2008a, p53). Moreover, a recent scoping document on the development of a national scheme to assess the ecological status of Australia's estuarine and marine waters has also stated the need for the above information to support particular stages of the assessment framework (Mount 2008). Thus, for each of the estuaries selected for study in south-western Australia, namely the Swan and Peel-Harvey estuaries, Broke and Wilson Inlets and Wellstead Estuary, the main aims of this component of the study were to determine the following.

1. Whether the compositions of the fish assemblages and, in selected systems, those of the benthic macroinvertebrate, nematode and hyperbenthic assemblages, differ significantly among the habitats that were identified quantitatively using the current classification approach (Chapter 3) and, if so, those species that are most characteristic of each habitat type.
2. Whether the relative differences among habitats, as defined by their faunal composition, are significantly correlated with those of the environmental data used to classify those habitats, and thus whether spatial differences in the latter characteristics provide a sound basis for predicting those in faunal composition.
3. Whether the above two aspects of the faunal assemblages recur consistently in all seasons.

Further to the above, it should be noted that this is one of the very few studies in which the species composition of the nematode fauna has been explored, both spatially and temporally, in the nearshore subtidal waters of a microtidal estuary, and the first time that such a study has been undertaken in Western Australia. Moreover, this is the only known study of hyperbenthic faunal assemblages in an Australian estuary. Lastly, this study is among the first to provide fully quantitative data at a high spatio-temporal resolution on the nearshore fish assemblages of Broke Inlet, the only estuary in south-western Australia that was classified as "near-pristine" by the most recent Australian Catchment, River and Estuary Assessment (Commonwealth of Australia 2002).

4.2 Materials and Methods

4.2.1 Field techniques

4.2.1.1 Collection of fish and benthic invertebrate assemblages

Samples of the fish assemblages were collected from sites in the nearshore shallow waters (<1.5 m deep) of the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary that represented the various habitat types identified in each of these systems in Chapter 3 of the current study. In each system, fish were sampled during the day in the last month of each of four to six seasons between autumn 2005 and winter 2008, which always included four consecutive seasons (Table 4.2.1.1). In each sampling season, fish were collected at two sites representing each habitat type, with four randomly-located replicate samples being taken at each site. The only exception was Broke Inlet, in which fish were collected at four sites representing each habitat, and two replicate samples were taken at each site. The latter sampling regime was adopted for the Broke Inlet in order to maximize statistical power for testing for ichthyofaunal differences among habitats, and to avoid preliminary testing for differences between sites prior to testing among habitats (see subsection 4.2.3). Collection of the replicate samples at each site in each estuary was staggered over one to three weeks in each sampling season to obtain a better representation of the temporal range of environmental conditions, and to reduce the likelihood of the resultant data being unduly influenced by an atypical catch.

Fish were collected using a seine net that was 21.5 m long and 1.5 m high, comprised 10 m long wings (6m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long central bunt (3 mm mesh) and swept an area of 116 m^2. Fish could not be collected at some habitats in each estuary as the particular physical features of those habitats precluded effective operation of the seine net, *e.g.* the substrate contained too many rocks or snags, the nearshore waters were too shallow throughout the year (*i.e.* typically less than 0.3 m deep) or the banks were too steep and quickly fell to depths >1.5 m. Furthermore, in some instances in the Swan and Peel-Harvey estuaries, some habitats were represented by only one site and/or could not be sampled in particular seasons due to unfavorable environmental conditions. The habitats and their representative sites that were able to be sampled in each estuary and season are given in Table 4.2.1.1.

Benthic macroinvertebrates, nematodes and hyperbenthic fauna were also collected from a subset of the habitats and seasons for which fish were sampled in the Swan Estuary, and the same was true for the latter group of invertebrates in the Peel-Harvey Estuary. The particular

Table 4.2.1.1: Summary of the sampling regimes undertaken for the fish and/or benthic invertebrate fauna and non-enduring environmental variables at each habitat type in the Swan and Peel-Harvey estuaries, Broke and Wilson Inlets and Wellstead Estuary between summer 2005 and winter 2008. * reduced number of sites sampled at a particular habitat (provided in brackets under "N^{o} sites per habitat"); $^{-}$ habitat, or one of its representative sites, unable to be sampled in particular seasons (habitats and seasons for which sampling was not undertaken are denoted by $^{-}$ under "Habitats" and "Sampling seasons").

	Year	**Swan Estuary**	**Peel-Harvey Estuary**	**Broke Inlet**	**Wilson Inlet**	**Wellstead Estuary**
Fish fauna						
Habitats		A, C, E, F*, G, I, J, M, N*, Q	B^{-}, C, D, E^{-}, H*, I^{-}, J, K*, L, M, Q^{-}	A^{-}, B, C, D, E, F, G, H, I, J*, K	C, D, F, G^{-}, I, J^{-}, L, O	A, C, D, E, F
N^{o} sites per habitat		2 (*1)	2 (*1)	4 (*3)	2	2
N^{o} reps per site		4	4	2	4	4
Sampling seasons	2005	A W SP	W^{-E} SP^{-I}			
	2006	S W	$S^{-B,I,Q}$ A W		W $SP^{-G,J}$	W SP
	2007	S	S^{-B}	SP	$S^{-G,J}$ $A^{-G,J}$ W	S A W
	2008			S^{-A} A^{-A} W	S	S
Benthic invertebrates						
Macroinvertebrates & Nematodes						
Habitats		A, C, F*, G, I*, J, M				
Sampling seasons	2005	S A W SP				
Hyperbenthos						
Habitats		A, C, E*, F*, G, I*, J, M	B^{-}, D, H*, K*, L, Q^{-}			
Sampling seasons	2005	W	W			
	2006	S	$S^{-B,Q}$			
N^{o} sites per habitat		2 (*1)	2 (*1)			
N^{o} reps per site		5	5			
Non-enduring environmental variables						
Water quality						
Habitats		As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna
N^{o} sites per habitat		As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna
N^{o} reps per site		3	3	2	3	3
Sampling seasons		As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna	As for fish fauna
Sediment parameters						
Habitats		As for macroinvertebrates				
N^{o} sites per habitat		2 (*1)				
N^{o} reps per site		3				
Sampling seasons		As for macroinvertebrates				

habitats and seasons in which each of these benthic invertebrate assemblages were sampled, as well those instances in which the regular sampling regime could not be carried out, are given in Table 4.2.1.1. Five randomly-located replicate samples of each invertebrate assemblage were collected in the shallows (*i.e.* 0.5-1.5 m deep) at each site in each sampling season and, as for the fish fauna, their collection was staggered over several weeks in a season. Benthic macroinvertebrates were collected using a cylindrical steel sediment corer that was 11 cm in diameter, sampled sediment to a depth of 10 cm and had a surface area of 96 cm^2. The sediment samples were immediately wet-sieved through a 500 µm mesh to discard any fine sedimentary material. Nematodes were collected using a cylindrical steel sediment corer that was 3.57 cm in diameter, sampled to a sediment depth of 10 cm and covered a surface area of 10 cm^2. The hyperbenthic fauna was sampled using a benthic sled that comprised a rectangular steel frame (50 cm long x 25 cm high), to which a plankton net was attached. The sled was mounted on two runners that maintained its base *ca* 3 cm above the substrate surface, and had a steel 'lip' at its entrance, which enabled it to effectively collect fauna resting on the substrate. The plankton net, which was made of 150 µm mesh, was 1.45 m in length and tapered gradually from its mouth to a cod-end that was 11 cm wide and comprised a Perspex cylinder with a 150 µm mesh draining port. The sled was towed manually for 50 m along a subtidal transect that lay parallel to the shoreline. A General Oceanics flowmeter was attached at the entrance of the net to record the volume of water filtered during each replicate tow. All benthic invertebrate samples were preserved in 5% formalin buffered in estuary water immediately after collection.

4.2.1.2 Collection of non-enduring environmental data

Measurements of a suite of water quality characteristics, namely salinity (‰), water temperature (°C) and dissolved oxygen (mg L^{-1}), were undertaken at the same sites and times at which fauna were collected in each of the study estuaries. Three replicate measurements of each variable were recorded in the middle of the water column at each site in each season using a Yellow Springs Instrument 556 water quality meter, except for in Broke Inlet, where only two replicates were recorded at each site on each sampling occasion (Table 4.2.1.1).

In addition to the above water quality measurements, the sediment mean grain size (µm), particulate organic matter content (POM; %), chlorophyll concentration (µg L^{-1}) and the depth (cm) below the sediment surface at which its colour changed from light to dark (*i.e.* where sedimentary conditions become anaerobic, and henceforth referred to as the transition zone) were also measured at the same sites and times at which the benthic macroinvertebrates and nematodes were collected in the Swan Estuary. Three replicate sediment cores for the measurement of sediment grain size, POM and transition zone depth were collected at each site in each sampling season using a steel corer that was 3.57 cm in diameter (10 cm^2) and sampled to a depth of 10 cm. An additional three replicate sediment cores were collected using disposable plastic corers that were 2.8 cm in diameter and sampled to a depth of 10 cm, to ascertain the quantity of sedimentary chlorophyll. These latter cores were immediately wrapped in aluminium foil to exclude light, stored on ice and then frozen.

4.2.2 Laboratory techniques

4.2.2.1 Faunal samples

The total number of individuals of each fish species in each replicate sample was recorded and the total length of each fish measured to the nearest 1 mm, except when a large number of a species was caught, in which case the lengths of 100 randomly-selected individuals were measured. Each species was assigned to one of the life-history categories described by Potter and Hyndes (1999).

All benthic macroinvertebrates in each replicate sample were separated from the sediment under a dissecting microscope, identified to the lowest possible taxon and then counted. All macroinvertebrates were stored in 70% ethanol to provide a reference collection.

The nematodes in each core were separated from the sediment using the laboratory procedures described in Hourston *et al.* (2005), except that a decantation step was added prior to using colloidal silica (Ludox™) to increase the efficiency with which nematodes were removed. Thus, each sample was suspended in 800 ml of tap water and the larger sediment grains allowed to settle briefly, after which the remaining suspension was decanted through nested sieves of 500 and 63 μm mesh. The sand from which the suspension was decanted was subjected to the above procedure four more times to ensure that all nematodes had been removed. The organisms were separated from the fine sand and debris particles remaining on the 63um sieve using Ludox™ and preserved in 70% ethanol. The procedures for isolating, subsampling, mounting and identifying the nematodes are also given in Hourston *et al.* (2005). Counts were conducted on sub-samples, generally comprising one quarter of each core, then multiplied appropriately to estimate the abundance of each taxon in the entire core.

Each sample of the hyperbenthos, which contained a mixture of fauna, sediment and plant material, was wet-sieved through nested 2 mm and 150 μm mesh sieves and the resultant size fractions removed and stored separately in 70% ethanol. The organisms retained on the 2 mm sieve fraction were then separated from the sediment under a dissecting microscope, sorted to the lowest possible taxon and counted. The organisms retained on the 150 μm sieve were stored in 200 ml of 70% ethanol, stirred thoroughly and three 1 ml subsamples removed using a pipette. The organisms in each subsample were identified to the lowest possible taxon and then counted. The mean number of individuals of each taxa in these subsamples was then multiplied appropriately to estimate their total number in 200 ml. The number of individuals of each taxon in both the 2 mm and 150 μm fractions were then summed to determine their total numbers in each replicate sample. In the few cases in which the quantity of sediment retained on the 150 μm mesh exceeded 200 ml, the hyperbenthic fauna was separated from the sediment using Ludox™. Thus, each sample was covered with sufficient Ludox™ to double its volume, stirred and left for 15 minutes. The organisms and fluid were decanted and the process repeated to minimize the chances of any organisms being retained in the sediment. Note that small juvenile hyperbenthos, which could not be reliably allocated to a taxon, were not included in subsequent analyses. However, these juveniles represented less than 2% of all hyperbenthos collected. All hyperbenthos were stored in 70% ethanol to provide a reference.

4.2.2.2 Sediment samples

Each of the sediment cores collected for grain size and POM analysis were dried at 70°C for 24 h, weighed to the nearest 1 mg, ashed at 550°C for 2 h and then reweighed. The ashed sediment weight was then subtracted from the total dried sediment weight to determine the percentage contribution of POM in each sample (Heiri *et al.* 2001). Each ashed sample was then wet-sieved through 63 μm mesh to remove any silt and clay particles, redried and weighed again. The latter dry weight was subtracted from the ashed sediment weight to determine the amount of silt and clay particles in each sample (Heiri *et al.* 2001). The remaining sample was wet-sieved through a series of nested sieves that correspond to the Wentworth scale of grain size distribution, *i.e.* 2000, 1000, 500, 250, 125 and 63 μm (Wentworth 1922), and the fraction of sediment retained on each mesh was then redried and weighed. The weights of each fraction were then converted to a percentage and used to calculate mean grain size. The quantity of total sedimentary chlorophyll in the top 2 cm of sediment in each of the second set of replicate cores was determined using the acetone extraction method described by Parsons *et al.* (1984).

4.2.3 Statistical Analyses

Each of the following data analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke and Gorley 2006) with the PERMANOVA+ add-on module (Anderson *et al.* 2008).

4.2.3.1 Univariate analyses

Spatial and temporal differences in faunal characteristics

The species abundances in each replicate sample of each faunal assemblage collected in each estuary were initially converted to densities. Thus, those for fish, benthic macroinvertebrates, nematodes and hyperbenthos were converted to number of individuals per 100 m^2, 0.1 m^2, 10 cm^2 and 1 m^3, respectively. Calculation of the species densities of hyperbenthos in each replicate sample was achieved by using the complementary volume of water filtered by the net, as determined by the following equations.

$$\text{Distance (m)} = (\text{Flowmeter reading} * 26873)/999999 \quad (1)$$

$$\text{Volume } (m^3) = (3.14 * (a * b) * \text{distance})/4 \qquad (2)$$

Where *a* and *b* are the height and width dimensions of the mouth of the net, respectively.

The number of species, density of individuals and quantitative average taxonomic distinctness (Δ^*) was then calculated for each replicate sample. The latter variable is a measure of species diversity that accounts for the relatedness of individuals from different species in a sample, based on their level of taxonomic separation through the hierarchical levels of the Linnaean tree (Warwick and Clarke 1995).

Prior to undertaking Permutational ANOVA and MANOVA (PERMANOVA; Anderson 2001) on the data for each of the above dependent variables, they were each examined to ascertain the type of transformation required, if any, to approximate the test assumption of homogeneous sample dispersions among groups. This was achieved by determining the slope of the linear relationship between the $\log_e$(mean) and $\log_e$(standard deviation) of groups of replicate samples of each dependent variable, and applying the criteria provided by Clarke and Warwick (2001). The type of transformation applied to the data for each of these dependent variables for each faunal assemblage in each study estuary is given in Table 4.2.3.1. Note that PERMANOVA, rather than standard parametric ANOVA, was employed to test for differences in the above univariate data, since the former permutational test does not make any assumptions about the distribution of the underlying data (Anderson 2001).

The transformed replicate data for each dependent variable of each faunal assemblage in each system were then used to construct separate Euclidean distance matrices, which were all subjected to PERMANOVA to ascertain the extent to which they differed spatially and temporally. For data collected from all estuaries except Broke Inlet, a preliminary PERMANOVA was used to ascertain whether there were any significant differences between

Table 4.2.3.1: Transformations applied to the data for the univariate faunal and non-enduring environmental variables recorded in the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary.

	Swan Estuary	**Peel-Harvey Estuary**	**Broke Inlet**	**Wilson Inlet**	**Wellstead Estuary**
Fish fauna					
N^{o} species	√	√	none	none	none
Density	$\log_e(n+1)$	$\log_e(n+1)$	$\log_e(n+1)$	$\log_e(n+1)$	$\log_e(n+1)$
Taxonomic distinctness	√	none	none	none	none
Benthic invertebrates					
Macroinvertebrates					
N^{o} species	√				
Density	√√				
Taxonomic distinctness	√				
Nematodes					
N^{o} species	none				
Density	√√				
Taxonomic distinctness	none				
Hyperbenthos					
N^{o} species	√√	none			
Density	$\log_e(n+1)$	$\log_e(n+1)$			
Taxonomic distinctness	none	√			
Non-enduring environmental variables					
Water quality					
Salinity	none	none	none	√	none
Temperature	none	none	none	none	none
Dissolved oxygen	none	none	none	none	none
Sediment parameters					
Mean grain size	√√				
Particulate organic matter	$\log_e(n)$				
Chlorophyll concentration	√√				
Transition zone depth	√				

sites assigned to the same habitat type, and thus whether the replicate samples collected from each site could be pooled to test for differences at the broader habitat level, or whether spatial differences were more appropriately examined at the site level. Thus, in this test, the factors included habitat, site nested within habitat type and sampling season, the latter of which was crossed with the first two. Site was considered to be a random factor, while both habitat and season were treated as fixed factors. If a significant site and/or site x season effect was detected in the above test, the data were then subjected to a two-way crossed site x season PERMANOVA to better elucidate the nature and extent of the spatio-temporal differences in the dependent variable. Note that, in these tests, site was considered a fixed factor, since pairwise comparisons between sites, and particularly those from different habitats, were of interest. Alternatively, if no significant site effects were detected, the replicates collected at each site were pooled to represent their assigned habitat type, and the data subsequently subjected to a habitat x season PERMANOVA. In all PERMANOVA tests, the null hypothesis of no significant differences among groups was rejected if the significance level (p) was ≤0.05. Furthermore, the magnitude of the components of variation for each term in the PERMANOVA model was used to ascertain their relative importance to differences in the dependent variable. The main causes of any significant differences detected by PERMANOVA were determined by examining plots of the marginal means of the dependent variable, back-transformed where necessary, with associated 95% confidence intervals.

The data contained in the two replicate samples collected at each of the four sites representing each habitat in Broke Inlet in each sampling season were averaged prior to analysis, and these means were treated as replicates of habitat type in subsequent tests. The greater replication that was undertaken at the habitat level in this system, combined with the use of site averages as replicates, thus precluded the necessity to undertake the preliminary three-way PERMANOVA test described above. The data were thus subjected only to a habitat x season PERMANOVA to elucidate their spatial and temporal differences.

Spatial and temporal differences in non-enduring environmental characteristics

Replicate data for each of the water quality parameters (*i.e.* salinity, temperature and dissolved oxygen concentration) and, where relevant, sediment parameters (*i.e.* mean grain size, POM, chlorophyll concentration and transition zone depth) recorded in each estuary were used to construct separate Euclidean distance matrices, which were then subjected to the same PERMANOVA analyses as described above. However, prior to analysis, a different technique was adopted for ascertaining which type of data transformation was required, if any, to meet test assumptions. The replicate data for the suite of water quality or sediment parameters were instead used to construct "Draftsman plots", or scatterplots of samples between every pair of variables, which allowed visual detection of whether the data distribution for any variable was notably skewed, and thus provided a basis for selecting an appropriate transformation to ameliorate any such effect. The data transformations applied to each non-enduring environmental variable in each estuary are given in Table 4.2.3.1.

4.2.3.2 Multivariate analyses

Spatial differences in faunal composition

The replicate species abundance data for each faunal assemblage in each estuary was initially subjected to dispersion weighting (Clarke *et al.* 2006) to downweight the contributions of those species that exhibited large and erratic differences in abundance within groups of replicate samples. This procedure was thus carried out for the group of replicates collected at each site in each season in the Swan and Peel-Harvey estuaries, Wilson Inlet and Wellstead Estuary, and for the site averages recorded at each habitat in each season in the Broke Inlet. The dispersion weighted data was then subjected to a square-root transformation to balance the contributions of highly abundant and consistently-occurring species with those that were less abundant. The pretreated replicate data were then used to construct separate Bray-Curtis similarity matrices for each faunal assemblage in each system.

Each of the above similarity matrices, except that for Broke Inlet, were subjected to the same preliminary three-way PERMANOVA test described in subsection 4.2.3.1 to ascertain whether spatial differences in faunal composition were most appropriately analysed at the habitat or site level. While significant site and/or site x season effects were detected in most cases (see Chapters 5.1, 6.1, 8.1 and 9.1), the relative importance of differences among habitat types was almost always far greater than that of site or the site x season interaction. Furthermore, when sub-matrices containing the replicates collected in any particular sampling season were constructed from each of the above Bray-Curtis matrices and then subjected to preliminary one-way Analysis of Similarities tests (ANOSIM; Clarke and Green 1988), the majority of significant differences in faunal composition between sites assigned to the same habitat were typically shown to be restricted to a small number of seasons (see Chapters 5.1, 6.1, 8.1 and 9.1). In these and all subsequent ANOSIM tests, the null hypothesis that there were no significant differences in faunal composition between groups was rejected if the p value was $\leq 5\%$, and the relative extent of any significant differences was determined by the magnitude of the associated R-statistic, *i.e.* values close to 0 indicate little difference in composition between groups, while those close to +1 indicate large compositional differences between groups (Clarke and Green 1988).

In view of the above results, the replicate samples recorded at the various sites were pooled to represent their respective habitat types, and the Bray-Curtis sub-matrices containing samples for any particular faunal assemblage, estuary and season were each then subjected to one-way ANOSIM tests to better examine the extent to which faunal composition differed among the levels of this broader spatial factor. Note that these tests were almost always carried out separately for the data recorded in each season, since significant seasonal differences were nearly always detected by the above preliminary PERMANOVA tests. The same Bray-Curtis sub-matrices were also each subjected to Multidimensional Scaling ordination (MDS), and the samples on the resultant plots coded for habitat type in order to illustrate the nature of differences in faunal composition among levels of this factor. Complementary one-way Similarity Percentages analyses (SIMPER; Clarke and Green 1988) were used to ascertain, in each season, which species best typified the faunal assemblages at each habitat type, and those that best distinguished the assemblages of pairs of habitats that were shown by ANOSIM to differ significantly. In these and all subsequent SIMPER analyses, emphasis was placed on those typifying and distinguishing species that (i) had relatively high similarity to standard deviation and dissimilarity to standard deviation ratios, respectively, and (ii) those that were relatively abundant.

The Bray-Curtis similarity matrix constructed from the average species abundance data recorded at replicate sites representing each habitat in Broke Inlet in each season was subjected to a two-way crossed habitat x season PERMANOVA to elucidate the extent of any significant differences among these main effects and the interaction term. As this test demonstrated that all terms were significant (see Chapter 7.1), the nature of differences in faunal composition among habitats was further explored by undertaking one-way ANOSIM tests, MDS ordination and one-way SIMPER analyses for this spatial factor using the data collected in each individual season.

Matching spatial patterns between the environmental and faunal assemblage characteristics of habitats

The RELATE routine was used to test the extent to which the pattern of resemblances between habitats, as defined by the composition of a given faunal assemblage in a particular estuary and sampling season, matched that defined by the complementary suites of (i) enduring environmental characteristics used to classify those habitats and (ii) non-enduring environmental characteristics, *i.e.* water or sediment parameters. This test was thus used to correlate the pattern of the rank orders of resemblance between habitats in a Bray-Curtis similarity matrix constructed from the pretreated average species composition, with those in complementary Manhattan distance matrices constructed from the pretreated average data for either the enduring or non-enduring environmental characteristics. Note that the enduring environmental data were pretreated in the same way as described in Chapter 3.2.3.1, while the pretreatment of the faunal assemblage and non-enduring environmental data were the same as those described above and/or shown in Table 4.2.3.1. The only exception was that the latter data, which contained variables measured in different units, were also subject to normalization prior to analysis to place all data on the same measurement scale. The null hypothesis that there were no similarities in the pattern of the rank order of resemblances between the complementary matrices was rejected if the significance level associated with the test statistic (rho; ρ) was ≤5%. The relative extent of any significant differences was determined by the magnitude of ρ, *i.e.* values close to 0 indicate little correlation in rank order pattern between complementary matrices, while those close to +1 indicate near perfect agreement in the underlying pattern of complementary matrices.

The Biota and Environment matching routine (BIOENV; Clarke and Ainsworth 1993) was then used to ascertain whether a greater correlation between complementary faunal and non-enduring environmental matrices could be obtained by using only a particular subset of water or sediment parameters, rather than the full suites. The null hypothesis, criteria for rejecting it and the test statistic were the same as those described above for RELATE. Note that, for all systems except Broke Inlet, the matrices employed in these BIOENV tests were constructed from the average data recorded at each site rather than habitat type, in order to increase the number of samples in the reference (faunal) matrices and thus minimize the likelihood of BIOENV finding a subset of water or sediment variables that provided a good match with those references by chance. It should also be noted that additional RELATE tests were undertaken between complementary faunal and non-enduring environmental matrices constructed from site rather than habitat averages, in order to verify whether the results obtained from the earlier (habitat) RELATE tests were comparable with those from BIOENV. In most cases, the RELATE results obtained from matching complementary faunal and water quality matrices constructed from habitat *vs* site averages were similar, but those instances in which notable discrepancies occurred are mentioned in Chapters 5.1, 6.1, 8.1 and 9.1.

Comparisons of the spatial patterns among sites exhibited by (i) the average composition of a given faunal assemblage in a particular estuary and sampling season *vs* (ii) the averages of the complementary non-enduring environmental variables selected by BIOENV, were illustrated by subjecting the Bray-Curtis similarity matrices constructed from the average faunal composition data at each site to MDS ordination, then overlaying circles ("bubbles") of proportionate sizes that represented the magnitude at each site of the selected non-enduring environmental variables.

Seasonal differences in faunal composition

The Bray-Curtis similarity matrices constructed from the pretreated replicate species abundance data for any given faunal assemblage in any particular estuary, *i.e.* those described in the above subsection entitled *Spatial differences in faunal composition,* were used to construct sub-matrices containing the replicate samples collected in the various seasons at each individual habitat type. Each of these sub-matrices were then subjected to one-way ANOSIM tests, MDS ordination and SIMPER analyses as described above, to better elucidate the nature of seasonal differences in faunal composition. Note that these analyses were performed separately for the data recorded at each habitat to overcome the confounding influence of that spatial factor.

5. Relationships between habitat types and faunal assemblages in the Swan Estuary

5.1 Results

5.1.1 Non-enduring environmental variables

5.1.1.1 Water quality parameters

Preliminary three-way PERMANOVA tests were used to ascertain whether habitat, or their representative sites, was the most appropriate spatial level for testing for differences in salinity, water temperature and dissolved oxygen concentration throughout the Swan Estuary between autumn 2005 and summer 2007. These tests demonstrated that, for the first two of these water quality variables, there were no significant differences between sites within the same habitat, nor were there any significant site x season interaction effects. In contrast, dissolved oxygen concentration did differ significantly between sites belonging to the same habitat, and the interaction between site and season was also significant. It should be noted, however, that the relative importance of these significant site effects were two to three times less than that of habitat type. In view of the above results, data for salinity and temperature were then each subjected to a two-way crossed habitat x season PERMANOVA test and dissolved oxygen subjected to a site x season PERMANOVA to explore more thoroughly the extent of the spatial and temporal differences in these water quality parameters in the Swan Estuary (Table 5.1.1.1).

Salinity varied significantly among both habitats and seasons (p=0.001), and the interaction between these factors was also significant (p=0.005). However, the components of variation for each of these significant effects clearly demonstrated that the overall influence of habitat, followed by that of season, were far greater than that for the interaction between these factors. Figure 5.1.1.1a clearly shows that, in virtually all sampling seasons, the salinities at the two riverine habitats A and C were significantly lower than those at all other habitats. The only exception to this was in summer 2007, during which the average salinity at C (*ca* 32‰) did not differ significantly from that at all basin and channel habitats (*ca* 36-37‰). Salinities at habitat J at the base of the Swan River were also notably lower than those at several of the other basin habitats and those in the channel in most seasons, particularly during winter 2005. The greatest salinities were generally recorded at the channel habitats E, M and N and, in some seasons, also at the shallow habitat Q in the middle reaches of the main basin. Pronounced seasonal differences in salinity were also evident, with the lowest salinities at each habitat generally being

Table 5.1.1.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on data for salinity and water temperature, and a site x season PERMANOVA on data for dissolved oxygen concentration recorded throughout the Swan Estuary during autumn, winter and spring 2005, summer and winter 2006 and summer 2007. df = degrees of freedom. Significant results are highlighted in bold.

	Salinity					Temperature				Dissolved Oxygen				
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p
Main Effects														
Habitat	9	**1806.600**	**117.210**	**7.552**	**0.001**	**4.339**	**3.037**	**0.304**	**0.002**					
Season	5	**1915.900**	**124.300**	**6.251**	**0.001**	**775.770**	**542.990**	**3.990**	**0.001**	5	**55.950**	**56.341**	**1.022**	**0.001**
Site										17	**22.268**	**22.424**	**1.101**	**0.001**
Two-way Interactions														
Habitat * Season	45	**27.462**	**1.782**	**1.513**	**0.005**	**5.202**	**3.641**	**0.847**	**0.001**					
Season * Site										85	**4.908**	**4.943**	**1.154**	**0.001**
Residual	258	15.414		3.926		1.429		1.195		210	0.993		0.997	

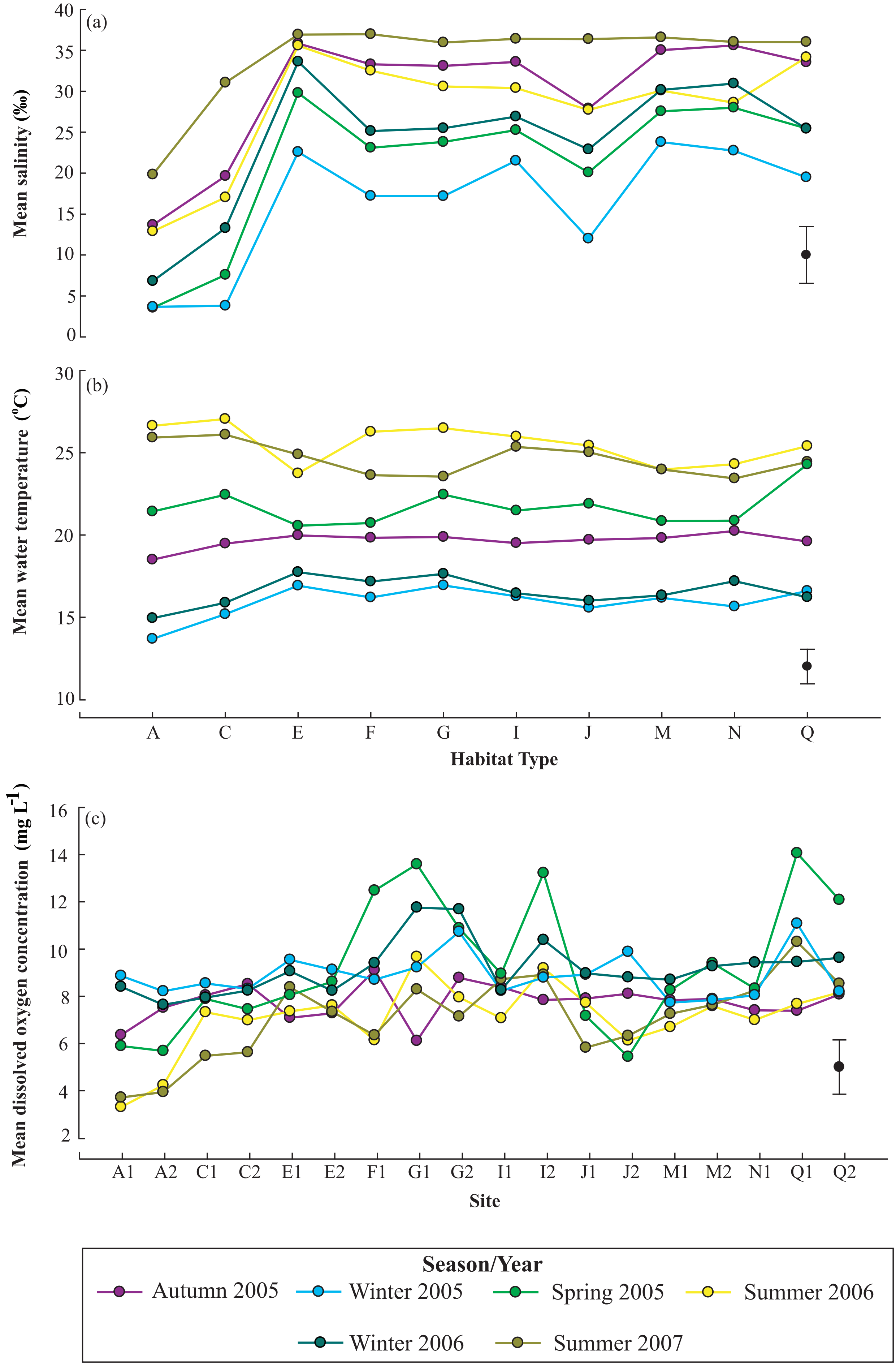


Figure 5.1.1.1: Mean (a) salinity, (b) water temperature and (c) dissolved oxygen concentration at each habitat type/site in the Swan Estuary between autumn 2005 and summer 2007. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

recorded in winter 2005 (*ca* 4‰ at habitats A and C – *ca* 23‰ at habitats E, M and N), followed by spring 2005, winter 2006, summer 2006, autumn 2006 and summer 2007 (*ca* 20‰ at habitat A – *ca* 36‰ at habitats, E, F, G, I, J, M, N and Q; Fig. 5.1.1.1a). Some small exceptions to this seasonal pattern in salinity occurred at some habitats, thus causing the small but significant interaction that was detected by PERMANOVA. The greatest seasonal range in average salinity occurred at habitat C (*ca* 4-32‰), while, as expected, the least occurred at channel habitats M and N (*ca* 23-36‰).

Significant differences in water temperature were detected among habitats and seasons and for the interaction between these two factors (p=0.001-0.002; Table 5.1.1.1). However, the influence of season was far greater than the interaction term, which in turn was more important than that attributable solely to habitat type. Water temperatures were clearly lowest in the winter of either 2005 or 2006 (*ca* 14°C at habitat A – *ca* 17.5°C at habitats E and G), followed by autumn then spring 2005, and greatest in summer 2006 or 2007 (*ca* 27°C at habitats A and C and *ca* 24°C at habitats E, M and N; Fig. 5.1.1.1b). The greatest seasonal variations in water temperature thus generally occurred in riverine habitats, while temperatures in channel habitats were typically more stable. The significant habitat x season interaction was largely attributable to variability in the pattern of temperature differences among habitats in the various seasons. For example, while appreciable temperature differences occurred among habitats in both winters and summers, relatively little spatial difference in water temperature was detected in autumn 2005 (Fig. 5.1.1.1b).

PERMANOVA showed that, while dissolved oxygen concentration differed significantly among both sites and seasons, the relative importance of each of these main effects was slightly less than that of the interaction term (p=0.001; Table 5.1.1.1). Figure 5.1.1.1c clearly illustrates the erratic spatial and temporal differences in this water quality parameter, and thus the overall cause of this interaction. Broadly speaking, the average dissolved oxygen concentration at most sites was lowest in summer 2006, 2007 and/or autumn 2005 (*ca* 3-10 mg L^{-1}, with most values <8 mg L^{-1}) and greatest in winter 2005, 2006 and/or spring 2005 (*ca* 5-14 mg L^{-1}, with most values >8 mg L^{-1}). Furthermore, the upper-most habitat (A) and, to a lesser extent, habitats C and J, generally experienced the lowest dissolved oxygen concentrations throughout the estuary in summer 2006, 2007 and spring 2005, whereas values were relatively similar among most sites in the remaining seasons (Fig. 5.1.1.1c). Dissolved oxygen concentrations varied the most among seasons at individual sites representing habitat A (*ca* 3-9 mg L^{-1}) and the shallow, vegetated basin habitats F, G and Q (*ca* 6-14 mg L^{-1}). In contrast, all representatives of the channel habitats

E, M and N typically displayed the least temporal variability in this water quality parameter (*ca* 7-9.5 mg L^{-1}; Fig. 5.1.1.1c).

5.1.1.2 Sediment parameters

Preliminary three-way PERMANOVA analyses were carried out on data for each of a range of sediment parameters (*i.e.* mean grain size, transition zone depth, organic matter content and chlorophyll concentration), recorded between summer and spring 2005 at sites representing the various habitats throughout the Swan Estuary, to determine whether spatial differences in their characteristics were most appropriately examined at the habitat or site level. Significant differences between sites representing the same habitat and/or a significant site x season interaction (p=0.001) were detected in all cases except chlorophyll concentration. Thus, for the first three sediment parameters, site x season PERMANOVA tests were subsequently used to more fully elucidate their spatio-temporal differences, while the latter variable was subjected to a habitat x season PERMANOVA.

Mean grain size differed significantly among sites (p=0.001) but not among seasons. While the interaction between these two main effects was also significant (p=0.031), its relative importance was about four times less than that of the site, based on a comparison of their respective components of variation (Table 5.1.1.2). Figure 5.1.1.2a illustrates that the main cause of the significant site differences were the considerably coarser sediments found at the riverine sites A2 and C1 than at all other sites throughout the estuary, and particularly when compared to A1 at the uppermost reaches of the estuary and F1, G2 and I1 in the main basin. The relatively weak interaction was attributable to differences among some sites in the seasons during which mean grain size was greater. Plots of the various grain size fractions at each site in each season illustrated that the main cause of the larger mean grain size at sites A2 and C1 was their far greater proportion of sediments in the 1000 µm size fraction (Fig. 5.1.1.3a-d). Moreover, in all seasons except summer, the latter site also had a considerably greater proportion of gravels in the 2000 µm size fraction. The remaining sites were often dominated by sediments in the 250 µm size fraction and, at sites such as F1, I1, M1 and M2, also by sediments in the 125 µm size fraction. Sediments in the 500 µm size fraction also made considerable contributions to sites A2, C1, G1, J1, J2, M1 and M2 in two or more seasons, while sites A1 and C2 generally had the greatest proportion of fines, particularly during autumn and, in the case of the former site, also during winter (Fig. 5.1.1.3a-d).

The mean depth of the transition zone beneath the sediment surface differed significantly among sites and seasons, and there was a significant interaction between these two effects. The

Table 5.1.1.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for a habitat x season PERMANOVA on the chlorophyll concentration and site x season PERMANOVAs on the transition zone depth, organic matter content and mean grain size of the sediment throughout the Swan Estuary during each season in 2005. df = degrees of freedom. Significant results are highlighted in bold.

	Mean Grain Size					**Transition Zone Depth**				**Organic Matter Content**				**Chlorophyll Concentration**				
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p
Main Effects																		
Habitat														6	**0.568**	**8.472**	**0.157**	**0.001**
Season	3	0.061	1.505	0.024	0.239	**3.093**	**11.151**	**0.280**	**0.001**	**0.875**	**3.305**	**0.130**	**0.038**	3	**0.462**	**6.897**	**0.110**	**0.001**
Site	11	**2.122**	**52.772**	**0.417**	**0.001**	**1.650**	**5.948**	**0.338**	**0.001**	**4.489**	**16.950**	**0.593**	**0.001**					
Two-way Interactions																		
Habitat * Season														18	**0.191**	**2.848**	**0.156**	**0.001**
Season * Site	33	**0.067**	**1.675**	**0.095**	**0.031**	**0.589**	**2.122**	**0.322**	**0.006**	0.334	1.261	0.152	0.193					
Residual	96	0.040		0.201		0.277		0.527		0.265		0.515		116	0.067		0.259	

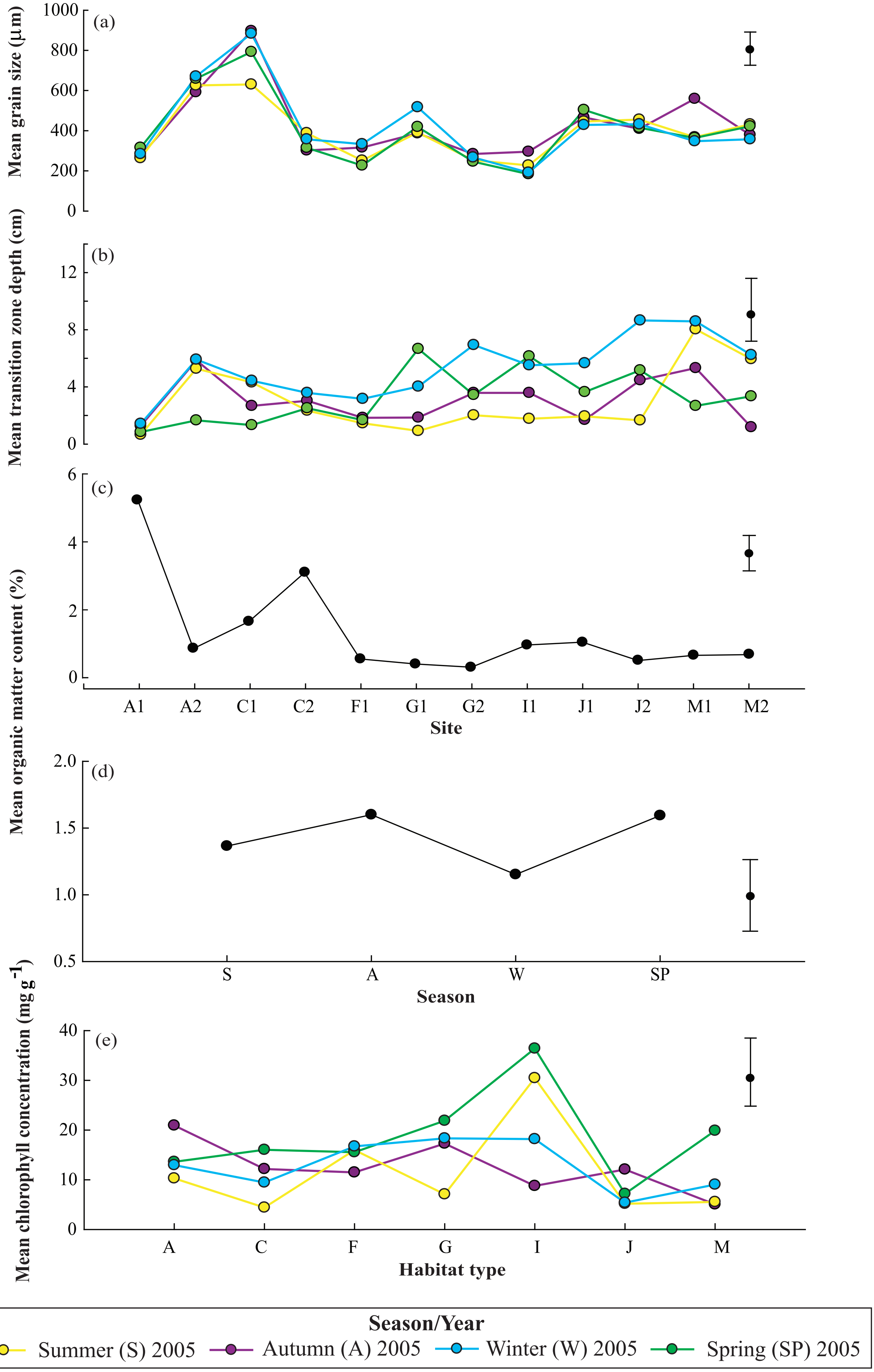


Figure 5.1.1.2: Mean (a) sediment grain size, (b) transition zone depth, (c-d) organic matter content and (e) chlorophyll concentration at each site/habitat throughout the Swan Estuary in each season in 2005. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

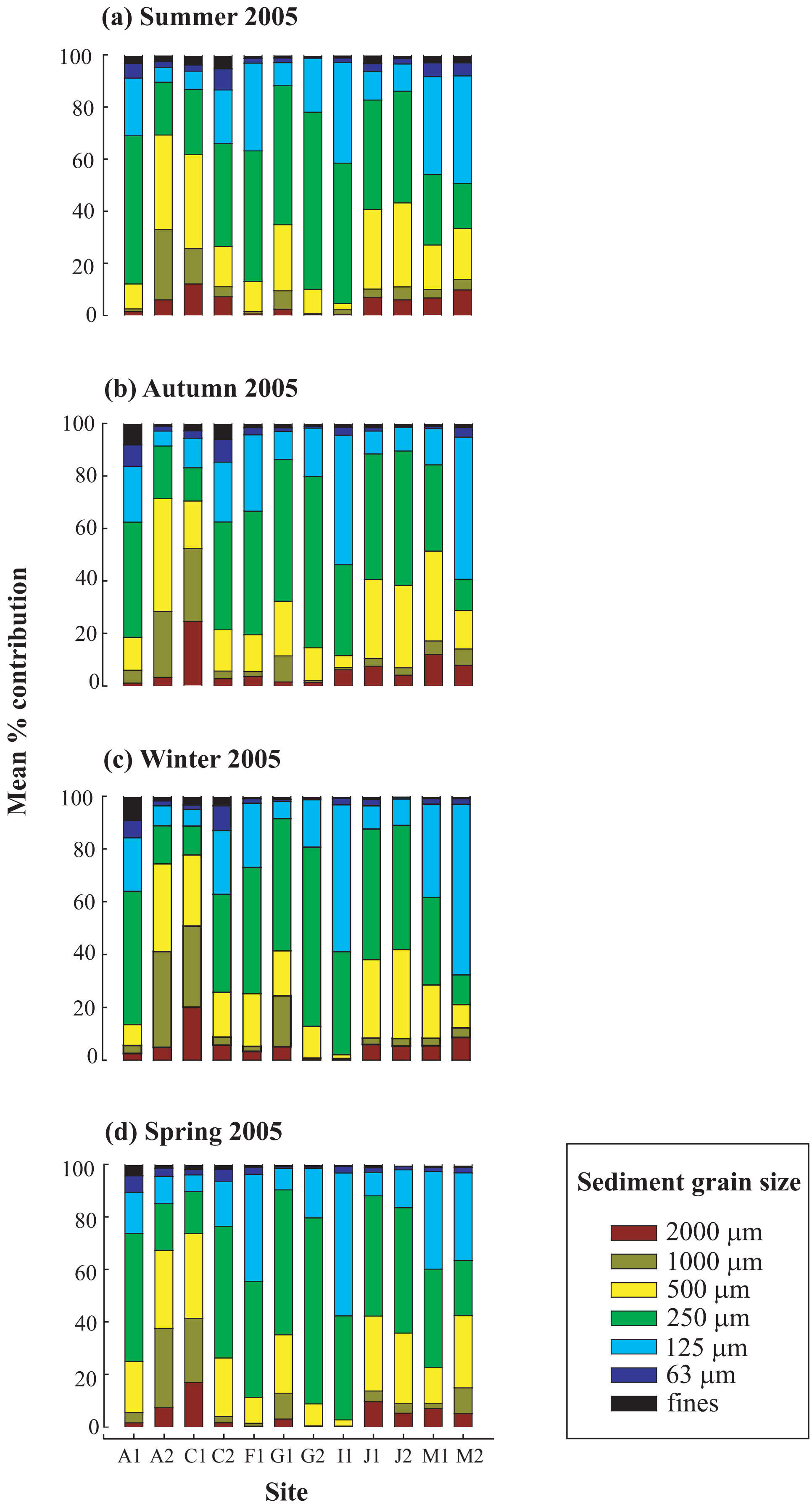


Figure 5.1.1.3: Mean percentage contribution of the various sediment grain size fractions recorded at each site throughout the Swan Estuary in (a) summer, (b) autumn, (c) winter and (d) spring 2005.

components of variation were similar for both site and the interaction term and were least for season, but each of these values were considerably less than that for the residual (error) term (Table 5.1.1.2). The relative importance of the residual term is also reflected by the sizeable average 95% confidence interval associated with the mean transition zone depth values plotted for each site and season in Fig. 5.1.1.2b. The uppermost site (A1) had the shallowest average transition zone depth in all seasons except autumn, during which that at M2 was only slightly shallower. Furthermore, transition zone depths at A1 remained remarkably consistent throughout the year, varying only between *ca* 0.6 and 1.4 cm. Transition zone depths also remained relatively low and consistent across seasons at the riverine sites C1 and C2, *i.e. ca* 1.3-4.4 and 2.3-3.5 cm, respectively, and the shallow basin site F1, *i.e.* 1.4-3.1 cm (Fig. 5.1.1.2b). Conversely, transition zone depths were either the greatest or second greatest at site M1 in the entrance channel during all seasons except spring, but varied considerably between *ca* 2.6 cm in that latter season and 8.6 cm in winter. Substantial seasonal variability was also detected at sites J2 (1.6-8.6 cm), M2 (1.2-6.2 cm), G1 (0.9-6.6 cm) and G2 (2.0-6.9 cm). Transition zone depths were generally greatest or second greatest in winter at all sites, and lowest or second lowest in summer at all sites except A2, C1, M1 and M2, at which they were the second greatest in that season (Fig. 5.1.1.2b).

Particulate organic matter content of the sediment differed significantly among both sites (p=0.001) and seasons (p=0.038). Based on their respective components of variation, the influence of the first of these factors was more than four times greater than that of the latter (Table 5.1.1.2). Site A1 had far greater quantities of organic matter comprising the sediment (*ca* 5.6%) than all other sites, followed by those at C2 and C1, *i.e. ca* 3.5 and 2.1%, respectively. The sediment at the remaining sites comprised between *ca* 1.5 and 0.7% organic matter (Fig. 5.1.1.2c). The lowest proportions of organic matter were recorded in winter and the greatest during autumn and spring (Fig. 5.1.1.2d).

Significant differences in sedimentary chlorophyll concentration were detected among habitats and seasons, and the interaction between those factors was also significant (p=0.001). The components of variation and thus relative importance of the first of these factors and the interaction term was almost equal and greater than that for season, but the importance of each of these terms was less than that for the residual (Table 5.1.1.2). This was also reflected by the considerable average 95% confidence interval associated with the mean chlorophyll concentration at each habitat type in each season (Fig. 5.1.1.2e). The lowest or second lowest chlorophyll concentrations were recorded at habitat J in all seasons except autumn, and varied relatively little between *ca* 5 mg g^{-1} in summer/winter and 12 mg g^{-1} in autumn. Relatively low and consistent values were also recorded at the channel habitat M in all seasons except spring (*ca* 5-9 mg g^{-1}), habitat A in all seasons except autumn (*ca* 10-14 mg g^{-1}) and habitat C in summer and winter (*ca* 4-9 mg g^{-1}). The greatest but most seasonally variable chlorophyll concentrations were recorded at habitat I (ca 9-36 mg g^{-1}). The lowest chlorophyll concentrations were recorded in either summer or autumn at all habitats, while the greatest or second greatest values were always recorded in spring (Fig. 5.1.1.2e).

5.1.2 Fish assemblages

5.1.2.1 Species mean density and length characteristics at each habitat type

A total of 60 fish species and 79 837 individuals (*i.e.* after the number of fish in each sample was adjusted to that in 100 m^2 and summed) were caught at the various nearshore habitat types sampled throughout the Swan Estuary between autumn 2005 and summer 2007 (Table 5.1.2.1). The greatest overall number of species (38) was recorded at the channel habitat E, followed by those at the two other channel habitats M (36) and N (33). Conversely, the least number of species were found at the uppermost habitat A (19), followed by those at the shallow basin habitat F (24), habitat C located just downstream of A and habitat J located downstream of C (25). The mean density of fish was greatest by far at habitat E, *i.e.* 420 fish 100 m^{-2}, with the next greatest mean densities occurring at habitat A and the middle-basin habitat Q, *i.e.* 214 and 210 fish 100 m^{-2}, respectively. The least mean density of fish was recorded at habitat C, followed closely by that at the basin habitat G, *i.e.* 113 and 118 fish 100 m^{-2}, respectively (Table 5.1.2.1).

The fish faunas at the upper estuary habitats A and C were both dominated by the estuarine species *Lepthatherina wallacei, Pseudogobius olorum* and *Acanthopagrus butcheri,* which collectively represented *ca* 83 and 51%, respectively, of the total number of fish caught in each of those habitats. The median length of the latter species at habitat A (90 mm), was substantially smaller than that recorded at any other habitat at which this species was caught throughout the estuary, *i.e.* 105-209. Other abundant species at habitat A (*i.e.* those contributing 5% or more to the total catch) included the estuarine atherinid *Atherinosoma mugiloides*, while habitat C was also dominated by the estuarine species *Papillogobius punctatus* and *Amniataba caudavittatus* and the marine estuarine-opportunist *Atherinomorus ogilbyi*. Furthermore, habitat A contained one species, the freshwater *Galaxias occidentalis*, that was not recorded at C, while C contained seven species, all of which were marine estuarine opportunists or estuarine and marine, which were not recorded at A.

The most abundant species by far at habitat J in the small basin at the foot of the Swan River was *A. mugiloides* (*ca* 35% of the catch), followed by the estuarine and marine species

Table 5.1.2.1: Mean density (M), standard deviation (^{SD}), percentage contribution to the overall catch (%), rank by density (R) and length range and median length (L^{Med}) of each fish species recorded at each habitat type sampled in the Swan Estuary between autumn 2005 and summer 2007. Abundant species (*i.e.* those that contribute >5% to the catch) are highlighted in grey. The life-history category of each species is also provided (*i.e.* ^{A}=semi-anadromous, ^{E}=estuarine, ^{EM}=estuarine and marine, ^{F}=freshwater, ^{O}=marine estuarine-opportunist, ^{S}=marine straggler). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of fish in each sample had been adjusted to that in 100 m^2 and summed) are given for each habitat type.

	Habitat type A				Habitat type C				Habitat type E			
Species name	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Leptatherina wallacei ^{E}	$124.26^{152.93}$	58.05	1	$15\text{-}62^{36}$	$27.60^{65.78}$	24.48	1	$25\text{-}68^{44}$	$0.62^{4.15}$	0.15	10	$27\text{-}46^{36}$
Pseudogobius olorum ^{E}	$41.49^{101.92}$	19.38	2	$14\text{-}59^{27}$	$6.90^{22.64}$	6.12	6	$16\text{-}93^{28}$	$0.02^{0.13}$	<0.01	32	36
Atherinosoma mugiloides ^{E}	$12.36^{37.87}$	5.77	3	$16\text{-}61^{42}$	$1.92^{6.39}$	1.70	10	$22\text{-}61^{42}$	$0.04^{0.18}$	0.01	27	$32\text{-}41^{36}$
Acanthopagrus butcheri ^{E}	$12.00^{17.89}$	5.61	4	$34\text{-}323^{90}$	$23.42^{35.78}$	20.77	2	$31\text{-}350^{143}$				
Gambusia affinis ^{F}	$6.48^{19.86}$	3.03	5	$13\text{-}42^{25}$	$0.05^{0.21}$	0.04	22	$25\text{-}42^{27}$				
Afurcagobius suppositus ^{E}	$4.65^{10.38}$	2.17	6	$14\text{-}84^{36}$	$3.86^{15.57}$	3.42	7	$14\text{-}56^{25}$	$0.02^{0.13}$	<0.01	32	27
Engraulis australis ^{EM}	$4.13^{28.62}$	1.93	7	$60\text{-}85^{73}$	$0.36^{2.36}$	0.32	15	$77\text{-}90^{82}$	$0.02^{0.13}$	<0.01	32	87
Nematalosa vlaminghi ^{A}	$2.78^{8.38}$	1.30	8	$37\text{-}229^{115}$	$1.85^{5.18}$	1.64	11	$89\text{-}230^{113}$				
Amniataba caudavittatus ^{E}	$1.80^{7.85}$	0.84	9	$30\text{-}198^{70}$	$10.63^{23.42}$	9.43	4	$50\text{-}248^{137}$				
Papillogobius punctatus ^{E}	$1.74^{7.76}$	0.81	10	$17\text{-}53^{31}$	$17.06^{37.05}$	15.13	3	$15\text{-}82^{26}$	$0.07^{0.40}$	0.02	22	$51\text{-}61^{58}$
Mugil cephalus ^{O}	$1.56^{3.08}$	0.73	11	$26\text{-}308^{160}$	$1.33^{5.53}$	1.18	12	$24\text{-}421^{29}$	$0.06^{0.38}$	0.01	25	$26\text{-}28^{27}$
Atherinosoma elongata ^{E}	$0.25^{1.74}$	0.12	12	$27\text{-}33^{30}$	$0.11^{0.75}$	0.10	21	$30\text{-}57^{50}$	$0.07^{0.30}$	0.02	22	$35\text{-}66^{48}$
Favonigobius lateralis ^{EM}	$0.25^{1.74}$	0.12	12	$34\text{-}58^{40}$	$0.16^{0.83}$	0.14	20	$19\text{-}30^{25}$	$25.11^{19.58}$	5.98	5	$12\text{-}70^{31}$
Galaxias occidentalis ^{F}	$0.20^{0.91}$	0.09	14	$33\text{-}67^{52}$								
Hyperlophus vittatus ^{O}	$0.04^{0.25}$	0.02	15	$36\text{-}41^{38}$	$0.25^{1.26}$	0.22	17	$27\text{-}40^{34}$	$0.15^{0.45}$	0.04	16	$34\text{-}89^{59}$
Atherinomorus ogilbyi ^{O}	$0.02^{0.12}$	0.01	16	56	$9.91^{36.52}$	8.79	5	$44\text{-}130^{72}$	$46.29^{276.86}$	11.03	3	$28\text{-}144^{84}$
Platycephalus endrachtensis ^{E}	$0.02^{0.12}$	0.01	16	322	$0.02^{0.12}$	0.02	24	460	$0.02^{0.13}$	<0.01	32	367
Gerres subfasciatus ^{O}	$0.02^{0.12}$	0.01	16	58	$0.20^{0.62}$	0.18	18	$146\text{-}196^{164}$				
Aldrichetta forsteri ^{O}	$0.02^{0.12}$	0.01	16	36	$0.99^{5.87}$	0.88	13	$30\text{-}109^{92}$	$0.04^{0.25}$	0.01	27	$33\text{-}34^{34}$
Torquigener pleurogramma ^{O}					$2.68^{11.09}$	2.38	8	$84\text{-}186^{108}$	$66.67^{121.38}$	15.89	2	$37\text{-}178^{81}$
Pelates octolineatus ^{O}					$2.28^{6.47}$	2.02	9	$35\text{-}169^{121}$	$2.79^{18.73}$	0.66	6	$13\text{-}48^{24}$
Apogon rueppellii ^{EM}					$0.56^{3.16}$	0.50	14	$35\text{-}58^{46}$	$1.61^{4.38}$	0.38	8	$19\text{-}79^{32}$
Amoya bifrenatus ^{EM}					$0.34^{1.68}$	0.30	16	$29\text{-}56^{37}$				
Leptatherina presbyteroides ^{EM}					$0.20^{1.01}$	0.18	18	$40\text{-}57^{52}$	$225.94^{477.44}$	53.84	1	$21\text{-}141^{57}$
Sillago burrus ^{O}					$0.04^{0.17}$	0.04	23	$106\text{-}157^{132}$				

Species name	Habitat type A				Habitat type C				Habitat type E			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Rhabdosargus sarba ^{O}					$0.02^{0.12}$	0.02	24	247				
Spratelloides robustus ^{O}									$44.39^{259.64}$	10.58	4	$35\text{-}102^{69}$
Stigmatophora argus ^{S}									$2.29^{3.81}$	0.55	7	$37\text{-}209^{120}$
Haletta semifasciata ^{S}									$0.94^{3.16}$	0.22	9	$20\text{-}177^{61}$
Gymnapistes marmoratus ^{O}									$0.50^{0.95}$	0.12	11	$36\text{-}92^{65}$
Neoodax balteatus ^{S}									$0.35^{1.01}$	0.08	12	$48\text{-}107^{77}$
Sillago schomburgkii ^{O}									$0.22^{0.75}$	0.05	13	$222\text{-}313^{258}$
Meuschenia freycineti ^{S}									$0.18^{0.62}$	0.04	14	$34\text{-}64^{42}$
Acanthaluteres spilomelanurus ^{S}									$0.17^{0.43}$	0.04	15	$13\text{-}73^{34}$
Ammotretis elongata ^{O}									$0.15^{0.41}$	0.04	16	$23\text{-}123^{74}$
Pugnaso curtirostris ^{S}									$0.13^{0.44}$	0.03	18	$93\text{-}148^{106}$
Scobinichthys granulatus ^{S}									$0.13^{0.44}$	0.03	18	$17\text{-}61^{42}$
Pseudorhombus jenynsii ^{O}									$0.11^{0.34}$	0.03	20	$72\text{-}328^{96}$
Enoplosus armatus ^{S}									$0.09^{0.63}$	0.02	21	$25\text{-}47^{32}$
Monacanthus chinensis ^{S}									$0.07^{0.30}$	0.02	22	$70\text{-}130^{102}$
Hyporhamphus regularis ^{E}									$0.06^{0.38}$	0.01	25	$235\text{-}255^{253}$
Sillaginodes punctata ^{O}									$0.04^{0.18}$	0.01	27	$42\text{-}100^{71}$
Siphonognathus radiatus ^{S}									$0.04^{0.18}$	0.01	27	$74\text{-}78^{76}$
Leatherjacket sp. (juvenile) $^{-}$									$0.04^{0.25}$	0.01	27	$37\text{-}40^{38}$
Platycephalus laevigatus ^{S}									$0.02^{0.13}$	<0.01	32	170
Arripis georgiana ^{O}									$0.02^{0.13}$	<0.01	32	50
Cristiceps australis ^{S}									$0.02^{0.13}$	<0.01	32	80
Number of species		**19**				**25**				**38**		
Total mean density		**214**				**113**				**420**		
Number of samples		**48**				**48**				**47**		
Total number of fish		**10 275**				**5 412**				**19 725**		

Species name	Habitat type F				Habitat type G				Habitat type I			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Leptatherina wallacei ^{E}	$3.95^{12.01}$	2.27	8	$20\text{-}61^{30}$	$8.76^{54.78}$	7.40	4	$19\text{-}65^{35}$				
Pseudogobius olorum ^{E}	$0.07^{0.24}$	0.04	16	$32\text{-}35^{34}$	$0.25^{0.73}$	0.21	14	$20\text{-}44^{32}$	$0.13^{0.50}$	0.10	17	$22\text{-}45^{34}$
Atherinosoma mugiloides ^{E}	$22.45^{29.65}$	12.92	4	$24\text{-}62^{42}$	$36.94^{55.81}$	31.23	1	$22\text{-}62^{39}$	$22.07^{43.91}$	17.45	2	$22\text{-}62^{42}$
Acanthopagrus butcheri ^{E}	$4.74^{10.63}$	2.73	6	$18\text{-}320^{200}$	$0.07^{0.24}$	0.06	16	$31\text{-}215^{208}$	$0.45^{1.80}$	0.36	13	$19\text{-}264^{163}$
Gambusia affinis ^{F}												
Afurcagobius suppositus ^{E}	$0.11^{0.53}$	0.06	13	$22\text{-}30^{30}$	$0.02^{0.12}$	0.02	22	54				
Engraulis australis ^{EM}												
Nematalosa vlaminghi ^{A}												
Amniataba caudavittatus ^{E}	$1.40^{2.84}$	0.81	10	$49\text{-}248^{212}$	$1.98^{5.03}$	1.67	9	$17\text{-}235^{194}$	$1.71^{7.22}$	1.35	11	$14\text{-}235^{26}$
Papillogobius punctatus ^{E}	$4.60^{7.07}$	2.65	7	$17\text{-}67^{31}$	$3.72^{7.65}$	3.14	5	$17\text{-}52^{29}$	$2.41^{8.47}$	1.91	9	$16\text{-}67^{36}$
Mugil cephalus ^{O}	$7.97^{38.88}$	4.59	5	$22\text{-}31^{27}$	$2.37^{15.92}$	2.00	8	$24\text{-}32^{27}$				
Atherinosoma elongata ^{E}	$1.90^{7.02}$	1.09	9	$40\text{-}67^{60}$	$3.09^{8.23}$	2.61	6	$31\text{-}71^{53}$	$0.48^{1.19}$	0.38	12	$24\text{-}108^{40}$
Favonigobius lateralis ^{EM}	$0.90^{1.71}$	0.52	11	$18\text{-}50^{29}$	$2.77^{6.70}$	2.34	7	$12\text{-}68^{27}$	$12.61^{14.44}$	9.97	5	$16\text{-}66^{35}$
Galaxias occidentalis ^{F}												
Hyperlophus vittatus ^{O}									$0.07^{0.39}$	0.06	19	$33\text{-}42^{34}$
Atherinomorus ogilbyi ^{O}	$57.29^{268.65}$	32.97	1	$48\text{-}101^{76}$	$1.67^{5.97}$	1.41	10	$50\text{-}103^{62}$	$5.12^{17.13}$	4.05	6	$19\text{-}79^{58}$
Platycephalus endrachtensis ^{E}	$0.11^{0.39}$	0.06	13	$148\text{-}173^{161}$	$0.09^{0.27}$	0.08	15	$28\text{-}101^{46}$	$0.05^{0.21}$	0.04	21	$214\text{-}383^{250}$
Gerres subfasciatus ^{O}												
Aldrichetta forsteri ^{O}	$0.11^{0.53}$	0.06	13	$60\text{-}77^{64}$	$0.86^{3.64}$	0.73	12	$38\text{-}159^{113}$	$3.41^{11.16}$	2.70	7	$34\text{-}312^{96}$
Torquigener pleurogramma ^{O}	$29.63^{33.05}$	17.05	3	$56\text{-}184^{98}$	$26.29^{40.88}$	22.22	3	$62\text{-}183^{102}$	$19.45^{27.72}$	15.38	3	$54\text{-}173^{90}$
Pelates octolineatus ^{O}	$0.04^{0.18}$	0.02	20	18	$0.36^{1.51}$	0.30	13	$35\text{-}91^{68}$	$33.01^{135.80}$	26.11	1	$15\text{-}107^{34}$
Apogon rueppellii ^{EM}	$0.90^{2.96}$	0.52	11	$41\text{-}65^{50}$	$1.13^{3.95}$	0.96	11	$17\text{-}57^{35}$	$3.11^{8.76}$	2.46	8	$17\text{-}64^{34}$
Amoya bifrenatus ^{EM}					$0.02^{0.12}$	0.02	22	54				
Leptatherina presbyteroides ^{EM}	$37.21^{85.42}$	21.42	2	$20\text{-}69^{37}$	$27.59^{67.39}$	23.32	2	$21\text{-}67^{33}$	$19.43^{33.99}$	15.37	4	$17\text{-}69^{34}$
Sillago burrus ^{O}	$0.04^{0.18}$	0.02	20	28	$0.05^{0.28}$	0.04	17	$52\text{-}74^{55}$	$1.94^{6.59}$	1.53	10	$19\text{-}79^{52}$
Rhabdosargus sarba ^{O}									$0.14^{1.00}$	0.11	16	$29\text{-}39^{37}$
Spratelloides robustus ^{O}												
Stigmatophora argus ^{S}									$0.02^{0.12}$	0.02	25	162
Haletta semifasciata ^{S}									$0.04^{0.17}$	0.03	23	$100\text{-}125^{112}$
Gymnapistes marmoratus ^{O}	$0.04^{0.18}$	0.02	20	61	$0.04^{0.17}$	0.03	19	$84\text{-}87^{86}$	$0.16^{0.52}$	0.13	15	$51\text{-}78^{58}$
Neoodax balteatus ^{S}									$0.02^{0.12}$	0.02	25	95
Sillago schomburgkii ^{O}	$0.07^{0.24}$	0.04	16	$267\text{-}284^{276}$					$0.31^{1.44}$	0.25	14	$32\text{-}193^{171}$

Species name	Habitat type F				Habitat type G				Habitat type I			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Meuschenia freycineti ^{S}												
Acanthaluteres spilomelanurus ^{S}												
Ammotretis elongata ^{O}					$0.02^{0.12}$	0.02	22	16	$0.07^{0.39}$	0.06	19	$75\text{-}87^{82}$
Pugnaso curtirostris ^{S}												
Scobinichthys granulatus ^{S}												
Pseudorhombus jenynsii ^{O}	$0.07^{0.24}$	0.04	16	$108\text{-}134^{121}$	$0.04^{0.17}$	0.03	19	$113\text{-}135^{124}$	$0.11^{0.42}$	0.09	18	$100\text{-}249^{122}$
Enoplosus armatus ^{S}									$0.02^{0.12}$	0.02	25	45
Monacanthus chinensis ^{S}												
Hyporhamphus regularis ^{E}												
Sillaginodes punctata ^{O}	$0.07^{0.35}$	0.04	16	$45\text{-}64^{54}$	$0.02^{0.12}$	0.02	22	36	$0.05^{0.28}$	0.04	21	$21\text{-}35^{28}$
Siphonognathus radiatus ^{S}												
Leatherjacket sp. (juvenile) $^{-}$												
Platycephalus laevigatus ^{S}												
Arripis georgiana ^{O}												
Cristiceps australis ^{S}												
Urocampus carinirostris ^{EM}	$0.04^{0.18}$	0.02	20	43	$0.05^{0.21}$	0.04	17	$42\text{-}55^{45}$				
Platycephalus speculator ^{EM}	$0.04^{0.18}$	0.02	20	48	$0.04^{0.17}$	0.03	19	$41\text{-}51^{46}$				
Platycephalus fuscus ^{S}					$0.02^{0.12}$	0.02	22	75				
Sillago bassensis ^{O}					$0.02^{0.12}$	0.02	22	59				
Arripis truttacea ^{O}					$0.02^{0.12}$	0.02	22	58				
Contusus brevicaudus ^{O}									$0.04^{0.25}$	0.03	23	$46\text{-}47^{46}$
Siphamia cephalotes ^{S}									$0.02^{0.12}$	0.02	25	29
Number of species		**24**				**28**				**28**		
Total mean density		**174**				**118**				**126**		
Number of samples		**24**				**48**				**48**		
Total number of fish		**4 170**				**5 678**				**6 070**		

Species name	Habitat type J				Habitat type M				Habitat type N			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Leptatherina wallacei ^{E}	$4.13^{9.05}$	2.64	8	$27\text{-}68^{46}$					$0.04^{0.18}$	0.03	22	49
Pseudogobius olorum ^{E}	$0.18^{0.69}$	0.11	18	$18\text{-}47^{26}$								
Atherinosoma mugiloides ^{E}	$54.24^{129.67}$	34.61	1	$20\text{-}68^{43}$	$0.36^{2.24}$	0.23	13	$41\text{-}53^{46}$	$2.55^{11.77}$	1.84	6	$38\text{-}52^{46}$
Acanthopagrus butcheri ^{E}	$10.58^{16.54}$	6.75	6	$27\text{-}345^{105}$	$1.15^{2.55}$	0.73	7	$119\text{-}244^{172}$	$0.04^{0.18}$	0.03	22	220
Gambusia affinis ^{F}												
Afurcagobius suppositus ^{E}	$0.23^{1.27}$	0.15	16	$19\text{-}45^{30}$								
Engraulis australis ^{EM}	$0.09^{0.41}$	0.06	22	$74\text{-}81^{77}$								
Nematalosa vlaminghi ^{A}	$0.11^{0.38}$	0.07	19	$136\text{-}217^{197}$								
Amniataba caudavittatus ^{E}	$1.33^{3.32}$	0.85	10	$51\text{-}238^{130}$	$0.02^{0.12}$	0.01	28	192	$0.04^{0.18}$	0.03	22	256
Papillogobius punctatus ^{E}	$1.58^{3.19}$	1.01	9	$17\text{-}49^{28}$	$0.40^{1.10}$	0.25	12	$35\text{-}61^{51}$	$1.94^{6.39}$	1.4	8	
Mugil cephalus ^{O}	$11.58^{64.71}$	7.39	5	$25\text{-}451^{30}$			37		$0.04^{0.18}$	0.03	22	349
Atherinosoma elongata ^{E}	$0.11^{0.46}$	0.07	19	$34\text{-}40^{36}$	$0.02^{0.12}$	0.01	28	55	$0.29^{1.41}$	0.21	15	$50\text{-}68^{58}$
Favonigobius lateralis ^{EM}	$0.52^{1.35}$	0.33	12	$16\text{-}62^{28}$	$7.65^{12.96}$	4.85	4	$15\text{-}97^{32}$	$32.90^{32.18}$	23.78	2	$16\text{-}70^{32}$
Galaxias occidentalis ^{F}												
Hyperlophus vittatus ^{O}					$0.31^{2.12}$	0.2	15	$28\text{-}36^{34}$				
Atherinomorus ogilbyi ^{O}	$1.17^{4.28}$	0.75	11	$40\text{-}94^{70}$	$56.45^{262.44}$	35.83	2	$34\text{-}111^{58}$	$12.61^{48.21}$	9.11	4	$35\text{-}127^{85}$
Platycephalus endrachtensis ^{E}	$0.05^{0.21}$	0.03	24	$116\text{-}405^{325}$	$0.02^{0.12}$	0.01	28					
Gerres subfasciatus ^{O}	$0.34^{1.41}$	0.22	15	$91\text{-}148^{109}$	$0.02^{0.12}$	0.01	28	16				
Aldrichetta forsteri ^{O}	$7.04^{17.61}$	4.49	7	$32\text{-}150^{97}$	$0.36^{2.13}$	0.23	13	$64\text{-}96^{79}$				
Torquigener pleurogramma ^{O}	$20.94^{30.50}$	13.36	3	$49\text{-}200^{114}$	$19.70^{27.88}$	12.5	3	$49\text{-}174^{89}$	$22.23^{23.40}$	16.07	3	$55\text{-}167^{110}$
Pelates octolineatus ^{O}	$0.43^{1.17}$	0.27	13	$72\text{-}186^{162}$	$1.08^{3.79}$	0.69	9	$12\text{-}172^{22}$	$9.41^{39.67}$	6.8	5	$16\text{-}170^{27}$
Apogon rueppellii ^{EM}	$27.71^{93.63}$	17.68	2	$23\text{-}78^{39}$	$1.13^{2.38}$	0.72	8	$16\text{-}62^{27}$	$2.01^{4.14}$	1.45	7	$15\text{-}73^{38}$
Amoya bifrenatus ^{EM}	$0.11^{0.42}$	0.07	19	$46\text{-}107^{74}$								
Leptatherina presbyteroides ^{EM}	$13.49^{76.08}$	8.61	4	$24\text{-}62^{50}$	$61.69^{204.85}$	39.15	1	$15\text{-}77^{50}$	$47.56^{82.70}$	34.37	1	$20\text{-}78^{41}$
Sillago burrus ^{O}	$0.43^{1.24}$	0.27	13	$38\text{-}151^{122}$	$0.14^{0.62}$	0.09	18	$31\text{-}124^{64}$	$0.04^{0.18}$	0.03	22	36
Rhabdosargus sarba ^{O}									$0.07^{0.24}$	0.05	19	$93\text{-}233^{163}$
Spratelloides robustus ^{O}					$3.07^{11.55}$	1.95	5	$41\text{-}86^{60}$	$1.51^{7.39}$	1.09	10	$74\text{-}87^{80}$
Stigmatophora argus ^{S}					$1.98^{4.31}$	1.26	6	$41\text{-}205^{117}$	$1.87^{4.71}$	1.35	9	$52\text{-}184^{126}$
Haletta semifasciata ^{S}					$0.47^{2.15}$	0.3	10	$28\text{-}181^{122}$	$1.40^{3.46}$	1.01	11	$40\text{-}127^{94}$
Gymnapistes marmoratus ^{O}					$0.41^{0.77}$	0.26	11	$28\text{-}83^{59}$	$0.32^{0.61}$	0.23	14	$23\text{-}79^{60}$
Neoodax balteatus ^{S}					$0.22^{0.70}$	0.14	16	$63\text{-}102^{76}$	$0.04^{0.18}$	0.03	22	81

Species name	Habitat type J				Habitat type M				Habitat type N			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Sillago schomburgkii ^{O}	$0.02^{0.12}$	0.01	25	126	$0.13^{0.64}$	0.08	19	$123\text{-}322^{305}$	$0.36^{1.59}$	0.26	12	$233\text{-}337^{292}$
Meuschenia freycineti ^{S}					$0.04^{0.25}$	0.03	25	$24\text{-}67^{46}$	$0.04^{0.18}$	0.03	22	36
Acanthaluteres spilomelanurus ^{S}					$0.05^{0.21}$	0.03	22	$31\text{-}40^{34}$	$0.04^{0.18}$	0.03	22	47
Ammotretis elongata ^{O}					$0.11^{0.38}$	0.07	21	$49\text{-}87^{70}$			34	$144\text{-}401^{240}$
Pugnaso curtirostris ^{S}												
Scobinichthys granulatus ^{S}					$0.05^{0.28}$	0.03	22	$42\text{-}43^{43}$	$0.11^{0.39}$	0.08	17	$32\text{-}44^{43}$
Pseudorhombus jenynsii ^{O}					$0.04^{0.17}$	0.03	25	$20\text{-}109^{64}$	$0.14^{0.33}$	0.1	16	$18\text{-}66^{39}$
Enoplosus armatus ^{S}									$0.07^{0.35}$	0.05	19	$31\text{-}33^{32}$
Monacanthus chinensis ^{S}					$0.04^{0.17}$	0.03	25	$42\text{-}82^{62}$	$0.04^{0.18}$	0.03	22	78
Hyporhamphus regularis ^{E}												
Sillaginodes punctata ^{O}	$0.09^{0.51}$	0.06	22	$32\text{-}101^{90}$	$0.18^{0.59}$	0.11	17	$27\text{-}189^{116}$	$0.36^{0.72}$	0.26	12	$30\text{-}184^{120}$
Siphonognathus radiatus ^{S}												
Leatherjacket sp. (juvenile) $^{-}$												
Platycephalus laevigatus ^{S}									$0.07^{0.35}$	0.05	19	$194\text{-}284^{239}$
Arripis georgiana ^{O}									$0.04^{0.18}$	0.03	22	
Cristiceps australis ^{S}					$0.02^{0.12}$	0.01	28	61				
Urocampus carinirostris ^{EM}					$0.13^{0.53}$	0.08	19	$52\text{-}66^{59}$	$0.11^{0.39}$	0.08	17	$56\text{-}59^{58}$
Platycephalus speculator ^{EM}												
Platycephalus fuscus ^{S}												
Sillago bassensis ^{O}												
Arripis truttacea ^{O}					$0.05^{0.37}$	0.03	22	$50\text{-}54^{52}$				
Contusus brevicaudus ^{O}												
Siphamia cephalotes ^{S}					$0.02^{0.12}$	0.01	28	34				
Sillago vittata ^{O}	$0.23^{1.50}$	0.15	16	$72\text{-}108^{94}$	$0.02^{0.12}$	0.01	28	120				
Filicampus tigris ^{S}					$0.02^{0.12}$	0.01	28	79				
Acanthaluteres brownii ^{S}					$0.02^{0.12}$	0.01	28	33				
Cnidoglanis macrocephalus ^{EM}									$0.04^{0.18}$	0.03	22	116
Parapercis haackei ^{S}									$0.04^{0.18}$	0.03	22	35
Number of species		**25**				**36**				**33**		
Total mean density		**157**				**158**				**138**		
Number of samples		**48**				**48**				**24**		
Total number of fish		**7 523**				**7 563**				**3 321**		

Species name	Habitat type Q			
	M^{SD}	%	R	L^{Med}
Leptatherina wallacei ^{E}	$3.56^{14.99}$	1.69	9	$15-60^{25}$
Pseudogobius olorum ^{E}	$0.56^{2.17}$	0.27	15	$26-49^{30}$
Atherinosoma mugiloides ^{E}	$38.49^{91.28}$	18.29	2	$21-65^{38}$
Acanthopagrus butcheri ^{E}	$0.05^{0.28}$	0.02	19	$185-210^{209}$
Gambusia affinis ^{F}				
Afurcagobius suppositus ^{E}	$0.04^{0.25}$	0.02	22	$36-40^{38}$
Engraulis australis ^{EM}				
Nematalosa vlaminghi ^{A}				
Amniataba caudavittatus ^{E}	$0.66^{3.42}$	0.31	14	$76-249^{210}$
Papillogobius punctatus ^{E}	$4.74^{12.86}$	2.25	8	$16-61^{29}$
Mugil cephalus ^{O}	$0.02^{0.12}$	0.01	25	26
Atherinosoma elongata ^{E}	$12.23^{35.77}$	5.81	7	$15-68^{37}$
Favonigobius lateralis ^{EM}	$15.63^{29.85}$	7.43	4	$15-67^{29}$
Galaxias occidentalis ^{F}				
Hyperlophus vittatus ^{O}				
Atherinomorus ogilbyi ^{O}	$1.81^{7.90}$	0.86	10	$33-121^{70}$
Platycephalus endrachtensis ^{E}	$0.13^{0.31}$	0.06	17	$26-306^{133}$
Gerres subfasciatus ^{O}				
Aldrichetta forsteri ^{O}	$1.15^{3.93}$	0.55	12	$33-380^{83}$
Torquigener pleurogramma ^{O}	$21.62^{35.97}$	10.28	3	$27-190^{88}$
Pelates octolineatus ^{O}	$12.79^{84.55}$	6.08	6	$13-56^{43}$
Apogon rueppellii ^{EM}	$1.44^{6.41}$	0.68	11	$20-73^{40}$
Amoya bifrenatus ^{EM}				
Leptatherina presbyteroides ^{EM}	$81.20^{224.02}$	38.59	1	$14-71^{37}$
Sillago burrus ^{O}	$0.90^{4.66}$	0.43	13	$25-55^{43}$
Rhabdosargus sarba ^{O}	$0.14^{0.88}$	0.07	16	$59-89^{62}$
Spratelloides robustus ^{O}				
Stigmatophora argus ^{S}				
Haletta semifasciata ^{S}				
Gymnapistes marmoratus ^{O}	$0.04^{0.17}$	0.02	22	$68-80^{74}$
Neoodax balteatus ^{S}				
Sillago schomburgkii ^{O}	$0.13^{0.87}$	0.06	17	$31-54^{38}$

Species name	Habitat type Q			
	M^{SD}	%	R	L^{Med}
Meuschenia freycineti ^{S}				
Acanthaluteres spilomelanurus ^{S}				
Ammotretis elongata ^{O}				
Pugnaso curtirostris ^{S}				
Scobinichthys granulatus ^{S}				
Pseudorhombus jenynsii ^{O}	$0.04^{0.17}$	0.02	22	$102\text{-}150^{126}$
Enoplosus armatus ^{S}				
Monacanthus chinensis ^{S}				
Hyporhamphus regularis ^{E}				
Sillaginodes punctata ^{O}	$0.05^{0.21}$	0.02	19	$38\text{-}94^{87}$
Siphonognathus radiatus ^{S}				
Leatherjacket sp. (juvenile) $^{-}$				
Platycephalus laevigatus ^{S}				
Arripis georgiana ^{O}				
Cristiceps australis ^{S}				
Urocampus carinirostris ^{EM}	$0.05^{0.21}$	0.02	19	$52\text{-}54^{53}$
Platycephalus speculator ^{EM}				
Platycephalus fuscus ^{S}				
Sillago bassensis ^{O}				
Arripis truttacea ^{O}	$0.02^{0.12}$	0.01	25	63
Contusus brevicaudus ^{O}				
Siphamia cephalotes ^{S}				
Sillago vittata ^{O}	$0.02^{0.12}$	0.01	25	60
Filicampus tigris ^{S}				
Acanthaluteres brownii ^{S}				
Cnidoglanis macrocephalus ^{EM}				
Parapercis haackei ^{S}				
Atherinid sp. (juvenile) $^{-}$	$12.90^{89.34}$	6.13	5	$11\text{-}22^{15}$
Number of species		**27**		
Total mean density		**210**		
Number of samples		**48**		
Total number of fish		**10 100**		

Apogon rueppellii and the marine estuarine-opportunist *Torguigener pleurogramma, i.e. ca* 18 and 13% of the catch, respectively (Table 5.1.2.1). *Leptatherina presbyteroides*, an estuarine and marine atherinid, the marine estuarine-opportunist *Mugil cephalus* (and mainly its small juveniles, as indicated by the median length of 30 mm for this species) and *A. butcheri* were also relatively abundant, collectively contributing a further 22.75% to the overall catch at this habitat.

Leptatherina presbyteroides and *T. pleurogramma* both ranked either second or third in terms of abundance at habitats F and G located in the upper to middle reaches of the main basin (Table 5.1.2.1). However, the most abundant species at F, *A. ogilbyi*, which contributed 32.97% to the overall catch at that habitat, ranked only tenth at G, where it contributed just 1.41% to the total catch. Likewise, *A. mugiloides*, which ranked first at habitat G and represented more than the 30% of the total catch, ranked fourth at F and comprised less than 13% of the overall catch. Furthermore, *L. wallacei* was abundant at habitat G, but not at F (Table 5.1.2.1). The fish fauna at the middle-basin habitat Q was dominated largely by *L. presbyteroides* (*ca* 39% of the total catch), followed by *A. mugiloides* and *T. pleurogramma*, *i.e.* 18.29 and 10.28% of the overall catch, respectively. However, abundant catches of the estuarine and marine goby *Favonigobius lateralis*, the marine estuarine-opportunist *Pelates octolineatus* and the estuarine atherinid *Atherinosoma elongata* were also recorded at Q, unlike habitats F and G (Table 5.1.2.1). Habitat I, located in the lowermost reaches of the main basin, shared several similar abundant species with habitats F, G and Q. However, the relative importance of those species was unique to this habitat. Thus, *P. octolineatus* was the highest ranking species and comprised *ca* 26% of the catch (which was represented largely by small juveniles, as indicated by its median length of 34 mm in this habitat), followed by *A. mugiloides, T. pleurogramma* and *L. presbyteroides*, which each contributed between 15 and 17.5% to the total number of fish. However, *L. wallacei*, which was either abundant or present at the other basin habitats, was never recorded at habitat I. Furthermore, several weed-associated species, such as the marine stragglers *Stigmatophora argus, Haletta semifasciata, Neoodax balteatus and Enoplosus armatus*, were caught at the more extensively vegetated habitat I, but not at F, G or Q (Table 5.1.2.1).

More than half of the catch at habitat E, located in the entrance channel and closest to the estuary mouth, comprised *L. presbyteroides*. This species also ranked first in terms of abundance and comprised more than a third of the overall catch at the two other channel habitats, M and N (Table 5.1.2.1). Other species that were abundant at all three channel habitats, although differing in their respective mean densities and rankings, included the marine estuarine-opportunists *T. pleurogramma* and *A. ogilbyi*. *Favonigobius lateralis* was also abundant at habitat E and particularly N, and the marine estuarine-opportunists *Spratelloides robustus* and *P. octolineatus* were also abundant at E and N, respectively. All three channel habitats were vegetated to some extent and contained numerous fish species that are typically associated with seagrass or macroalgae, 13 of which were not recorded at any other habitat. Moreover, habitat E, which had the most extensive beds of vegetation, contained several species that were not recorded at M and/or N, such as *Pugnaso curtirostris, Enoplosus armatus, Hyporhamphus regularis, Siphonognathus radiatus* and very small monocanthid juveniles, *i.e.* minimum length of 38 mm.

5.1.2.2 Spatial and temporal differences in mean number of species, density and taxonomic diversity

Preliminary three-way PERMANOVA tests were used to ascertain whether spatial differences in the mean number of fish species, density of fish and taxonomic distinctness of the fish assemblages recorded seasonally at sites representing the various habitats throughout the Swan Estuary were most appropriately analysed at the site or habitat level. Significant differences between sites belonging to the same habitat and/or a significant site x season interaction were detected for each of these dependent variables (p=0.001-0.003), and thus each were then subjected to a site x season PERMANOVA to explore more fully the extent of their spatial and temporal differences.

The mean number of species differed significantly among both sites and seasons and the interaction between these factors was also significant (p=0.001; Table 5.1.2.2). However, the components of variation for each of these terms demonstrated that the seasonal main effect was substantially more important than either site or the interaction, which each made similar contributions to the overall variation in the PERMANOVA model. It is also of interest that the components of variation associated with the residual term was greater than that for any other term, which is also reflected by the relatively large confidence interval associated with the means plotted in Fig. 5.1.2.1a. The mean number of species at each site was almost always lowest in either winter 2005 or 2006 and greatest in summer 2006 or 2007. The mean number of species exhibited considerable seasonal variability at site A2 (*ca* 2-9), both sites representing habitat J (*i.e. ca* 3-10 at J1 and *ca* 2-8 at J2) and site M1 (*ca* 2-8). In contrast, relatively little difference in mean species richness was recorded among seasons at sites representing habitat E (*ca* 4-6 at E1 and *ca* 5-8 at E2), F1 (*ca* 4-5) and G1 (*ca* 3-6; Fig. 5.1.2.1a). Such differences in the seasonal range of the mean number of species among sites, combined with differences in the seasonal pattern at each site, contributed to the significant site x season interaction detected by PERMANOVA. Clear differences in the mean number of species among sites were less obvious, but it was almost always the case that less than six species were recorded at sites A1, F1, G1, G2

Table 5.1.2.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for site x season PERMANOVAs on the number of species, density and quantitative taxonomic distinctness of fish assemblages recorded throughout the Swan Estuary during autumn, winter and spring 2005, summer and winter 2006 and summer 2007. df = degrees of freedom. Significant results are highlighted in bold.

		Number of Species				**Density**				**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Site	17	**0.728**	**4.842**	**0.155**	**0.001**	**6.964**	**7.152**	**0.500**	**0.001**	**4.654**	**2.762**	**0.352**	**0.001**
Season	5	**7.112**	**47.283**	**0.311**	**0.001**	**14.910**	**15.311**	**0.441**	**0.001**	**6.496**	**3.854**	**0.259**	**0.002**
Two-way Interaction													
Site * Season	85	**0.289**	**1.922**	**0.186**	**0.001**	**2.470**	**2.537**	**0.612**	**0.001**	**3.361**	**1.994**	**0.648**	**0.001**
Residual	323	0.150		0.388		0.974		0.987		1.685		1.298	

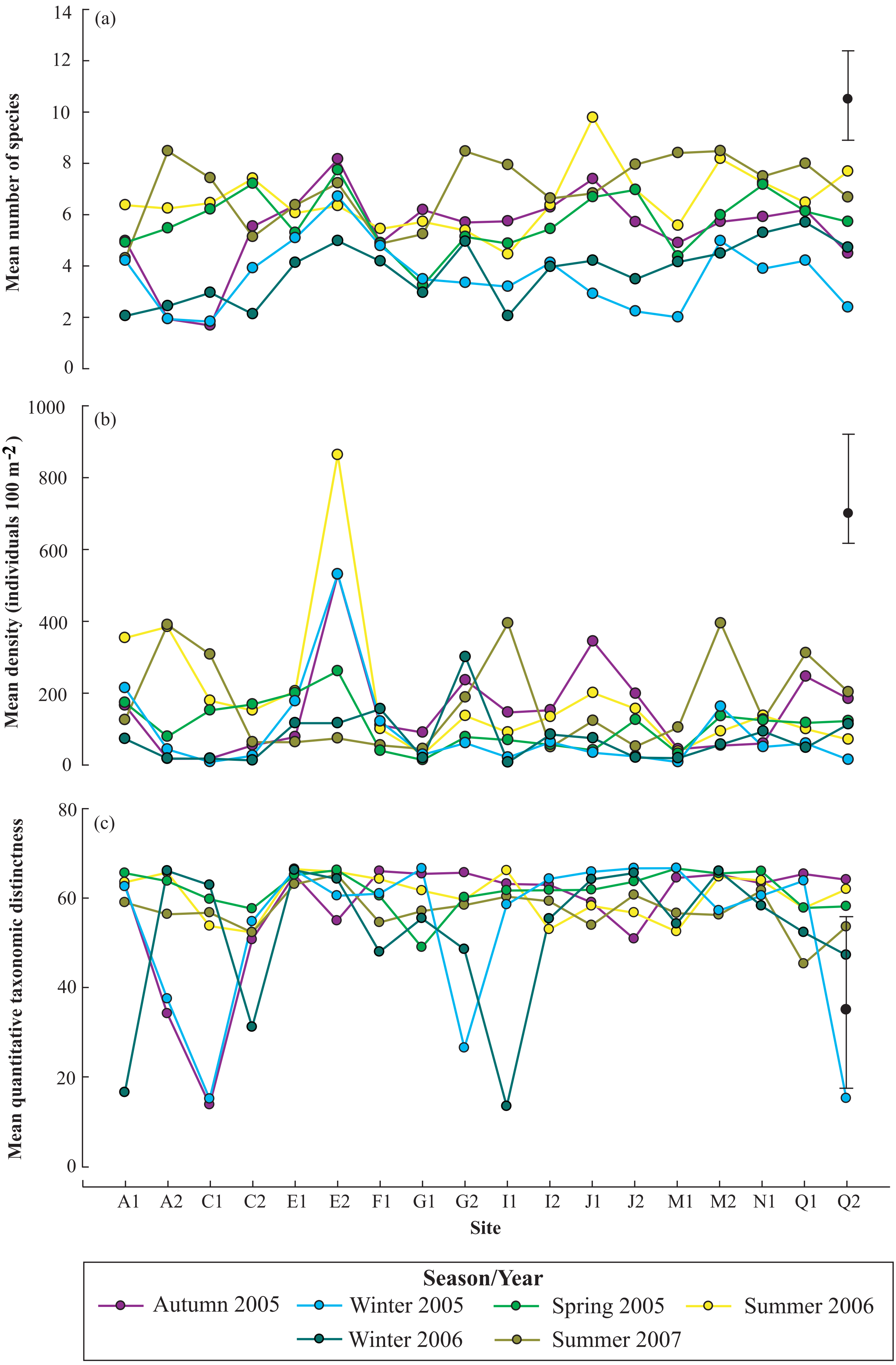


Figure 5.1.2.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the fish assemblages recorded at each site in the Swan Estuary between autumn 2005 and summer 2007. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

and I1 in each season, while greater than five species were recorded in each season at sites E1, E2, M2, N1 and Q1 (Fig. 5.1.2.1a).

Significant differences in the mean density of fish were also detected among sites, seasons and the interaction between these factors (p=0.001; Table 5.1.2.2). The components of variation associated with each term in this PERMANOVA test showed that the influence of the interaction term was greatest, followed by that for site and then season. However, the relative importance of the residual was also substantially greater than that of any of the above terms, which was again reflected by the relatively large confidence interval associated the mean fish density at each site in each season shown in Fig. 5.1.2.1b. Pronounced differences in the seasonal patterns and magnitudes of fish densities among the various sites were clearly the cause of the relatively important interaction term in this case. Thus, the greatest seasonal variability by far was recorded at the channel site E2, where mean densities ranged between *ca* 860 fish 100 m^{-2} in summer 2006 to *ca* 74 fish 100 m^{-2} in summer 2007. The greatest densities were also recorded at this site in every season except winter 2006 and summer 2007 (Fig. 5.1.2.1b). Relatively large seasonal differences in fish density were also recorded at sites A2 (*ca* 390-18 fish 100 m^{-2}), I1 (*ca* 394-7 fish 100 m^{-2}) and M2 (*ca* 394-57 fish 100 m^{-2}). In contrast, relatively constant seasonal densities, which were also among the lowest throughout the estuary, were recorded at the basin sites F1, G1, I2 and the channel sites M1 and N1, *i.e. ca* 156-8 fish 100 m^{-2}. The greatest densities at most sites were recorded in either summer 2006 or 2007 and, in many cases, these were considerably greater than those recorded in any other season. The densities at most sites were lowest in either winter 2005 or 2006 (Fig. 5.1.2.1b).

The taxonomic distinctness of the fish assemblage varied significantly among sites and seasons and a significant interaction between these two factors was also detected (p=0.001-0.002; Table 5.1.2.2). The influence of this interaction was approximately twice that attributable to site or season. However, the variation due to the residual term was about twice that of the interaction, which is reflected by the large confidence interval associated with each mean on the plot shown in Fig. 5.1.2.1c. The importance of the site x season interaction is clearly reflected by the fact that the seasonal order of mean taxonomic distinctness often varied between sites, with no clear trend being evident. Markedly lower mean values of this diversity index were recorded during either autumn 2005, winter 2005 and/or winter 2006 at each of the sites representing habitats A and C and the basin sites G2, I1 and Q2 (Fig. 5.1.2.1c).

5.1.2.3 Composition of fish assemblages among habitats

Three-way PERMANOVA was used initially to determine whether habitats, or their representative sites, were most appropriate for examining spatial differences in the composition of the nearshore fish assemblages recorded throughout the Swan Estuary between autumn 2005 and summer 2007. While this test detected significant differences for all terms in the model, the associated components of variation demonstrated that the influence of habitat alone was almost twice that of site and the site x season interaction. Furthermore, one-way ANOSIM tests for site, carried out separately for the data collected in each sampling season in view of the above significant seasonal main effect and interactions, detected few significant differences in fish faunal composition between sites assigned to the same habitat in all seasons except summer 2006 and, to a lesser extent, summer 2007. Moreover, for those few cases in which significant intra-habitat differences were detected in the remaining four seasons, the associated R-statistic was usually <0.400. During summer 2006 and 2007, significant differences were detected between the ichthyofaunal compositions of sites assigned to the same habitat in six and four cases, respectively, and, in most of those cases, the associated R-statistic exceeded 0.400. However, given the relatively minor intra-habitat differences in fish faunal composition overall, particularly when compared to the extent of inter-habitat differences, the following analyses of spatial differences in the fish assemblage throughout the Swan Estuary were carried out at the habitat rather than site level. They were also carried out separately for the data recorded in each individual season, given the significant seasonal main effects and interactions that were detected by the above PERMANOVA test.

One-way ANOSIM tests for habitat type, carried out separately for data collected in each sampling season, demonstrated that fish faunal composition differed significantly among habitats in each case (p=0.1%), and that the greatest overall differences occurred in spring 2005 and summer 2007 (Global R=0.713 and 0.676, respectively), while the least occurred in winter and autumn 2005 (Global R=0.435 and 0.508, respectively; Table 5.1.2.3). Significant differences were detected between most pairs of habitat types in all seasons except the latter two, during which 11-14 of the 45 pairwise comparisons had a significance level exceeding 5%. In all seasons, the ichthyofaunal composition at habitat A was particularly distinct from that at all others (*i.e.* pairwise R typically greater than 0.800) except the other riverine habitat (C), from which it was either not significantly different or exhibited relatively small significant differences, *i.e.* pairwise R=0.144-0.502. The fish fauna at habitat C was also markedly distinct from that at all basin and channel habitats in most seasons (*i.e.* pairwise R typically greater than 0.600 and, in spring 2005 and summer 2007, almost always greater than 0.900), except habitat J in the small

Table 5.1.2.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the fish faunal composition among habitat types in the Swan Estuary during (a) autumn 2005, (b) winter 2005, (c) spring 2005, (d) summer 2006, (e) winter 2006 and (f) summer 2007. Insignificant pairwise comparisons are highlighted in grey.

(a) Autumn 2005; p=0.1%, Global R=0.508

	A	C	E	F	G	I	J	M	N
C	0.107								
E	0.964	0.744							
F	0.835	0.296	0.704						
G	0.919	0.574	0.763	-0.154					
I	0.946	0.634	0.491	0.202	0.103				
J	0.782	0.491	0.929	0.480	0.479	0.377			
M	0.962	0.655	0.054	0.419	0.579	0.268	0.733		
N	0.938	0.528	0.149	0.531	0.849	0.531	0.893	-0.011	
Q	0.946	0.667	0.709	0.116	-0.148	0.004	0.504	0.554	0.818

(b) Winter 2005; p=0.1%, Global R=0.435

	A	C	E	F	G	I	J	M	N
C	0.144								
E	0.997	0.772							
F	0.805	0.313	0.779						
G	0.994	0.615	0.613	0.257					
I	0.851	0.541	0.319	0.287	0.194				
J	0.958	0.500	0.669	0.142	-0.004	0.250			
M	0.893	0.572	0.293	0.081	0.115	-0.002	0.076		
N	1.000	0.607	0.368	0.323	0.270	-0.156	0.364	-0.097	
Q	0.908	0.652	0.396	0.458	0.261	-0.086	0.333	0.085	-0.103

(c) Spring 2005; p=0.1%, Global R=0.713

	A	C	E	F	G	I	J	M	N
C	0.502								
E	1.000	0.994							
F	0.994	0.932	0.882						
G	0.999	0.978	0.886	0.160					
I	1.000	0.989	0.397	0.515	0.545				
J	0.828	0.607	0.971	0.355	0.835	0.825			
M	1.000	0.985	0.296	0.476	0.549	0.257	0.834		
N	1.000	0.996	0.112	0.698	0.700	0.059	0.917	0.195	
Q	0.989	0.985	0.706	0.382	0.344	0.123	0.868	0.650	0.355

(d) Summer 2006; p=0.1%, Global R=0.603

	A	C	E	F	G	I	J	M	N
C	0.304								
E	0.996	0.999							
F	0.862	0.425	0.810						
G	0.814	0.662	0.648	-0.009					
I	0.909	0.771	0.450	0.169	0.164				
J	0.795	0.369	0.940	0.018	0.363	0.327			
M	0.988	0.933	0.252	0.645	0.660	0.311	0.723		
N	1.000	1.000	0.034	0.885	0.577	0.344	0.963	0.154	
Q	0.984	0.892	0.486	0.335	0.281	0.193	0.624	0.389	0.314

(e) Winter 2006; p=0.1%, Global R=0.579

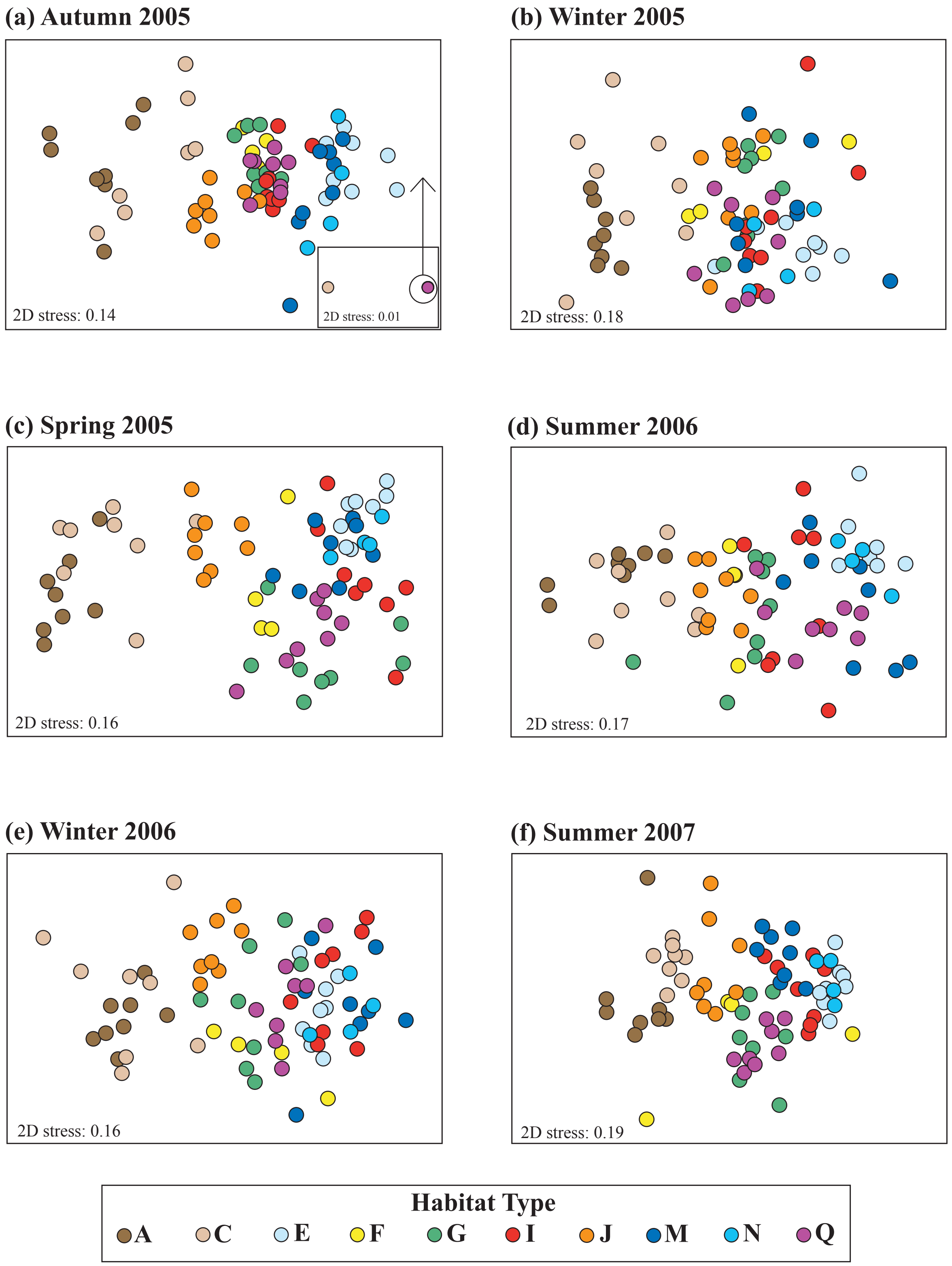
	A	C	E	F	G	I	J	M	N
C	0.136								
E	0.996	0.831							
F	0.736	0.450	0.729						
G	0.815	0.593	0.440	-0.055					
I	0.977	0.771	0.249	0.411	0.400				
J	0.852	0.597	0.914	0.846	0.379	0.950			
M	0.926	0.746	0.131	0.432	0.427	0.100	0.844		
N	1.000	0.745	0.116	0.609	0.404	0.066	1.000	-0.195	
Q	0.991	0.813	0.467	0.283	0.121	0.273	0.942	0.275	0.496

(f) Summer 2007; p=0.1%, Global R=0.676

	A	C	E	F	G	I	J	M	N
C	0.473								
E	1.000	1.000							
F	0.628	0.415	0.741						
G	0.766	0.811	0.746	0.222					
I	0.973	0.959	0.497	0.721	0.468				
J	0.540	0.401	0.855	0.358	0.409	0.711			
M	0.916	0.950	0.447	0.533	0.683	0.581	0.682		
N	1.000	1.000	0.235	0.365	0.673	0.412	0.770	0.561	
Q	0.844	0.994	0.836	0.403	0.188	0.717	0.679	0.799	0.816

basin at the foot of the Swan River and F in the upper reaches of the main basin (*i.e.* although always significantly different, pairwise R often less than 0.500; Table 5.1.2.3). Such results are clearly illustrated by the MDS ordination plots of the ichthyofaunal composition at the various habitats in each season (Fig. 5.1.2.2). Thus, samples representing A and C clearly tended to lie to one side of those for the remaining habitats on each plot and, in seasons such as autumn, winter and spring 2005, samples from habitat A formed a discrete group that lay a considerable distance from those for all basin and channel habitats. It is also interesting that, in all seasons except summer 2006 and 2007, samples from habitat C were more dispersed than those from A and, in winter 2005 and 2006, were among the most dispersed of any habitat type. Samples from habitat J tended to lie between those for C and the remaining basin and channel habitats and, particularly in seasons such as autumn and spring 2005, formed a comparatively tight and distinct group (Fig. 5.1.2.2). Samples from habitat F also formed a comparatively tight group in autumn and spring 2005 and summer 2006, and were generally located between those for J and the remaining basin and channel habitats. However, in each of the other seasons, samples from F were dispersed throughout those for the other basin and channel habitats (Fig. 5.1.2.2).

Habitat E, located closest to the mouth of the estuary, contained fish faunas that were largely dissimilar to those at all other habitats in the middle and upper reaches of the estuary in each season (*i.e.* pairwise R often greater than 0.700), except I in the lowermost reaches of the main basin, *i.e.* although always significantly different, pairwise R less than 0.500 (Table 5.1.2.3). The other channel habitats, M and N, both of which either did not differ significantly from E or each other in each season or exhibited relatively small significant differences, also contained fish faunas that always differed markedly from those in the upper reaches of the estuary, *i.e.* habitats A, C and J, with some exceptions in winter 2005. However, the extent to which the ichthyofaunas at N and particularly M differed from those at habitats in main basin of the estuary, *e.g.* F, G, I and Q, was typically less than that for E. Thus, while both M and N almost always differed significantly from the above the four basin habitats in all seasons except winter 2005, the relevant pairwise R-statistics were often less than 0.600. The MDS plots of the ichthyofaunal data collected in autumn 2005, summer 2006 and summer 2007 (Fig. 5.1.2.2a, d and f, respectively), clearly illustrate that the compositions of samples from habitats E, N and to a lesser extent M, differed the most from those in upper estuary habitats. In the remaining seasons, samples from these channel habitats were still among the most distinct from those in the upper estuary, but tended to intermingle more with samples from basin habitats, particularly in the case of habitat M (Fig. 5.1.2.2b, c and e).



(a) Autumn 2005

(b) Winter 2005

(c) Spring 2005

(d) Summer 2006

(e) Winter 2006

(f) Summer 2007

Figure 5.1.2.2: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample at each habitat type in the Swan Estuary during (a) autumn 2005, (b) winter 2005, (c) spring 2005, (d) summer 2006, (e) winter 2006 and (f) summer 2007.

Several comparisons of the fish faunal compositions between pairs of habitats located in the main basin of the Swan Estuary, *i.e.* F, G, I and Q, were not significantly different in each season, particularly during autumn 2005 (Table 5.1.2.3). This is also illustrated on the associated MDS plots, in which groups of samples from these habitat types often exhibited considerable overlap (Fig. 5.1.2.2). However, samples from habitat I in the lowermost reaches of the basin, which often lay alongside or intermingled with those from the channel on the MDS plots shown in Fig. 5.1.2.2, was comparatively distinct from the remaining basin habitats during spring 2005, winter 2006 and summer 2007, *i.e.* significantly different and pairwise R=0.400-0.721 in almost all cases.

One-way SIMPER analyses among habitats, which were also carried out separately for data collected in each season to complement the above ANOSIM analyses, were then used to identify those species that best typified and distinguished the fish faunas at each habitat (Table 5.1.2.4). The fish faunas at the uppermost habitat (A) were characterised in every season by abundant and consistent occurrences of the atherinid *L. wallacei*, and this species also always distinguished the assemblages at this habitat from that at every other habitat from which it was significantly different. *Pseudogobius olorum* and *A. butcheri* also commonly characterised and distinguished the fish faunas at habitat A from those at other habitats in most seasons (Table 5.1.2.4). At least one of the above three species also typified the assemblages at habitat C in each season and, on those occasions for which *A. butcheri* characterised this habitat, it was always more abundant than in A. *Amniataba caudavittatus* also commonly typified and/or distinguished the ichthyofauna at C, particularly during spring 2005, summer 2007 and to a lesser extent, summer 2006. *Acanthopagrus butcheri* also typified the fish fauna at habitat J in all seasons except winter 2005. However, this estuarine species was always more abundant at habitat C than J, except during winter 2006 in which it was more prevalent at the latter habitat than at both C and A. Habitat J was also characterised by consistent catches of *T. pleurogramma* in almost every season and, in both summers and autumn 2005, also by *A. mugiloides*. Various other species typified the faunas at this habitat in particular seasons, such as *L. wallacei* in autumn 2005, *A. forsteri* in summer 2006 and *A. rueppellii* in summer 2007 (Table 5.1.2.4).

The fish assemblages at the channel habitats E, M and N were each characterised by *F. lateralis* in every season and also by *T. pleurogramma* in all but one season. Various other species either characterised or distinguished at least two of these habitats in particular seasons, such as *Gymnapistes marmoratus* in autumn 2005, *L. presbyteroides* in spring 2005, summer 2006 and summer 2007 and *S. argus* in winter 2006 (Table 5.1.2.4). During those seasons in which the ichthyofauna at E differed significantly from that at M and/or N, it was almost always

Table 5.1.2.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each habitat in the Swan Estuary during (a) autumn 2005, (b) winter 2005, (c) spring 2005, (d) summer 2006, (e) winter 2006 and (f) summer 2007, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Autumn 2005

	A	C	E	F	G	I	J	M	N	Q
A	*L. wallacei* *A. butcheri*									
C	▨	*A. butcheri* *P. punctatus* *A. caudavittatus*								
E	*F. lateralis*^{E} *G. marmoratus*^{E} *T. pleurogramma*^{E} *L. wallacei*^{A} *S. argus*^{E}	*F. lateralis*^{E} *G. marmoratus*^{E} *T. pleurogramma*^{E} *A. butcheri*^{C} *S. argus*^{E}	*F. lateralis* *G. marmoratus* *T. pleurogramma*							
F	*T. pleurogramma*^{F} *L. wallacei*^{A} *P. punctatus*^{F} *A. butcheri*^{A} *F. lateralis*^{F}	▨	*F. lateralis*^{E} *G. marmoratus*^{E} *T. pleurogramma*^{F} *P. punctatus*^{F} *S. argus*^{E}	*T. pleurogramma* *P. punctatus*						
G	*T. pleurogramma*^{G} *L. wallacei*^{A} *A. mugiloides*^{G} *A. butcheri*^{A} *P. punctatus*^{G}	*T. pleurogramma*^{G} *A. butcheri*^{C} *P. punctatus*^{C} *A. caudavittatus*^{C}	*G. marmoratus*^{E} *F. lateralis*^{E} *T. pleurogramma*^{G} *A. mugiloides*^{G} *S. argus*^{E}	▨	*T. pleurogramma* *A. mugiloides*					
I	*T. pleurogramma*^{I} *A. mugiloides*^{I} *F. lateralis*^{I} *L. wallacei*^{A} *A. butcheri*^{A} *L. presbyteroides*^{I}	*T. pleurogramma*^{I} *F. lateralis*^{I} *A. mugiloides*^{I} *A. butcheri*^{C} *P. punctatus*^{C} *L. presbyteroides*^{I}	*G. marmoratus*^{E} *F. lateralis*^{E} *A. mugiloides*^{I} *L. presbyteroides*^{E} *T. pleurogramma*^{I} *S. argus*^{E}	▨	▨	*T. pleurogramma* *A. mugiloides* *F. lateralis* *L. presbyteroides*				
J	*A. mugiloides*^{J} *T. pleurogramma*^{J} *A. butcheri*^{A} *L. wallacei*^{A}	*A. mugiloides*^{J} *T. pleurogramma*^{J} *A. butcheri*^{C} *L. wallacei*^{J}	*A. mugiloides*^{J} *F. lateralis*^{E} *G. marmoratus*^{E} *L. presbyteroides*^{E} *T. pleurogramma*^{E} *A. butcheri*^{J} *S. argus*^{E} *L. wallacei*^{J}	*A. mugiloides*^{J} *T. pleurogramma*^{F} *P. punctatus*^{F} *A. butcheri*^{J} *L. wallacei*^{J} *F. lateralis*^{F}	*T. pleurogramma*^{G} *A. mugiloides*^{J} *A. butcheri*^{J} *L. wallacei*^{J}	*A. mugiloides*^{J} *F. lateralis*^{I} *T. pleurogramma*^{I} *L. presbyteroides*^{J} *A. butcheri*^{J} *L. wallacei*^{J}	*A. mugiloides* *T. pleurogramma* *A. butcheri* *L. wallacei*			

	A	C	E	F	G	I	J	M	N	Q
M	*L. wallacei*^{A} *T. pleurogramma*^{M} *A. butcheri*^{A} *F. lateralis*^{M} *G. marmoratus*^{M}	*T. pleurogramma*^{M} *A. butcheri*^{C} *F. lateralis*^{M} *G. marmoratus*^{M}		*T. pleurogramma*^{F} *P. punctatus*^{F} *G. marmoratus*^{M} *F. lateralis*^{M}	*T. pleurogramma*^{G} *A. mugiloides*^{G} *G. marmoratus*^{M} *F. lateralis*^{M}	*A. mugiloides*^{I} *T. pleurogramma*^{I} *F. lateralis*^{I} *G. marmoratus*^{M} *L. presbyteroides*^{I}	*A. mugiloides*^{J} *F. lateralis*^{M} *G. marmoratus*^{M} *A. butcheri*^{J} *L. wallacei*^{J}	*T. pleurogramma* *F. lateralis* *G. marmoratus*		
N	*L. wallacei*^{A} *F. lateralis*^{N} *A. butcheri*^{A} *T. pleurogramma*^{N}	*F. lateralis*^{N} *A. butcheri*^{C} *T. pleurogramma*^{N}		*T. pleurogramma*^{F} *P. punctatus*^{F} *F. lateralis*^{N}	*T. pleurogramma*^{G} *A. mugiloides*^{G} *F. lateralis*^{N}	*A. mugiloides*^{I} *T. pleurogramma*^{I} *F. lateralis*^{N} *G. marmoratus*^{N} *L. presbyteroides*^{I}	*A. mugiloides*^{J} *F. lateralis*^{N} *S. punctata*^{N} *A. butcheri*^{J} *L. wallacei*^{J}		*F. lateralis* *T. pleurogramma* *G. marmoratus*	
Q	*T. pleurogramma*^{Q} *A. mugiloides*^{Q} *L. wallacei*^{A} *F. lateralis*^{Q} *A. butcheri*^{A} *P. punctatus*^{Q} *L. presbyteroides*^{Q}	*T. pleurogramma*^{Q} *A. mugiloides*^{Q} *F. lateralis*^{Q} *A. butcheri*^{C} *P. punctatus*^{C}	*A. mugiloides*^{Q} *T. pleurogramma*^{E} *G. marmoratus*^{E} *F. lateralis*^{E} *S. argus*^{E}				*T. pleurogramma*^{Q} *A. mugiloides*^{J} *F. lateralis*^{Q} *A. butcheri*^{J} *L. wallacei*^{J}	*A. mugiloides*^{Q} *T. pleurogramma*^{Q} *F. lateralis*^{Q} *G. marmoratus*^{M} *L. presbyteroides*^{M}	*T. pleurogramma*^{Q} *A. mugiloides*^{Q} *F. lateralis*$^{-}$	*T. pleurogramma* *A. mugiloides* *F. lateralis*

(b) Winter 2005

	A	C	E	F	G	I	J	M	N	Q
A	*L. wallacei* *P. olorum*									
C	*L. wallacei*^{A} *P. olorum*^{A}	*L. wallacei* *P. olorum* *M. cephalus*								
E	*T. pleurogramma*^{E} *F. lateralis*^{E} *L. wallacei*^{A} *L. presbyteroides*^{E} *S. argus*^{E} *P. olorum*^{A}	*T. pleurogramma*^{E} *F. lateralis*^{E} *L. presbyteroides*^{E} *S. argus*^{E} *L. wallacei*^{C} *P. olorum*^{C}	*F. lateralis* *T. pleurogramma* *L. presbyteroides* *S. argus*							
F	*L. wallacei*^{A} *A. ogilbyi*^{F} *T. pleurogramma*^{F} *P. olorum*^{A}	*A. ogilbyi*^{F} *T. pleurogramma*^{F} *L. wallacei*^{C} *P. olorum*^{C} *F. lateralis*^{F}	*F. lateralis*^{E} *T. pleurogramma*^{E} *L. presbyteroides*^{E} *A. ogilbyi*^{F} *S. argus*^{E} *L. wallacei*^{F}	*T. pleurogramma* *L. wallacei*						
G	*L. wallacei*^{A} *T. pleurogramma*^{G} *P. olorum*^{A}	*T. pleurogramma*^{G} *F. lateralis*^{G} *L. wallacei*^{C} *P. punctatus*^{G} *P. olorum*^{C}	*F. lateralis*^{E} *T. pleurogramma*^{E} *L. presbyteroides*^{E} *S. argus*^{E}		*T. pleurogramma* *F. lateralis*					
I	*L. wallacei*^{A} *F. lateralis*^{I} *P. olorum*^{A}	*F. lateralis*^{I} *P. punctatus*^{I} *T. pleurogramma*^{I} *L. wallacei*^{C} *P. olorum*^{C}	*T. pleurogramma*^{E} *L. presbyteroides*^{E} *F. lateralis*^{E} *S. argus*^{E}		*F. lateralis*^{I} *T. pleurogramma*^{G} *P. punctatus*^{I}	*F. lateralis* *T. pleurogramma*				
J	*L. wallacei*^{A} *T. pleurogramma*^{J} *P. olorum*^{A}	*T. pleurogramma*^{J} *L. wallacei*^{C} *P. olorum*^{C} *P. punctatus*^{J} *M. cephalus*^{J}	*F. lateralis*^{E} *T. pleurogramma*^{E} *L. presbyteroides*^{E} *S. argus*^{E}			*F. lateralis*^{I} *T. pleurogramma*^{J} *P. punctatus*^{I}	*T. pleurogramma*			
M	*L. wallacei*^{A} *T. pleurogramma*^{M} *P. olorum*^{A} *F. lateralis*^{M}	*T. pleurogramma*^{M} *F. lateralis*^{M} *L. wallacei*^{C} *P. olorum*^{C}	*T. pleurogramma*^{E} *F. lateralis*^{E} *L. presbyteroides*^{E} *S. argus*^{E}					*T. pleurogramma* *F. lateralis*		
N	*L. wallacei*^{A} *F. lateralis*^{N} *P. olorum*^{A}	*F. lateralis*^{N} *T. pleurogramma*^{N} *P. olorum*^{C}	*T. pleurogramma*^{E} *L. presbyteroides*^{E} *S. argus*^{E} *F. lateralis*^{E}	*F. lateralis*^{F} *A. ogilbyi*^{N} *T. pleurogramma*^{F} *L. wallacei*^{F} *A. mugiloides*^{F}			*F. lateralis*^{N} *T. pleurogramma*^{J} *P. punctatus*^{N}		*F. lateralis* *T. pleurogramma*	
Q	*L. wallacei*^{A} *F. lateralis*^{Q} *P. olorum*^{A}	*F. lateralis*^{Q} *L. wallacei*^{C} *T. pleurogramma*^{Q} *P. olorum*^{C}	*T. pleurogramma*^{E} *L. presbyteroides*^{E} *F. lateralis*^{E} *S. argus*^{E}	*A. ogilbyi*^{F} *F. lateralis*^{Q} *T. pleurogramma*^{F} *L. wallacei*^{F} *A. mugiloides*^{F}	*F. lateralis*^{Q} *T. pleurogramma*^{G} *P. punctatus*^{G}		*F. lateralis*^{Q} *T. pleurogramma*^{J} *P. punctatus*^{Q}		*F. lateralis*^{N} *T. pleurogramma*^{Q} *P. punctatus*^{N}	*F. lateralis*

(c) Spring 2005

	A	C	E	F	G	I	J	M	N	Q
A	*A. butcheri* *L. wallacei* *P. olorum*									
C	*A. butcheri*^{C} *A. caudavittatus*^{C} *L. wallacei*^{A} *N. vlaminghi*^{C} *P. octolineatus*^{C} *P. olorum*^{A}	*A. butcheri* *A. caudavittatus*								
E	*T. pleurogramma*^{E} *F. lateralis*^{E} *L. wallacei*^{A} *A. butcheri*^{A} *M. freycineti*^{E} *P. olorum*^{A}	*A. butcheri*^{C} *T. pleurogramma*^{E} *F. lateralis*^{E} *A. caudavittatus*^{C} *M. freycineti*^{E} *P. octolineatus*^{C} *P. olorum*^{C}	*T. pleurogramma* *F. lateralis*							
F	*L. wallacei*^{A} *A. butcheri*^{A} *T. pleurogramma*^{F} *P. punctatus*^{F} *P. olorum*^{A}	*A. butcheri*^{C} *A. caudavittatus*^{C} *P. punctatus*^{F} *T. pleurogramma*^{F} *P. octolineatus*^{C} *P. olorum*^{C}	*T. pleurogramma*^{E} *F. lateralis*^{E} *M. freycineti*^{E} *P. punctatus*^{F}	*T. pleurogramma* *P. punctatus*						
G	*L. wallacei*^{A} *A. butcheri*^{A} *P. punctatus*^{G} *P. olorum*^{A} *F. lateralis*^{G}	*A. butcheri*^{C} *A. caudavittatus*^{C} *P. punctatus*^{G} *F. lateralis*^{G} *P. octolineatus*^{C} *P. olorum*^{C}	*T. pleurogramma*^{E} *F. lateralis*^{E} *M. freycineti*^{E} *L. presbyteroides*^{E} *P. punctatus*^{G}		*F. lateralis* *P. punctatus* *L. presbyteroides*					
I	*L. wallacei*^{A} *A. butcheri*^{A} *F. lateralis*^{I} *T. pleurogramma*^{I} *P. olorum*^{A} *L. presbyteroides*^{I}	*A. butcheri*^{C} *A. caudavittatus*^{C} *F. lateralis*^{I} *T. pleurogramma*^{I} *P. octolineatus*^{C} *L. presbyteroides*^{I} *P. olorum*^{C}	*T. pleurogramma*^{E} *M. freycineti*^{E} *L. presbyteroides*^{E} *F. lateralis*^{E}	*F. lateralis*^{I} *P. punctatus*^{F} *T. pleurogramma*^{F} *L. presbyteroides*^{I} *A. mugiloides*^{F}	*F. lateralis*^{I} *P. punctatus*^{G} *T. pleurogramma*^{I} *L. presbyteroides*^{G} *A. mugiloides*^{I}	*F. lateralis* *T. pleurogramma*				
J	*L. wallacei*^{A} *T. pleurogramma*^{J} *A. butcheri*^{A} *P. olorum*^{A} *P. punctatus*^{J}	*A. butcheri*^{C} *A. caudavittatus*^{C} *T. pleurogramma*^{J} *P. octolineatus*^{C} *P. olorum*^{C}	*F. lateralis*^{E} *T. pleurogramma*^{E} *A. butcheri*^{J} *M. freycineti*^{E} *P. punctatus*^{J}	*A. butcheri*^{J} *T. pleurogramma*^{J} *P. punctatus*^{F} *A. mugiloides*^{J}	*A. butcheri*^{J} *T. pleurogramma*^{J} *P. punctatus*^{G} *F. lateralis*^{G}	*F. lateralis*^{I} *A. butcheri*^{J} *T. pleurogramma*^{J} *P. punctatus*^{J} *L. presbyteroides*^{I}	*T. pleurogramma* *A. butcheri*			

	A	C	E	F	G	I	J	M	N	Q
M	*T. pleurogramma*^{M} *L. wallacei*^{A} *A. butcheri*^{A} *F. lateralis*^{M} *P. olorum*^{A} *L. presbyteroides*^{M}	*A. butcheri*^{C} *A. caudavittatus*^{C} *T. pleurogramma*^{M} *F. lateralis*^{M} *L. presbyteroides*^{M} *P. octolineatus*^{C} *P. olorum*^{C}	*T. pleurogramma*^{E} *F. lateralis*^{E} *M. freycineti*^{E} *S. argus*^{E} *L. presbyteroides*^{E}	*T. pleurogramma*^{M} *P. punctatus*^{F} *F. lateralis*^{M} *L. presbyteroides*^{M}	*T. pleurogramma*^{M} *P. punctatus*^{G} *L. presbyteroides*^{M} *G. marmoratus*^{M} *F. lateralis*^{M}	*T. pleurogramma*^{M} *F. lateralis*^{I} *L. presbyteroides*^{M}	*A. butcheri*^{J} *T. pleurogramma*^{M} *F. lateralis*^{M} *L. presbyteroides*^{M} *P. punctatus*^{J}	*T. pleurogramma* *F. lateralis* *L. presbyteroides*		
N	*F. lateralis*^{N} *T. pleurogramma*^{N} *L. wallacei*^{A} *A. butcheri*^{A} *S. argus*^{N} *L. presbyteroides*^{N} *P. olorum*^{A}	*A. butcheri*^{C} *F. lateralis*^{N} *A. caudavittatus*^{C} *T. pleurogramma*^{N} *S. argus*^{N} *L. presbyteroides*^{N} *P. octolineatus*^{C} *P. olorum*^{C}	▨	*F. lateralis*^{N} *S. argus*^{N} *T. pleurogramma*^{N} *P. punctatus*^{F} *L. presbyteroides*^{N} *A. rueppellii*^{F}	*F. lateralis*^{N} *T. pleurogramma*^{N} *S. argus*^{N} *P. punctatus*^{G} *L. presbyteroides*^{N}	*S. argus*^{N} *T. pleurogramma*^{N} *F. lateralis*^{N} *L. presbyteroides*^{N} *A. rueppellii*^{I}	▨	▨	*F. lateralis* *T. pleurogramma* *S. argus* *L. presbyteroides*	
Q	*F. lateralis*^{Q} *A. butcheri*^{A} *L. wallacei*^{A} *P. olorum*^{A} *A. mugiloides*^{Q} *T. pleurogramma*^{Q}	*A. butcheri*^{C} *F. lateralis*^{Q} *A. caudavittatus*^{C} *P. octolineatus*^{C} *A. mugiloides*^{Q} *P. olorum*^{C}	*T. pleurogramma*^{E} *M. freycineti*^{E} *F. lateralis*^{Q} *L. presbyteroides*^{E} *A. mugiloides*^{Q}	*F. lateralis*^{Q} *P. punctatus*^{Q} *T. pleurogramma*^{F} *A. mugiloides*^{Q}	*F. lateralis*^{Q} *P. punctatus*^{Q} *T. pleurogramma*^{Q}	*F. lateralis*^{Q} *P. punctatus*^{Q} *A. forsteri*^{I} *T. pleurogramma*^{I} *L. presbyteroides*^{Q} *A. mugiloides*^{Q}	▨	*F. lateralis*^{Q} *T. pleurogramma*^{M} *P. punctatus*^{Q} *L. presbyteroides*^{M}	*T. pleurogramma*^{N} *S. argus*^{N} *F. lateralis*^{N} *L. presbyteroides*^{N} *A. mugiloides*^{Q}	*F. lateralis* *P. punctatus*

(d) Summer 2006

	A	C	E	F	G	I	J	M	N	Q
A	*L. wallacei* *P. olorum* *A. butcheri* *A. caudavittatus* *N. vlaminghi*									
C	*L. wallacei*^{A} *P. olorum*^{A} *P. punctatus*^{C} *A. butcheri*^{C} *A. caudavittatus*$^{-}$ *N. vlaminghi*^{A} *A. suppositus*^{A}	*A. butcheri* *P. punctatus* *P. olorum*								
E	*L. wallacei*^{A} *P. olorum*^{A} *L. presbyteroides*^{E} *A. butcheri*^{A} *T. pleurogramma*^{E} *F. lateralis*^{E} *N. vlaminghi*^{A} *A. caudavittatus*^{A}	*A. butcheri*^{C} *L. presbyteroides*^{E} *T. pleurogramma*^{E} *F. lateralis*^{E} *P. olorum*^{C}	*F. lateralis* *T. pleurogramma* *L. presbyteroides*							
F	*L. wallacei*^{A} *P. olorum*^{A} *T. pleurogramma*^{F} *A. butcheri*^{F} *A. mugiloides*^{F} *N. vlaminghi*^{A}	*P. punctatus*^{C} *T. pleurogramma*^{F} *A. butcheri*^{C} *P. olorum*^{C} *A. mugiloides*^{F} *A. caudavittatus*^{C} *A. elongata*^{F}	*A. butcheri*^{F} *L. presbyteroides*^{E} *F. lateralis*^{E} *A. mugiloides*^{F} *T. pleurogramma*^{E} *A. caudavittatus*^{F}	*A. butcheri* *T. pleurogramma* *A. mugiloides* *A. caudavittatus*						
G	*L. wallacei*^{A} *P. olorum*^{A} *A. butcheri*^{A} *T. pleurogramma*^{G} *A. mugiloides*^{G} *N. vlaminghi*^{A} *A. suppositus*^{A}	*A. butcheri*^{C} *P. punctatus*^{C} *T. pleurogramma*^{G} *P. olorum*^{C} *A. mugiloides*^{G} *A. caudavittatus*^{G}	*L. presbyteroides*^{E} *F. lateralis*^{E} *T. pleurogramma*^{E} *A. mugiloides*^{G} *A. caudavittatus*^{G}		*T. pleurogramma* *A. caudavittatus* *A. mugiloides*					
I	*L. wallacei*^{A} *P. olorum*^{A} *A. butcheri*^{A} *T. pleurogramma*^{I} *N. vlaminghi*^{I} *A. caudavittatus*^{A} *F. lateralis*^{I}	*A. butcheri*^{C} *P. punctatus*^{C} *T. pleurogramma*^{I} *P. olorum*^{C} *A. caudavittatus*^{C} *F. lateralis*^{I}	*L. presbyteroides*^{E} *F. lateralis*^{E} *S. burrus*^{I} *T. pleurogramma*^{E}		*S. burrus*^{I} *T. pleurogramma*^{I} *A. mugiloides*^{G} *A. forsteri*^{I} *A. caudavittatus*^{G} *F. lateralis*^{I}	*T. pleurogramma* *S. burrus* *F. lateralis* *A. mugiloides* *L. presbyteroides*				

	A	C	E	F	G	I	J	M	N	Q
J	*P. olorum*^{A} *L. wallacei*^{A} *A. butcheri*^{J} *T. pleurogramma*^{J} *N. vlaminghi*^{A} *P. punctatus*^{J}	*P. punctatus*^{C} *A. rueppellii*^{J} *A. forsteri*^{J} *A. butcheri*^{C} *P. olorum*^{C} *T. pleurogramma*^{J} *A. caudavittatus*^{C}	*A. butcheri*^{J} *L. presbyteroides*^{E} *F. lateralis*^{E} *T. pleurogramma*^{J} *A. caudavittatus*^{J} *P. punctatus*^{J}		*A. butcheri*^{J} *A. mugiloides*^{J} *A. rueppellii*^{J} *A. forsteri*^{J} *T. pleurogramma*^{G} *A. caudavittatus*^{G} *P. punctatus*^{J} *L. wallacei*^{J}	*A. butcheri*^{J} *A. mugiloides*^{J} *A. rueppellii*^{J} *S. burrus*^{I} *A. forsteri*^{J} *T. pleurogramma*^{I} *A. caudavittatus*^{J} *P. punctatus*^{J} *F. lateralis*^{I}	*A. butcheri* *T. pleurogramma* *A. forsteri* *A. caudavittatus* *A. mugiloides*			
M	*L. wallacei*^{A} *P. olorum*^{A} *A. butcheri*^{M} *N. vlaminghi*^{A} *F. lateralis*^{M} *T. pleurogramma*^{M} *S. argus*^{M} *L. presbyteroides*^{M}	*A. butcheri*^{C} *P. punctatus*^{C} *P. olorum*^{C} *T. pleurogramma*^{M} *F. lateralis*^{M} *S. argus*^{M} *L. presbyteroides*^{M} *A. rueppellii*^{M} *A. ogilbyi*^{M}	*L. presbyteroides*^{E} *T. pleurogramma*^{E} *F. lateralis*^{E} *S. argus*^{M} *A. rueppellii*^{M}	*A. butcheri*^{F} *A. mugiloides*^{F} *T. pleurogramma*^{F} *F. lateralis*^{M} *A. caudavittatus*^{F} *S. argus*^{M} *L. presbyteroides*^{M} *A. rueppellii*^{M} *A. ogilbyi*^{M}	*A. mugiloides*^{G} *T. pleurogramma*^{G} *A. caudavittatus*^{G} *F. lateralis*^{M} *S. argus*^{M} *L. presbyteroides*^{M} *A. ogilbyi*^{M}	*S. burrus*^{I} *T. pleurogramma*^{I} *A. forsteri*^{I} *S. argus*^{M} *F. lateralis*^{M} *A. rueppellii*^{M}	*A. butcheri*^{J} *A. rueppellii*^{J} *A. forsteri*^{J} *F. lateralis*^{M} *T. pleurogramma*$^{-}$ *S. argus*^{M} *A. caudavittatus*^{J} *L. presbyteroides*^{M} *P. punctatus*^{J}	*F. lateralis* *L. presbyteroides* *T. pleurogramma* *S. argus*		
N	*L. wallacei*^{A} *F. lateralis*^{N} *P. olorum*^{A} *T. pleurogramma*^{N} *A. butcheri*^{A} *N. vlaminghi*^{A} *A. caudavittatus*^{A} *A. rueppellii*^{N}	*F. lateralis*^{N} *A. butcheri*^{C} *P. punctatus*^{C} *T. pleurogramma*^{N} *P. olorum*^{C} *A. rueppellii*^{N}		*F. lateralis*^{N} *A. butcheri*^{F} *A. mugiloides*^{F} *T. pleurogramma*^{N} *A. caudavittatus*^{F} *A. rueppellii*^{N} *L. presbyteroides*^{N}	*F. lateralis*^{N} *T. pleurogramma*^{N} *A. mugiloides*^{G} *A. caudavittatus*^{G} *A. rueppellii*^{N}	*F. lateralis*^{N} *S. burrus*^{I} *T. pleurogramma*^{N} *A. rueppellii*^{N} *L. presbyteroides*^{I}	*F. lateralis*^{N} *A. butcheri*^{J} *A. rueppellii*^{J} *T. pleurogramma*^{N} *A. caudavittatus*^{J} *P. punctatus*^{J} *L. presbyteroides*^{N}		*F. lateralis* *T. pleurogramma* *A. rueppellii*	
Q	*L. wallacei*^{A} *P. olorum*^{A} *A. butcheri*^{A} *F. lateralis*^{Q} *A. caudavittatus*^{A} *N. vlaminghi*^{A} *A. mugiloides*^{Q} *T. pleurogramma*^{Q} *A. elongata*^{Q}	*A. butcheri*^{C} *P. punctatus*^{C} *P. olorum*^{C} *F. lateralis*^{Q} *A. caudavittatus*^{C} *A. mugiloides*^{Q} *T. pleurogramma*^{Q} *A. elongata*^{Q}	*L. presbyteroides*^{E} *F. lateralis*^{E} *T. pleurogramma*^{E} *A. mugiloides*^{Q} *A. elongata*^{Q}	*A. butcheri*^{F} *F. lateralis*^{Q} *T. pleurogramma*^{F} *A. mugiloides*^{F} *A. caudavittatus*^{F} *A. elongata*^{Q} *P. punctatus*^{F}	*F. lateralis*^{Q} *A. caudavittatus*^{G} *T. pleurogramma*^{G} *A. mugiloides*^{G} *A. elongata*^{Q} *P. punctatus*^{Q}		*A. butcheri*^{J} *A. rueppellii*^{J} *A. mugiloides*^{J} *A. forsteri*^{J} *F. lateralis*^{Q} *A. caudavittatus*^{J} *A. elongata*^{Q} *T. pleurogramma*^{J} *P. punctatus*^{J}	*F. lateralis*^{Q} *A. mugiloides*^{Q} *T. pleurogramma*^{M} *S. argus*^{M} *A. elongata*^{Q} *L. presbyteroides*^{M} *A. ogilbyi*^{M} *P. octolineatus*^{M}	*F. lateralis*^{N} *T. pleurogramma*^{N} *A. mugiloides*^{Q} *A. elongata*^{Q} *A. rueppellii*^{N} *L. presbyteroides*^{N} *P. octolineatus*^{N}	*T. pleurogramma* *F. lateralis* *A. mugiloides* *A. elongata* *A. rueppellii*

(e) Winter 2006

	A	C	E	F	G	I	J	M	N	Q
A	*L. wallacei*									
C		*L. wallacei* *M. cephalus* *H. vittatus*								
E	*F. lateralis*^{E} *L. wallacei*^{A} *L. presbyteroides*^{E} *S. argus*^{E}	*F. lateralis*^{E} *L. presbyteroides*^{E} *S. argus*^{E} *L. wallacei*^{C}	*F. lateralis* *L. presbyteroides* *S. argus* *T. pleurogramma*							
F	*A. mugiloides*^{F} *L. wallacei*^{A} *L. presbyteroides*^{F} *M. cephalus*^{F}	*A. mugiloides*^{F} *L. presbyteroides*^{F} *M. cephalus*^{F} *L. wallacei*^{C}	*F. lateralis*^{E} *A. mugiloides*^{F} *L. presbyteroides*^{E} *S. argus*^{E}	*A. mugiloides* *L. presbyteroides*						
G	*L. wallacei*^{A} *A. mugiloides*^{G} *L. presbyteroides*^{G} *T. pleurogramma*^{G}	*A. mugiloides*^{G} *L. presbyteroides*^{G} *L. wallacei*^{G} *T. pleurogramma*^{G}	*F. lateralis*^{E} *L. presbyteroides*^{E} *A. mugiloides*^{G} *S. argus*^{E} *T. pleurogramma*^{E}		*A. mugiloides* *T. pleurogramma* *L. presbyteroides*					
I	*L. wallacei*^{A} *F. lateralis*^{I}	*F. lateralis*^{I} *L. wallacei*^{C} *A. mugiloides*^{I} *H. vittatus*^{C}	*F. lateralis*^{E} *L. presbyteroides*^{E} *S. argus*^{E} *T. pleurogramma*^{E}	*A. mugiloides*^{F} *F. lateralis*^{I} *L. presbyteroides*^{F} *M. cephalus*^{F}	*F. lateralis*^{I} *A. mugiloides*^{G} *L. presbyteroides*^{G}	*F. lateralis*				
J	*T. pleurogramma*^{J} *L. wallacei*^{A} *M. cephalus*^{J} *A. butcheri*^{J}	*T. pleurogramma*^{J} *M. cephalus*^{J} *A. butcheri*^{J} *L. wallacei*^{C}	*F. lateralis*^{E} *L. presbyteroides*^{E} *S. argus*^{E} *T. pleurogramma*^{J} *A. butcheri*^{J}	*T. pleurogramma*^{J} *M. cephalus*$^{-}$ *A. mugiloides*^{F} *L. presbyteroides*^{F} *A. butcheri*^{J}	*A. mugiloides*^{G} *M. cephalus*^{J} *T. pleurogramma*^{J} *L. presbyteroides*^{G}	*F. lateralis*^{I} *T. pleurogramma*^{J} *A. mugiloides*^{I} *M. cephalus*^{J}	*T. pleurogramma* *A. butcheri*			
M	*L. wallacei*^{A} *S. argus*^{M} *F. lateralis*^{M}	*S. argus*^{M} *F. lateralis*^{M}	*S. argus*^{M} *F. lateralis*^{E} *L. presbyteroides*^{E}	*S. argus*^{M} *A. mugiloides*^{F} *F. lateralis*^{M} *L. presbyteroides*^{F}	*S. argus*^{M} *F. lateralis*^{M} *A. mugiloides*^{G} *L. presbyteroides*^{G} *T. pleurogramma*^{G}	*S. argus*^{M} *F. lateralis*^{I}	*S. argus*^{M} *F. lateralis*^{M} *T. pleurogramma*^{J}	*F. lateralis* *S. argus*		
N	*F. lateralis*^{N} *L. wallacei*^{A} *S. argus*^{N} *P. punctatus*^{N} *T. pleurogramma*^{N}	*F. lateralis*^{N} *S. argus*^{N} *T. pleurogramma*^{N}			*F. lateralis*^{N} *S. argus*^{N} *A. mugiloides*^{G} *L. presbyteroides*^{N} *T. pleurogramma*^{G}	*F. lateralis*^{N} *S. argus*^{N} *A. mugiloides*^{I} *L. presbyteroides*^{N} *P. punctatus*^{N} *T. pleurogramma*^{N}	*F. lateralis*^{N} *S. argus*^{N} *T. pleurogramma*^{J} *L. presbyteroides*^{N}	*F. lateralis*^{N} *S. argus*^{M} *L. presbyteroides*^{N} *P. punctatus*^{N} *T. pleurogramma*^{N}	*F. lateralis* *S. argus*	
Q	*L. wallacei*^{A} *L. presbyteroides*^{Q} *A. elongata*^{Q} *F. lateralis*^{Q} *T. pleurogramma*^{Q}	*L. presbyteroides*^{Q} *A. elongata*^{Q} *F. lateralis*^{Q} *L. wallacei*^{C} *T. pleurogramma*^{Q}	*L. presbyteroides*^{Q} *F. lateralis*^{E} *S. argus*^{E} *T. pleurogramma*^{E}	*L. presbyteroides*^{Q} *A. mugiloides*^{F} *M. cephalus*^{Q} *A. elongata*^{Q} *F. lateralis*^{Q} *T. pleurogramma*^{Q}	*L. presbyteroides*^{Q} *A. mugiloides*^{G} *A. elongata*^{Q} *F. lateralis*^{Q} *T. pleurogramma*^{G}	*L. presbyteroides*^{Q} *F. lateralis*^{I} *A. elongata*^{Q} *A. mugiloides*^{I} *T. pleurogramma*^{Q}	*L. presbyteroides*^{Q} *T. pleurogramma*^{J} *A. elongata*^{Q} *F. lateralis*^{Q} *A. mugiloides*^{Q} *A. butcheri*^{J}	*S. argus*^{M} *L. presbyteroides*^{Q} *F. lateralis*^{M} *T. pleurogramma*^{Q}	*F. lateralis*^{N} *L. presbyteroides*^{Q} *S. argus*^{N} *P. punctatus*^{N} *T. pleurogramma*^{N}	*F. lateralis* *L. presbyteroides* *A. elongata* *T. pleurogramma*

(f) Summer 2007

	A	C	E	F	G	I	J	M	N	Q
A	*P. olorum* *L. wallacei* *A. butcheri* *A. suppositus*									
C	*P. olorum*^{A} *L. wallacei*^{A} *P. punctatus*^{C} *A. caudavittatus*^{C} *A. suppositus*^{A} *A. mugiloides*^{A} *A. butcheri*^{C}	*A. butcheri* *A. caudavittatus* *P. punctatus*								
E	*P. olorum*^{A} *F. lateralis*^{E} *L. wallacei*^{A} *T. pleurogramma*^{E} *A. butcheri*^{A} *A. mugiloides*^{A} *S. argus*^{E} *A. suppositus*^{A} *L. presbyteroides*^{E} *A. rueppellii*^{E}	*F. lateralis*^{E} *A. butcheri*^{C} *P. punctatus*^{C} *A. caudavittatus*^{C} *T. pleurogramma*^{E} *S. argus*^{E} *A. rueppellii*^{E} *L. presbyteroides*^{E}	*F. lateralis* *T. pleurogramma* *S. argus* *L. presbyteroides*							
F	*P. olorum*^{A} *L. wallacei*^{A} *A. mugiloides*^{A} *A. butcheri*^{A} *A. suppositus*^{A}	*P. punctatus*^{C} *A. butcheri*^{C} *A. caudavittatus*^{C} *T. pleurogramma*^{F} *A. mugiloides*^{F}	*F. lateralis*^{E} *T. pleurogramma*^{E} *S. argus*^{E} *L. presbyteroides*^{F} *P. punctatus*^{F} *A. caudavittatus*^{F} *A. mugiloides*^{F} *A. rueppellii*^{E}	*P. punctatus* *A. caudavittatus* *L. presbyteroides* *T. pleurogramma* *A. butcheri*						
G	*P. olorum*^{A} *L. wallacei*^{A} *A. mugiloides*^{A} *A. butcheri*^{A} *T. pleurogramma*^{G} *A. suppositus*^{A}	*A. butcheri*^{C} *P. punctatus*^{C} *A. caudavittatus*^{C} *A. mugiloides*^{G} *T. pleurogramma*^{G} *A. elongata*^{G} *A. rueppellii*^{G}	*F. lateralis*^{E} *A. mugiloides*^{G} *S. argus*^{E} *T. pleurogramma*^{E} *A. elongata*^{G} *L. presbyteroides*^{G} *A. rueppellii*^{G}		*A. mugiloides* *T. pleurogramma* *A. elongata*					
I	*P. olorum*^{A} *F. lateralis*^{I} *L. wallacei*^{A} *A. mugiloides*^{A} *A. butcheri*^{A} *A. suppositus*^{A} *A. rueppellii*^{I} *T. pleurogramma*^{I}	*F. lateralis*^{I} *A. butcheri*^{C} *A. caudavittatus*^{C} *P. punctatus*^{C} *P. octolineatus*^{I} *P. octolineatus*^{I} *A. rueppellii*^{I} *T. pleurogramma*^{I} *A. ogilbyi*^{I} *A. elongata*^{I} *L. presbyteroides*^{I}	*P. octolineatus*^{I} *S. argus*^{E} *A. rueppellii*^{I} *T. pleurogramma*^{E} *F. lateralis*^{E} *A. elongata*^{I} *S. granulatus*^{E} *A. ogilbyi*^{I} *L. presbyteroides*^{E}	*P. octolineatus*^{I} *F. lateralis*^{I} *T. pleurogramma*^{F} *L. presbyteroides*^{F} *A. rueppellii*^{I} *A. caudavittatus*^{F} *P. punctatus*^{F} *A. butcheri*^{F} *A. mugiloides*^{F} *A. ogilbyi*^{I}	*P. octolineatus*^{I} *F. lateralis*^{I} *A. mugiloides*^{G} *A. rueppellii*^{I} *T. pleurogramma*^{G} *L. presbyteroides*^{G} *A. elongata*^{G} *A. ogilbyi*^{I}	*F. lateralis* *T. pleurogramma* *A. rueppellii* *L. presbyteroides*				

	A	C	E	F	G	I	J	M	N	Q
J	*P. olorum*^{A} *A. rueppellii*^{J} *L. wallacei*^{A} *A. mugiloides*^{A} *A. suppositus*^{A} *A. butcheri*^{J} *T. pleurogramma*^{J}	*A. rueppellii*^{J} *P. punctatus*^{C} *A. caudavittatus*^{C} *A. butcheri*^{C} *T. pleurogramma*^{J}	*A. rueppellii*^{J} *F. lateralis*^{E} *A. butcheri*^{J} *S. argus*^{E} *T. pleurogramma*^{E} *L. presbyteroides*^{E}	*A. rueppellii*^{J} *A. butcheri*^{J} *T. pleurogramma*^{F} *A. mugiloides*^{F} *P. endrachtensis*^{F} *A. caudavittatus*^{F} *P. punctatus*^{F} *A. ogilbyi*^{F}	*A. rueppellii*^{J} *A. butcheri*^{J} *A. mugiloides*^{G} *T. pleurogramma*^{G} *A. caudavittatus*^{G} *A. elongata*^{G}	*A. rueppellii*^{J} *F. lateralis*^{I} *P. octolineatus*^{I} *A. butcheri*^{J} *A. mugiloides*^{J} *A. elongata*^{I} *A. ogilbyi*^{I} *T. pleurogramma*^{I} *L. presbyteroides*^{I}	*A. butcheri* *A. rueppellii* *A. mugiloides*			
M	*P. olorum*^{A} *L. wallacei*^{A} *A. mugiloides*^{A} *L. presbyteroides*^{M} *A. suppositus*^{A} *F. lateralis*^{M} *T. pleurogramma*^{M} *S. argus*^{M} *A. butcheri*^{A} *A. rueppellii*^{M}	*P. punctatus*^{C} *A. caudavittatus*^{C} *L. presbyteroides*^{M} *A. butcheri*^{C} *F. lateralis*^{M} *T. pleurogramma*^{M} *S. argus*^{M} *A. rueppellii*^{M}	*A. ogilbyi*^{M} *F. lateralis*^{E} *A. butcheri*^{M} *L. presbyteroides*^{M} *S. argus*^{E} *T. pleurogramma*^{E} *A. rueppellii*^{M}	*A. ogilbyi*^{M} *L. presbyteroides*^{M} *T. pleurogramma*^{F} *A. butcheri*^{M} *F. lateralis*^{M} *P. punctatus*^{F} *S. argus*^{M} *A. rueppellii*^{M} *A. caudavittatus*^{F}	*A. ogilbyi*^{M} *A. mugiloides*^{G} *L. presbyteroides*^{M} *A. butcheri*^{M} *T. pleurogramma*^{G} *F. lateralis*^{M} *A. elongata*^{G} *S. argus*^{M} *A. rueppellii*^{G}	*P. octolineatus*^{I} *A. ogilbyi*^{M} *F. lateralis*^{I} *A. butcheri*^{M} *L. presbyteroides*^{M} *A. rueppellii*^{I} *S. argus*^{M} *A. elongata*^{I} *T. pleurogramma*^{M}	*A. rueppellii*^{J} *A. ogilbyi*^{M} *L. presbyteroides*^{M} *F. lateralis*^{M} *S. argus*^{M} *A. butcheri*^{J} *T. pleurogramma*^{M}	*A. butcheri* *F. lateralis* *T. pleurogramma* *L. presbyteroides* *A. rueppellii*		
N	*P. olorum*^{A} *F. lateralis*^{N} *L. wallacei*^{A} *H. semifasciata*^{N} *T. pleurogramma*^{N} *A. mugiloides*^{A} *A. butcheri*^{A} *A. suppositus*^{A} *A. rueppellii*^{N}	*F. lateralis*^{N} *H. semifasciata*^{N} *A. butcheri*^{C} *P. punctatus*^{C} *A. caudavittatus*^{C} *T. pleurogramma*^{N}			*H. semifasciata*^{N} *F. lateralis*^{N} *A. mugiloides*^{G} *T. pleurogramma*^{N} *L. presbyteroides*^{N} *A. elongata*^{G} *A. rueppellii*^{G} *A. ogilbyi*^{N}	*H. semifasciata*^{N} *P. octolineatus*^{I} *T. pleurogramma*^{N} *A. rueppellii*^{I} *L. presbyteroides*^{N} *A. elongata*^{I} *F. lateralis*^{N} *A. ogilbyi*^{I}	*F. lateralis*^{N} *A. rueppellii*^{J} *H. semifasciata*^{N} *A. butcheri*^{J} *T. pleurogramma*^{N}	*H. semifasciata*^{N} *A. ogilbyi*^{M} *F. lateralis*^{N} *L. presbyteroides*^{M} *A. butcheri*^{M} *T. pleurogramma*^{N} *S. argus*^{M} *A. rueppellii*^{M}	*F. lateralis* *H. semifasciata* *T. pleurogramma* *A. rueppellii*	
Q	*P. olorum*^{A} *A. elongata*^{Q} *L. wallacei*^{A} *L. presbyteroides*^{Q} *A. mugiloides*^{A} *T. pleurogramma*^{Q} *A. butcheri*^{A} *A. suppositus*^{A} *P. punctatus*^{Q}	*A. elongata*^{Q} *A. butcheri*^{C} *A. caudavittatus*^{C} *P. punctatus*^{C} *L. presbyteroides*^{Q} *A. mugiloides*^{Q} *T. pleurogramma*^{Q} *F. lateralis*^{Q}	*A. elongata*^{Q} *F. lateralis*^{E} *A. mugiloides*^{Q} *S. argus*^{E} *L. presbyteroides*^{Q} *T. pleurogramma*^{E} *A. rueppellii*^{E} *P. punctatus*^{Q}	*A. elongata*^{Q} *L. presbyteroides*^{Q} *T. pleurogramma*^{Q} *A. mugiloides*^{Q} *P. endrachtensis*^{F} *S. burrus*^{Q} *F. lateralis*^{Q} *A. butcheri*^{F} *A. caudavittatus*^{F}	*A. elongata*^{Q} *L. presbyteroides*^{Q} *T. pleurogramma*^{Q} *A. mugiloides*^{Q} *A. rueppellii*^{G} *P. punctatus*^{Q} *F. lateralis*^{Q}	*A. elongata*^{Q} *P. octolineatus*^{I} *F. lateralis*^{I} *A. mugiloides*^{Q} *L. presbyteroides*^{Q} *A. rueppellii*^{I} *A. ogilbyi*^{I} *P. punctatus*^{Q}	*A. elongata*^{Q} *A. rueppellii*^{J} *L. presbyteroides*^{Q} *A. butcheri*^{J} *T. pleurogramma*^{Q} *A. mugiloides*^{Q} *F. lateralis*^{Q} *P. punctatus*^{Q}	*A. elongata*^{Q} *A. ogilbyi*^{M} *A. mugiloides*^{Q} *L. presbyteroides*^{Q} *A. butcheri*^{M} *F. lateralis*^{M} *S. argus*^{M} *A. rueppellii*^{M} *P. punctatus*^{Q}	*A. elongata*^{Q} *H. semifasciata*^{N} *F. lateralis*^{N} *A. mugiloides*^{Q} *T. pleurogramma*^{N} *L. presbyteroides*^{Q} *P. punctatus*^{Q} *A. rueppellii*^{N}	*L. presbyteroides* *A. mugiloides* *T. pleurogramma* *A. elongata* *P. punctatus*

distinguished by greater abundances of *T. pleurogramma*, *F. lateralis* and/or *L. presbyteroides*, and on those occasions that M and N differed significantly, their assemblages were typically distinguished by at least one of the above three species and/or a variety of weed-associated species, such as *H. semifasciata, S. argus* and *A. rueppellii.*

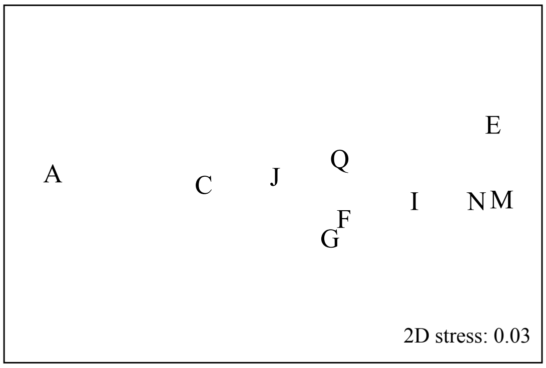
Habitats in the middle reaches of the estuary (*i.e.* F, G, I and Q) were also almost always characterised by the consistent occurrence of *T. pleurogramma* and/or *F. lateralis* in every season (Table 5.1.2.4). However, species such as *A. mugiloides* and *P. punctatus* also typified the faunas at several of these habitats in a number of seasons. On those occasions for which the composition of the fish faunas differed significantly between pairs of the above basin habitats, they were often distinguished by a greater prevalence of one or more of the above species. However, a considerably greater diversity of species distinguished the faunas of pairs of these habitats in summer 2006 and particularly summer 2007, *e.g. Sillago burrus, A. caudavittatus, A. butcheri, P. octolineatus, A. rueppellii* and *A. elongata* (Table 5.1.2.4).

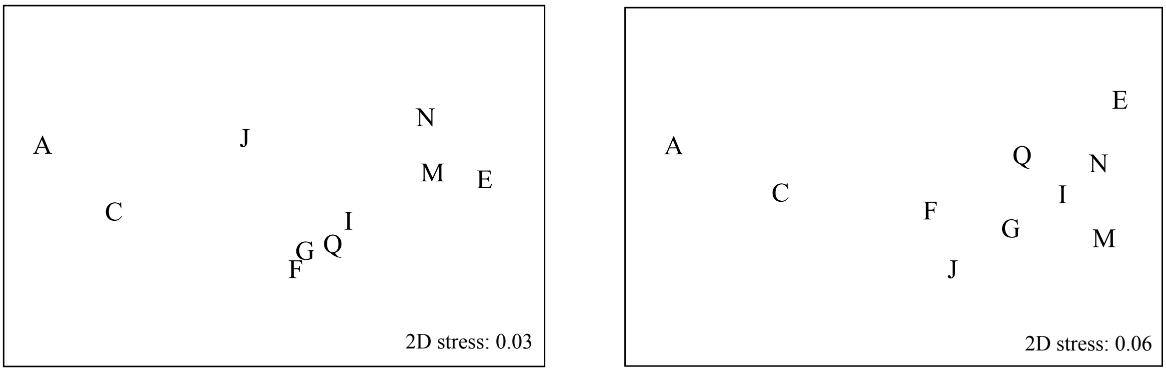
5.1.2.4 Matching spatial patterns between the environmental and fish assemblage characteristics of habitats

The extent to which the spatial pattern among habitats, as defined by the average of their enduring environmental characteristics, was correlated with that defined by the average composition of their fish faunas, was determined for each sampling season using the RELATE routine. This test detected a significant (p=0.1-0.2%) and high (*ρ*=0.775-0.886) correlation in each case, thus demonstrating that the relative spatial differences in the enduring environmental characteristics of habitat types provided an excellent surrogate for spatial differences in the composition of the fish fauna throughout the estuary in each season. Such results are illustrated by the very similar distribution of points representing the various habitats on the MDS plots shown in Fig. 5.1.2.3 of (a) the average enduring environmental composition at each habitat type and (b-g) the average fish faunal composition at each habitat type in each season. The RELATE results obtained for each individual season are also provided on the plots shown in Fig. 5.1.2.3b-g.

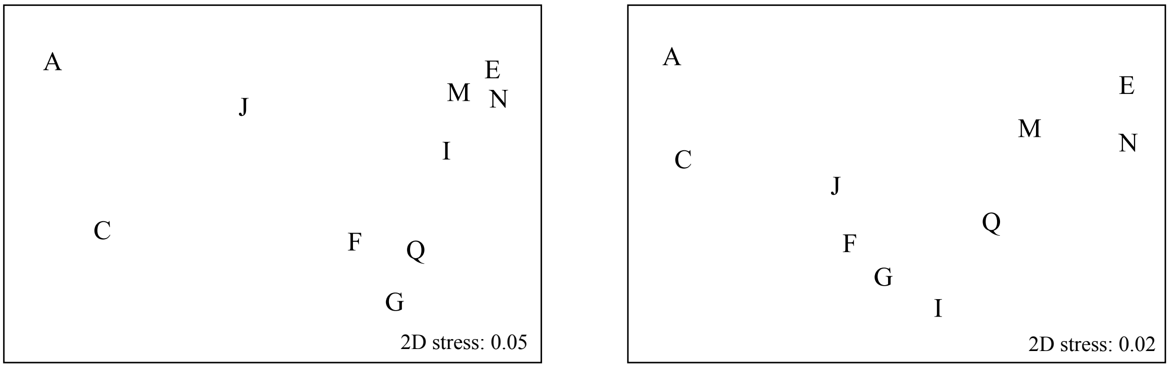
When each of the matrices constructed from the average species abundances at each habitat in each individual season were matched with the complementary matrices constructed from the suite of non-enduring water quality parameters (*i.e.* salinity, temperature and dissolved oxygen), RELATE detected a significant correlation in each case (p=0.1-0.2%), but the extent of those correlations were lower than those found between the enduring environmental matrix and the matrices constructed from the fish assemblage data in each season, *i.e. ρ*=0.794 (autumn

(a) Enduring environmental data

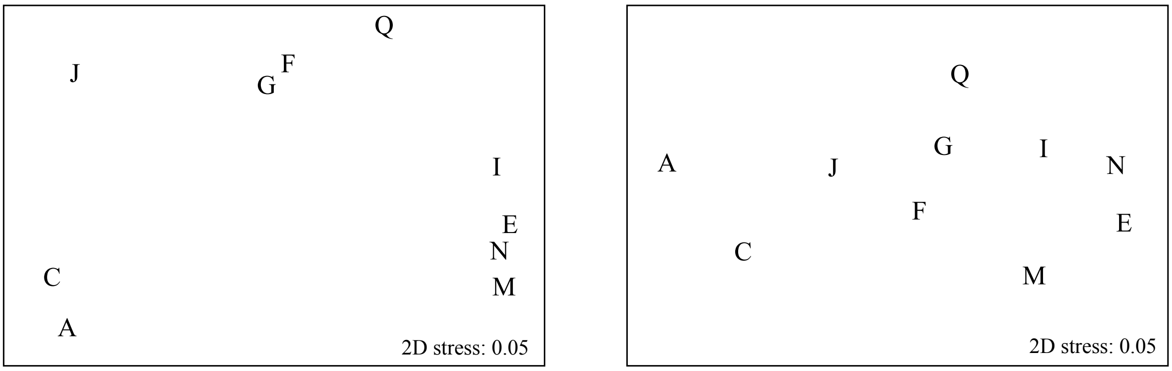



(b) Autumn 2005; p=0.1%, ρ=0.886

(c) Winter 2005; p=0.2%, ρ=0.816


(d) Spring 2005; p=0.1%, ρ=0.818

(e) Summer 2006; p=0.1%, ρ=0.775


(f) Winter 2006; p=0.1%, ρ=0.830

(g) Summer 2007; p=0.1%, ρ=0.849

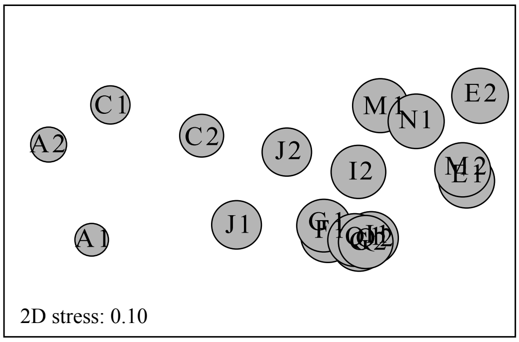
Figure 5.1.2.3: MDS ordination plots constructed from the averages at each habitat type in the Swan Estuary of their (a) enduring environmental measurements and (b-g) fish faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the fish faunal data are also provided for each season.

2005), 0.749 (winter 2005), 0.800 (spring 2005), 0.676 (summer 2006), 0.566 (winter 2006) and 0.662 (summer 2007).

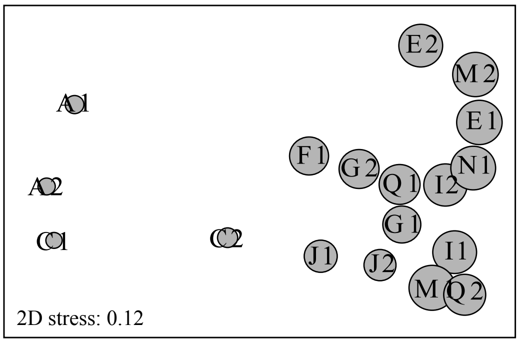
BIOENV was then used to ascertain whether the correlation between the complementary fish and water quality matrices could be improved by employing only data for particular subsets of water quality variables rather than the full suite. Note that these analyses were carried out using the averages of data collected at each representative site rather than habitat type, in order to maximise the number of samples in the reference (fish) matrices and thus minimise the likelihood of BIOENV finding a subset of water quality variables that provided a good match with those references by chance. For comparability, it should also be noted that, when the RELATE routine was used to match the complementary fish and water quality matrices constructed from the averages recorded at each site, the significance and correlation values were almost identical to those obtained above when habitat averages were employed, except for during winter and spring 2005, *i.e.* p=0.1%, ρ=0.588 and 0.696, respectively. BIOENV demonstrated that, in all seasons except summer 2006 and summer 2007, a significant (p=1%) and better correlation was obtained with the fish matrices when only salinity data were employed in the complementary water quality matrices, *i.e.* ρ=0.667 (winter 2006) - 0.874 (autumn 2005; Fig. 5.1.2.4). BIOENV also detected a significant (p=1%) and slightly better correlation between the fish and water quality matrices in summer 2006, but only when both salinity and temperature were used, *i.e.* ρ=0.702 (Fig. 5.1.2.4d, e). Dissolved oxygen data alone provided the best match with the complementary fish faunal matrix in summer 2007, but the improvement in the associated correlation value from when employing all water quality variables was negligible, *i.e.* ρ=0.674 (Fig. 5.1.2.4g).

The relationships between the spatial patterns exhibited by the composition of the fish assemblages and the magnitude of the water quality parameter(s) selected by the BIOENV procedure are illustrated, for each sampling occasion, by the MDS and associated bubble plots shown in Fig. 5.1.2.4. The pronounced difference between the ichthyofaunal compositions of sites representing the riverine habitats A and C *vs* those throughout the rest of the estuary in winter and spring 2005 and, to a lesser extent, winter 2006, typically mirrored the markedly lower salinities recorded at those former two habitats in those seasons (Fig. 5.1.2.4b, c and f, respectively). Moreover, sites representing the channel habitats E, M and N and the lower basin habitat I, which generally lay on the opposite side of the MDS plot to those from A and C and thus had notably different fish compositions, had the greatest salinities in the above seasons. However, differences in the magnitude of salinity sometimes did not clearly explain the spatial pattern in ichthyofaunal composition during the above sampling occasions. For instance, whereas

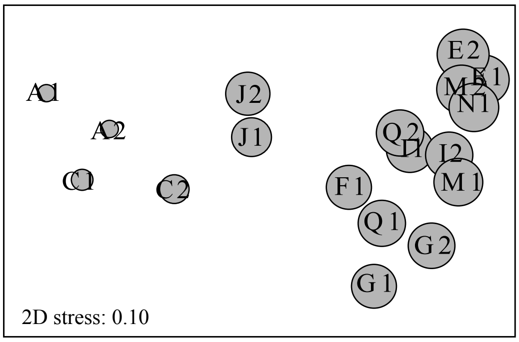
(a) Autumn 2005; p=1%, ρ=0.874



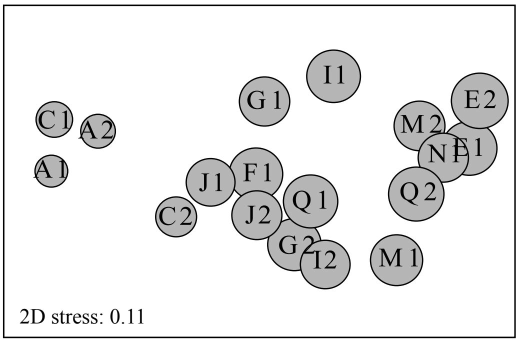
(b) Winter 2005; p=1%, ρ=0.696



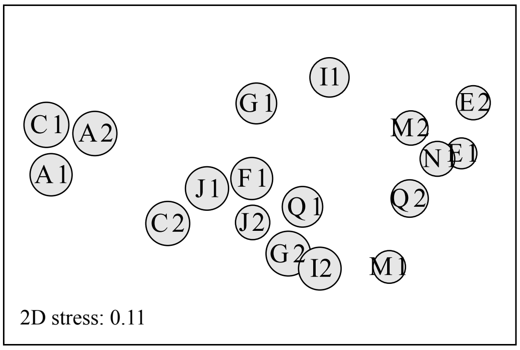
(c) Spring 2005; p=1%, ρ=0.828



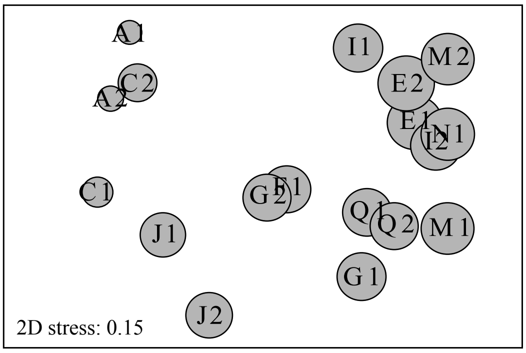
(d) Summer 2006; p=1%, ρ=0.702



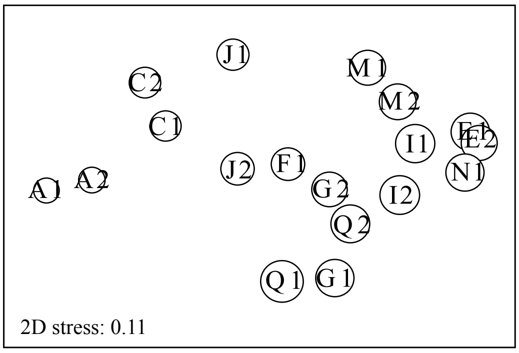
(e) Summer 2006; p=1%, ρ=0.702



(f) Winter 2006; p=1%, ρ=0.667



(g) Summer 2007; p=1%, ρ=0.674



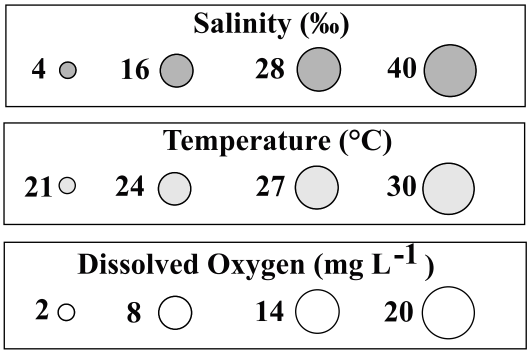


Figure 5.1.2.4: MDS ordination plots derived from the average fish faunal composition recorded at each site in the Swan Estuary in a particular sampling season. The magnitude of those water quality variables selected by the BIOENV routine when one of the matrices constructed from the above faunal data was matched with that constructed from the complementary water quality data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

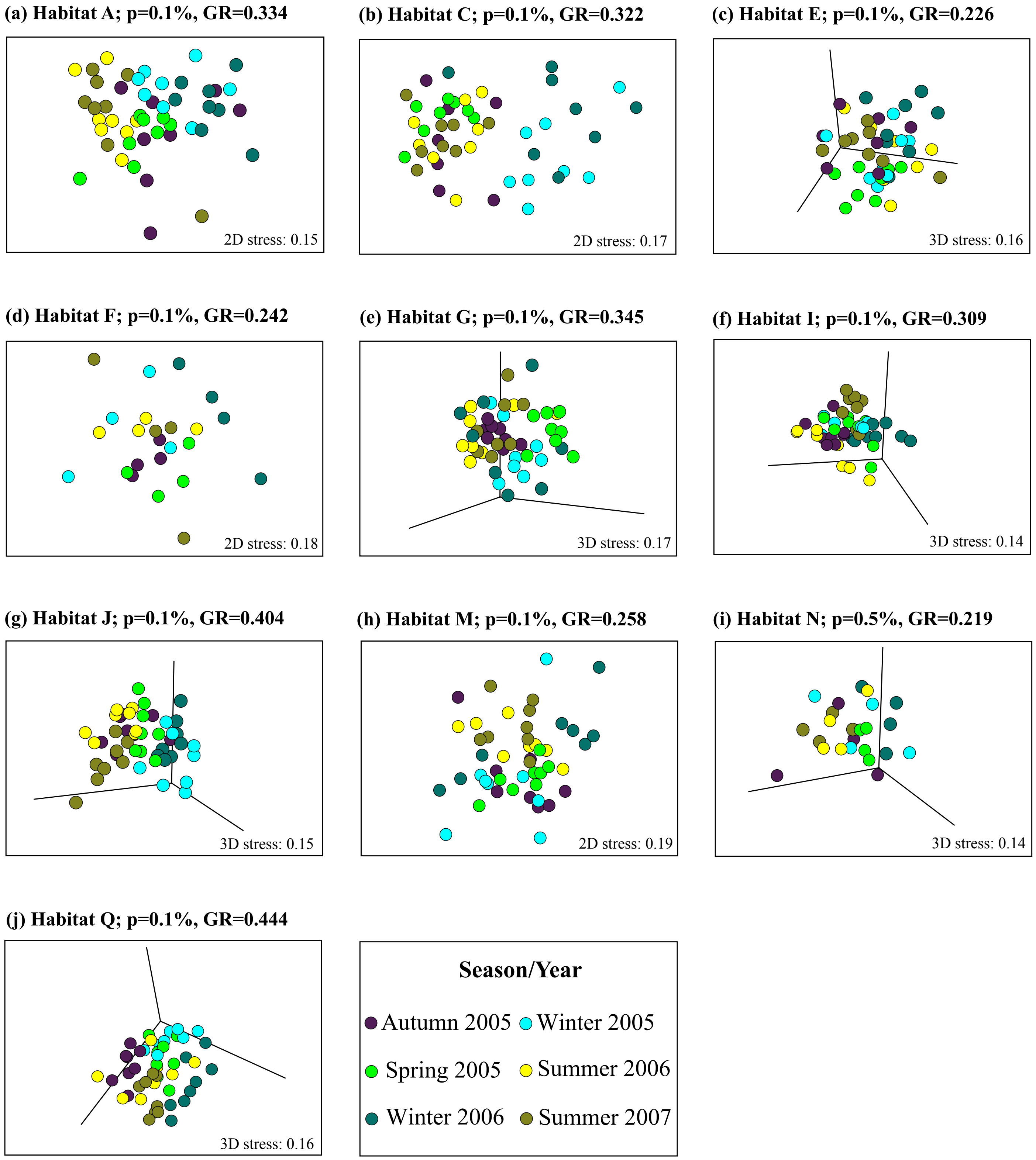
the average salinity at site C2 was similar to that at the other sites in the upper estuary during winter 2005, its ichthyofaunal composition was more similar to those of sites representing basin habitats than to those representing upper estuary habitats (Fig. 5.1.2.4b). Furthermore, while sites A2 and C2 clearly had very similar ichthyofaunal compositions in winter 2006, their average salinities were conspicuously different (Fig. 5.1.2.4f).

The more gradational shifts in ichthyofaunal composition from riverine to channel sites that were evident on the MDS plots constructed from data recorded in autumn 2005 and summer 2006, generally matched the trend of increasing salinities from the upper to lower reaches in those seasons (Fig. 5.1.2.4a and d, respectively). The same was also true of water temperature in the latter season, with the exception that the magnitude of this water quality variable decreased from the upper to lower estuary (Fig. 5.1.2.4e). However, there were also several examples of where the relative differences in fish faunal composition between sites in these seasons was clearly not explained by salinity and/or water temperature. For instance, whereas sites representing habitats J and M had similar mean salinities in summer 2006, their ichthyofaunal compositions were considerably different (Fig. 5.1.2.4d). The gradational shift in fish assemblage composition from the upper to lower estuary in summer 2007 was partly explained by the concomitant increase in dissolved oxygen concentration. However, the greatest average dissolved oxygen concentration was recorded at the shallow basin site Q1, and yet the fish composition at this site was clearly intermediate between those found at the upper *vs* lower estuary sites (Fig. 5.1.2.4g).

5.1.2.5 Composition of fish assemblages among seasons

One-way ANOSIM tests for sampling season, carried out separately for the fish faunal data recorded at each habitat type, demonstrated that, while significant differences were detected in each case (0.1-0.5%), the overall extents of these temporal differences in ichthyofaunal composition were generally less than those for habitat type. Thus, whereas the Global R-statistic for differences among habitat types in each season ranged between 0.435 and 0.713, those for differences among sampling occasions at each habitat type ranged between 0.219 and 0.444 (Fig. 5.1.2.5). The relatively small temporal differences in ichthyofaunal composition are also illustrated on the associated MDS plots shown in Fig. 5.1.2.5 by the fact that, at many habitats, samples from each of the different seasons often did not tend to form discrete groups.

The greatest seasonal differences overall were detected at habitat Q in the middle reaches of the main basin and habitat J in the small basin at the foot of the Swan River (Global R=0.444 and 0.404, respectively). All pairwise comparisons were significant in each case, except for



(a) Habitat A; p=0.1%, GR=0.334

(b) Habitat C; p=0.1%, GR=0.322

(c) Habitat E; p=0.1%, GR=0.226

(d) Habitat F; p=0.1%, GR=0.242

(e) Habitat G; p=0.1%, GR=0.345

(f) Habitat I; p=0.1%, GR=0.309

(g) Habitat J; p=0.1%, GR=0.404

(h) Habitat M; p=0.1%, GR=0.258

(i) Habitat N; p=0.5%, GR=0.219

(j) Habitat Q; p=0.1%, GR=0.444

Figure 5.1.2.5: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample in each sampling season at habitat (a) A, (b) C, (c) E, (d) F, (e) G, (f) I, (g) J, (h) M, (i) N and (j) Q in the Swan Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

spring 2005 *vs* winter 2005 at habitat Q and summer 2006 *vs* summer 2007, summer 2006 *vs* spring 2005 and winter 2005 *vs* winter 2006 at habitat J. The seasonal differences at habitat Q were greatest between autumn 2005 and winter 2006 (R=0.741), which is illustrated by the fact that their representative samples were located on opposite sides of the associated MDS plot (Fig. 5.1.2.5j). Furthermore, the other comparisons between autumn 2005, whose representative samples formed a relatively tight group on the MDS plot, and the remaining seasons, were also relatively high (R=0.526-0.670). SIMPER showed that the fish fauna in this season was characterised by particularly consistent and abundant catches of *T. pleurogramma* and *A. mugiloides* and, to a lesser extent, *F. lateralis*. Each of these species was caught inconsistently and/or in comparatively low numbers in winter 2006, while the reverse was true of *L. presbyteroides*. The prevalence of *T. pleurogramma* and *A. mugiloides* in autumn 2005 was also partly responsible for distinguishing the ichthyofauna in this season from those in all others, in conjunction with more abundant catches of particular species in several other seasons, such as *A. elongata* and *L. presbyteroides* in both summers and *F. lateralis* in spring 2005. Differences in fish composition were also pronounced between summer 2007 and winter 2005 at this habitat (R=0.714), which was primarily due to relatively large and consistent catches of *A. elongata, L. presbyteroides, A. mugiloides, T. pleurogramma* and *P. punctatus* in the first of these seasons and *F. lateralis* in the latter. With respect to habitat J, samples from both summers were located on the opposite side of the associated MDS plot to those from both winters, with samples from spring and autumn 2005 distributed in between (Fig. 5.1.2.5j). This was also reflected by the magnitude of the pairwise R-statistics, which were greatest for the comparisons between summer and winter samples (*i.e.* R=0.583-0.703). One-way SIMPER demonstrated that the species most responsible for these temporal differences were *A. butcheri, A. rueppellii, A. mugiloides* and *P. punctatus*, which were always more abundant in summer than winter, and *T. pleurogramma*, for which the reverse was true. Furthermore, *A. caudavittatus* and *A. forsteri* were consistently more abundant in summer 2006 than both winters.

Moderate to low seasonal differences in the composition of the nearshore fish fauna were detected at the riverine habitats A and C and habitats G and I located in the upper and lower reaches of the main basin, respectively, *i.e.* Global R=0.309-0.345. In the case of the uppermost habitat A, the ichthyofaunal compositions recorded in both summers were particularly distinct from those in winter 2006 (p=0.1%, R=0.707-0.824) and, to a lesser extent, winter 2005 (p=0.1-0.2%, R=0.454-0.461), which was illustrated by the relative locations of these groups of samples on the associated MDS plot (Fig. 5.1.2.5a). This was due mainly to *P. olorum, A. butcheri, L. wallacei,* and *A. suppositus* being more prevalent in both summers than winters. Samples from autumn and spring generally lay between those for summer and winter, but those representing the first of these seasons were particularly widely dispersed (Fig. 5.1.2.5a), which was reflected by the fact that its composition did not differ significantly from that recorded in either winter or spring 2005, and the only species that was recorded with any relative consistency was *L. wallacei*. The samples recorded during both winters at habitat C formed a dispersed but discrete group that lay to the right of an intermingled group containing samples from all other seasons (Fig. 5.1.2.5b). Accordingly, ANOSIM demonstrated that, while the compositions of the catches found in both winters differed significantly from that in every other season (p=0.1-0.4%, R=0.342-0.719), either no or very small significant differences (*i.e.* p=2.1-4.6%, R <0.176) were detected between the ichthyofaunal compositions recorded in the remaining pairs of seasons. SIMPER reflected the highly dispersed nature of the group containing samples from both winters by the fact that their average similarities were both relatively low and that no species were caught in any particular abundance or with any relative consistency. However, *L. wallacei* and *M. cephalus* were among the most prevalent species in both of these seasons, in addition to *P. olorum* in winter 2005 and *Hyperlophus vittatus* in winter 2006. In contrast, the fish assemblages in the remaining seasons at this habitat were mainly characterised by *A. butcheri, A. caudavittatus* and *P. punctatus*.

The seasonal differences in ichthyofaunal composition at habitat G in the upper reaches of the main basin were greatest for spring 2005 *vs* both autumn 2005 and summer 2006 (p=0.2%, R=0.761 and 0.718, respectively). Most samples from the latter two seasons were located on the opposite side of the associated MDS plot from those representing spring and, while samples from autumn formed a relatively tight group, those from summer were more highly dispersed (Fig. 5.1.2.5e). SIMPER demonstrated that these differences were due mainly to more abundant and consistent catches of *T. pleurogramma* and *A. mugiloides* in autumn and summer than in spring, while the reverse was true for *P. punctatus*. *Pelates octolineatus* was also found consistently in summer, but was not recorded in spring. ANOSIM showed that all remaining pairwise comparisons between seasons were significant at this habitat (p=0.1-4%; R=0.207-0.493), except for that between the two summers and, interestingly, that between summer 2007 and winter 2006. Samples for the latter season were particularly widely dispersed on the MDS plot (Fig. 5.1.2.5e), which was also reflected by SIMPER, in that the average similarity for that season was notably low and the three species that comprised 90% of the catch in that season (*i.e. A. mugiloides, T. pleurogramma* and *L. presbyteroides*) were not recorded consistently. The greatest seasonal differences in fish assemblage composition at habitat I in the lower basin occurred between both summers *vs* winter 2006, summer 2006 *vs* summer 2007 and autumn

2005 *vs* summer 2007 (p=0.1-0.2%, R=0.498-0.561), which was illustrated by the fact that samples representing each of these seasons tended form relatively tight and/or largely discrete groups on the associated MDS plot (Fig. 5.1.2.5f). The only species that was caught more consistently in both summers than in winter 2006 was *T. pleurogramma*, while the remaining species that were more prevalent in summer 2006 (*i.e. S. burrus*, *A. muglioides* and *A. forsteri*), differed from those that predominated in summer 2007 (*i.e. P. octolineatus, F. lateralis, A. rueppellii* and *A. elongata*). Apart from *F. lateralis*, no other species was recorded in consistently greater numbers in winter 2006 than either summer. The relatively large differences in ichthyofaunal composition between autumn 2005 and summer 2007 were attributable largely to greater catches of *T. pleurogramma* and *A. mugiloides* in the former season and of *P. octolineatus, F. lateralis*, *A. rueppellii* and *A. elongata* in the latter.

The extent of seasonal differences in ichthyofaunal composition at channel habitats E, M and N and habitat F in the main basin were low (*i.e.* Global R=0.219-0.258), which was reflected by the high degree of intermingling of samples from different seasons on the associated MDS plots (Fig. 5.1.2.5c, d, h and i) and the fact that a considerable number of the ANOSIM pairwise comparisons were not significant. Among the greatest seasonal differences in the fish faunal composition at habitats E, M and N occurred between spring 2005 and summer 2007 (R=0.485-0.604, p=0.1-2.9%). In all cases, this was partly attributable to considerably greater and more consistent catches of *T. pleurogramma* in spring. *Leptatherina presbyteroides* was also more prevalent in this season at E and N, while the reverse was true at M, and *A. rueppellii* was caught in greater numbers in summer 2007 at both E and M. Moreover, several other species were considerably more prevalent in one of these seasons at particular channel habitats, such as *M. freycineti* and *S. argus* in spring 2005 at E and N, respectively, *A. ogilbyi* and *A. butcheri* in summer 2007 at M and *H. semifasciata* in summer 2007 at N. Other notable seasonal differences in ichthyofaunal composition occurred between spring 2005 and winter 2006 at habitat E (p=0.1%, R=0.460), which were due mainly to greater catches of *T. pleurogramma, M. freycineti, S. argus* and *F. lateralis* in the former season, autumn 2005 and summer 2007 at habitat M (p=0.2%, R=0.530), attributable largely to a greater prevalence of *A. ogilbyi, A. butcheri, L. presbyteroides* and *A. rueppellii* in summer and of *G. marmoratus, T. pleurogramma* and *F. lateralis* in autumn, and summer 2007 and winter 2006 at habitat N (p=2.9%, R=0.615), at which greater numbers of *H. semifasciata* and *T. pleurogramma* were caught in summer and *F. lateralis, G. marmoratus* and *L. presbyteroides* were caught in winter. The greatest seasonal differences at habitat F occurred between autumn 2005 and both summer and winter 2006, and between spring 2005 and winter 2006 (p=2.9%, R=0.635-0.656). Greater catches of both *T. pleurogramma* and *P. punctatus* in autumn partly contributed to the differences in fish faunal composition between this season and both summer and winter 2006, as did notably greater and consistent catches of *A. butcheri*, *A. mugiloides* and *P. octolineatus* in summer and *L. presbyteroides* and *A. mugiloides* in winter. The prevalence of the latter two species in winter 2006 also helped distinguished the ichthyofauna in this season from that found in spring 2005, as did greater catches of *T. pleurogramma* and *P. punctatus* in the latter season.

5.1.3 Benthic macroinvertebrate assemblages

5.1.3.1 Species mean density at each habitat type

Sampling of the benthic macroinvertebrate assemblages at seven habitat types throughout the Swan Estuary in 2005 yielded 314 944 individuals, *i.e.* after the number in each sample was adjusted to that in 0.1 m^2 and summed. These individuals represented 69 species and comprised eight phyla, namely Annelida, Arthropoda, Mollusca, Sipuncula, Nematoda, Platyhelminthes, Cnidaria and Nemertea. The Polychaeta, Crustacea and Bivalvia were the most speciose classes, and were represented by 32, 12 and 13 species, respectively (Table 5.1.3.1).

The greatest number of species was recorded at the channel habitat M (47), which was far greater than that found at the next most speciose habitat, C, located in the upper reaches (29). The least number of species was recorded at the uppermost habitat A (21), followed closely by that at habitat type J located at the foot of the Swan River and habitats F and I in the upper and lower reaches, respectively of the main basin (22; Table 5.1.3.1). The greatest mean density of benthic macroinvertebrates was recorded at habitat G in the middle to upper reaches of the main basin (2033), followed by that at habitat I in the lower reaches of that region (1687). By far the lowest mean density was recorded at the uppermost habitat A (457; Table 5.1.3.1).

The species assemblages at the upper estuary habitats A and C were both dominated by the polychaete *Ceratonereis aequisetis* and the bivalve *Arthritica semen.* However, whereas *C. aequisetis* contributed *ca* 15% to the total number of individuals at habitat A, it represented only 9.7% of that at C, while the opposite trend was true for *A. semen*. Furthermore, the second most abundant species at C, the amphipod *Paracorophium excavatum*, was not abundant at habitat type A (*i.e.* it contributed <5% to the total number of individuals), whereas the polychaete *Leitoscoloplos normalis,* which was the second most abundant at A, was not abundant at C. Differences between the species assemblages at these two upper estuary habitats were further exemplified by the fact that 11 of the species found at C were never recorded at A (Table 5.1.3.1).

Table 5.1.3.1: Mean density (M), standard deviation (SD), percentage contribution to the overall mean density (%) and the rank by density (R) of the benthic macroinvertebrate taxa recorded at each habitat type sampled in the Swan Estuary in each season in 2005. Abundant taxa at each habitat type (*i.e.* those that contribute >5% to the overall mean density) are highlighted in grey. Each taxon has been assigned to its respective phyla (P) and class (C) (*i.e.* A, Annelida, Ar-Arthropoda, Mo-Mollusca, S-Sipuncula, Pl-Platyhelminthes, N-Nematoda, Ne-Nemertea, P-Polychaeta, O-Oligochaeta, B-Bivalvia, G-Gastropoda, C-Crustacea, I-Insecta, U-Unknown). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of individuals in each sample had been adjusted to that in 0.1 m^2 and summed) are also provided for each habitat type.

		Habitat type A				Habitat type C				Habitat type F				Habitat type G			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Ceratonereis aequisetis	A/P	136.5	120.2	14.9	1	274.5	263.1	9.7	3	205.2	130.6	9.0	2	323.7	248.6	7.9	3
Leitoscoloplos normalis	A/P	90.6	102.1	9.9	2	65.1	65.2	2.3	6	104.2	117.9	4.5	5	88.0	87.8	2.2	7
Arthritica semen	Mo/B	68.0	77.4	7.4	3	344.5	540.4	12.2	1	39.6	58.4	1.7	8	108.6	116.1	2.7	6
Desdemona ornata	A/P	31.8	146.0	3.5	4	5.2	18.9	0.2	14								
Grandidierella propodentata	Ar/C	22.4	105.9	2.4	5	63.8	80.7	2.3	7	156.3	245.7	6.8	3	268.8	359.3	6.6	5
Boccardiella limnicola	A/P	19.3	45.3	2.1	6	25.5	36.8	0.9	11					0.8	2.8	<0.1	19
Musculista senhausia	Mo/B	18.5	39.3	2.0	7	80.2	291.8	2.8	5								
Corophium minor	Ar/C	17.4	74.0	1.9	8	104.2	218.7	3.7	4	149.5	176.1	6.5	4	301.8	316.0	7.4	4
Oligochaete spp.	A/O	17.4	91.3	1.9	8	33.6	154.0	1.2	9	6.8	24.0	0.3	11	362.2	875.2	8.9	1
Paracorophium excavatum	Ar/C	10.2	22.9	1.1	10	293.5	406.9	10.4	2								
Capitella capitata	A/P	6.3	16.5	0.7	11	56.0	76.7	2.0	8	324.5	294.9	14.2	1	361.5	271.9	8.9	2
Sanguinolaria biradiata	Mo/B	6.0	34.7	0.7	12	31.5	72.0	1.1	10	62.0	79.1	2.7	6	71.1	92.6	1.7	8
Pseudopolydora kempi	A/P	5.2	19.0	0.6	13	3.6	9.6	0.1	17	44.8	73.3	2.0	7	54.4	67.6	1.3	10
Paratanytarsus grimmii	Ar/I	3.1	15.0	0.3	14	0.3	1.6	<0.1	23								
Polydora sp.2	A/P	1.0	3.9	0.1	15												
Prionospio cirrifera	A/P	0.8	3.6	0.1	16	7.6	22.7	0.3	12	15.1	45.4	0.7	9	0.5	2.3	<0.1	20
Manerogenia maneroo	Ar/C	0.8	4.9	0.1	16	0.3	1.6	<0.1	23	0.5	2.3	<0.1	20				
Caraziella victoriensis	A/P	0.5	3.3	0.1	18	0.3	1.6	<0.1	23					3.1	9.5	0.1	13
Velacumantus australis	Mo/G	0.5	3.3	0.1	18					6.3	13.3	0.3	12	1.0	3.2	<0.1	17
Spisula trigonella	Mo/B	0.3	1.6	<0.1	20	4.7	18.7	0.2	15	1.6	5.1	0.1	16	2.9	12.0	0.1	14
Caraziella sp.2	A/P	0.3	1.6	<0.1	20												
Paranthurid sp.2	Ar/C					7.6	39.5	0.3	12					0.3	1.6	<0.1	23
Ficopomatus sp.	A/P					4.2	26.4	0.1	16								
Marphysa sanguinea	A/P					1.8	5.2	0.1	18					0.5	2.3	<0.1	20
Amphipod sp.34	Ar/C					1.3	5.9	<0.1	19								
Platyhelminthes sp.	Pl/U					0.8	4.9	<0.1	20	1.0	4.7	<0.1	18				
Microspio sp.	A/P					0.5	3.3	<0.1	21								
Orbiniella sp.	A/P					0.5	3.3	<0.1	21								

Species name	P/C	Habitat type A				Habitat type C				Habitat type F				Habitat type G			
		M	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Tanais dulongii	Ar/C					0.3	1.6	<0.1	23	4.7	15.3	0.2	14	5.2	32.9	0.1	12
Nassarius sp.	Mo/G					0.3	1.6	<0.1	23	1.0	4.7	<0.1	18	1.0	3.2	<0.1	17
Polydora socialis	A/P					0.3	1.6	<0.1	23								
Bivalve sp.3	M/B					0.3	1.6	<0.1	23								
Sphaeromatid sp.1	Ar/C									7.8	32.6	0.3	10				
Nematode sp.	N/U									5.7	19.0	0.3	13	66.7	179.5	1.6	9
Tellina deltoidalis	Mo/B									2.6	7.5	0.1	15				
Venerupis crenata	M/B									1.6	3.8	0.1	16				
Australonereis elhersii	A/P									0.5	2.3	<0.1	20	5.7	11.1	0.1	11
Apistobranchid sp.	A/P									0.5	2.3	<0.1	20				
Bivalve sp.1	Mo/B													2.6	16.5	0.1	15
Bivalve sp.4	Mo/B													1.8	11.5	<0.1	16
Sipunculan sp.1	S/U													0.5	2.3	<0.1	20
Gastrosaccus sorrentoensis	Ar/C													0.3	1.6	<0.1	23
Decamastus sp.	A/P													0.3	1.6	<0.1	23
Number of species			**21**				**29**				**22**				**25**		
Total mean density			**457**				**1 412**				**1 142**				**2 033**		
Number of samples			**40**				**40**				**20**				**40**		
Total number of fauna			**18 276**				**56 492**				**22 836**				**81 332**		

Species name	P/C	Habitat type I				Habitat type J				Habitat type M			
		M	SD	%	R	M	SD	%	R	M	SD	%	R
Ceratonereis aquisetis	A/P	152.6	360.5	4.5	6	209.6	218.9	9.4	1	71.1	123.5	2.4	8
Leitoscoloplos normalis	A/P	163.0	303.2	4.8	5	134.6	135.4	6.1	4	113.5	138.2	3.9	6
Arthritica semen	M/B	39.1	89.9	1.2	9	79.9	158.8	3.6	6	22.4	103.2	0.8	10
Desdemona ornata	A/P					178.4	790.2	8.0	2				
Grandidierella propodentata	Ar/C	249.0	454.2	7.4	3	175.5	203.7	7.9	3	239.3	499.4	8.2	2
Boccardiella limnicola	A/P					9.1	15.9	0.4	11	0.8	4.9	<0.1	27
Musculista senhousia	M/B	0.5	2.3	<0.1	17	2.1	6.3	0.1	18				
Corophium minor	Ar/C	45.8	76.9	1.4	8	85.9	223.7	3.9	5	170.6	285.8	5.9	3
Oligochaete spp.	A/O	114.1	359.7	3.4	7	4.7	11.5	0.2	14	169.8	555.5	5.8	4
Paracorophium excavatum	Ar/C					8.3	38.1	0.4	12				
Capitella capitata	A/P	412.0	379.0	12.2	1	36.7	63.2	1.7	9	118.5	152.0	4.1	5
Sanguinolaria biradiata	M/B	292.7	331.9	8.7	2	52.1	65.2	2.3	8	112.2	173.2	3.9	7
Pseudopolydora kempi	A/P	168.8	196.4	5.0	4	76.0	155.0	3.4	7	330.5	404.0	11.4	1
Paratanytarsus grimmii	Ar/I												
Polydora sp.2	A/P												
Prionospio cirrifera	A/P	0.5	2.3	<0.1	17	3.6	9.9	0.2	16	2.1	5.9	0.1	17
Manerogenia maneroo	Ar/C												
Caraziella victoriensis	A/P	1.6	3.8	<0.1	14	3.4	10.1	0.2	17	11.5	23.6	0.4	13
Velacumantus australis	M/G	7.3	13.6	0.2	11	0.5	3.3	<0.1	21	2.1	6.8	0.1	17
Spisula trigonella	M/B	0.5	2.3	<0.1	17	4.7	10.3	0.2	14	2.1	6.3	0.1	17
Caraziella sp.2	A/P												
Paranthurid sp.2	Ar/C					6.5	18.5	0.3	13	0.5	2.3	<0.1	30
Ficopomatus sp.	A/P												
Marphysa sanguinea	A/P					2.1	4.2	0.1	18	1.0	6.6	<0.1	22
Amphipod sp.34	Ar/C												
Platyhelminthes sp.	Pl/U												
Microspio sp.	A/P									1.0	5.2	<0.1	22
Orbiniella sp.	A/P												
Tanais dulongii	Ar/C	1.6	7.0	<0.1	14					14.6	24.6	0.5	11
Nassarius sp.	M/G	3.6	6.1	0.1	13	1.0	3.2	<0.1	20	2.9	8.5	0.1	16
Polydora socialis	A/P									0.3	1.6	<0.1	34
Bivalve sp.3	M/B												
Sphaeromatid sp.1	Ar/C									0.3	1.6	<0.1	34
Nematode sp.	N/U	4.2	11.4	0.1	12					6.0	21.0	0.2	15
Tellina deltoidalis	M/B												
Venerupis crenata	M/B												
Australonereis elhersii	A/P	27.6	41.8	0.8	10	31.5	62.3	1.4	10	26.0	44.7	0.9	9
Apistobranchid sp.	A/P												

		Habitat type I				Habitat type J				Habitat type M			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Bivalve sp.1	M/B												
Bivalve sp.4	M/B												
Sipunculan sp.5	S/U	1.0	4.7	<0.1	16					0.5	3.3	<0.1	30
Gastrosaccus sorrentoensis	Ar/C									1.0	5.2	<0.1	22
Decamastus sp.	A/P												
Fusinus sp.	M/G	0.5	2.3	<0.1	17								
Laturnula sp.	M/B	0.5	2.3	<0.1	17								
Sipunculan sp.3	S/U	0.5	2.3	<0.1	17								
Sphaeromatid sp.2	Ar/C					0.3	1.6	<0.1	22				
Heteromastus sp.	A/P									11.7	23.3	0.4	12
Syllid sp.7	A/P									6.3	25.5	0.2	14
Nephtys graverii	A/P									1.8	5.7	0.1	20
Paranthurid sp.3	Ar/C									1.6	7.3	0.1	21
Phyllodoce sp.	A/P									1.0	3.9	<0.1	22
Bivalve sp.2	M/B									1.0	6.6	<0.1	22
Rhyncospio sp.	A/P									0.8	4.9	<0.1	27
Sipunculan sp.1	S/U									0.8	4.9	<0.1	27
Pseudopolydora sp.	A/P									0.5	3.3	<0.1	30
Nemertean sp.	Ne/U									0.5	3.3	<0.1	30
Lumbrinerid sp.	A/P									0.3	1.6	<0.1	34
Polydorella sp.	A/P									0.3	1.6	<0.1	34
Brania sp.	A/P									0.3	1.6	<0.1	34
Syllid sp.8	A/P									0.3	1.6	<0.1	34
Syllid sp.9	A/P									0.3	1.6	<0.1	34
Magelona sp.	A/P									0.3	1.6	<0.1	34
Maldanis sp.	A/P									0.3	1.6	<0.1	34
Cirriformia filigera	A/P									0.3	1.6	<0.1	34
Bivalve sp.5	M/B									0.3	1.6	<0.1	34
Ostracod sp.3	Ar/C									0.3	1.6	<0.1	34
Tanaid sp.	Ar/C									0.3	1.6	<0.1	34
Diogenid sp.	Ar/C									0.3	1.6	<0.1	34
Number of species		**22**				**22**				**47**			
Total mean density		**1 687**				**1 107**				**1 450**			
Number of samples		**20**				**40**				**40**			
Total number of fauna		**33 740**				**44 260**				**58 008**			

The species assemblages at habitat types F, G, I and J, located in different regions of the middle estuary, shared some similarities, but also exhibited pronounced differences. Thus, *Grandidierella propodentata* was abundant and ranked either third or fifth in each of these habitats, *Capitella capitata* ranked first or second at all habitats except J, at which it was not abundant, and *C. aquisetis* ranked first, second and third at habitats J, F and G, respectively, but was not abundant at habitat I in the lower reaches of the basin (Table 5.1.3.1). However, Oligochaete spp., which ranked first at habitat G, was not abundant at any other middle estuary habitat. Moreover, the bivalve *Sanguinolaria biradiata* and the polychaete *Pseudopolydora kempi* were only abundant at habitat I, at which they ranked second and fourth, respectively, while the same was true of the polychaetes *Desdemona ornata* and *L. normalis* at habitat J. The amphipod *Corophium minor* was also abundant at habitats F and G, but was not abundant at either I or J. Fifteen additional species were recorded in one or more of the above basin habitats that were never recorded in at least one of the upper estuary habitats, while the reverse was true for six other species (Table 5.1.3.1).

The assemblage at habitat M in the channel of the estuary, which contained 22 species never found at any other habitat, was dominated by *P. kempi* and *G. propodentata,* with the percentage contribution and mean density of the former species being considerably greater than at habitat I, the only other habitat at which it was abundant. *Corophium minor* and Oligochaete spp. were also abundant at habitat M, the latter of which had a lower contribution and mean density at this habitat than G, at which it was most abundant (Table 5.1.3.1).

5.1.3.2 Spatial and temporal differences in mean species richness, density and taxonomic diversity

The replicate data for the number of species, density and taxonomic distinctness of benthic macroinvertebrates collected seasonally throughout the Swan Estuary during 2005 were each subjected to a preliminary three-way PERMANOVA to determine whether habitat type or their representative sites was the most appropriate level for examining spatial differences within each of these dependent variables. These tests showed that mean number of species was not significantly influenced by site or the site x season interaction, and thus these data were subsequently subjected to a habitat x season PERMANOVA to more fully elucidate the spatio-temporal differences. In contrast, the influence of site and/or the site x season interaction was significant ($p=0.001$) and relatively important for the latter two dependent variables, and thus they were each then subjected to a site x season PERMANOVA.

The mean number of species differed significantly among habitat types, seasons and the interaction between these factors and, based on a comparison of their associated components of variation, the relative importance of each of these terms was similar (Table 5.1.3.2). Mean density and taxonomic distinctness of benthic macroinvertebrates differed significantly among sites, seasons and, in the case of density, also the site x season interaction. The influence of the interaction term was greatest for mean density, followed by that for site, while the components of variation were similar for both site and season in the case of taxonomic distinctness (Table 5.1.3.2). However, in all cases, the greatest overall variability was attributable to the error term, which is reflected by the relatively large confidence intervals associated with the means plotted in Fig. 5.1.3.1.

In each season, but particularly winter and spring, the mean number of species was least at the uppermost habitat A (*ca* 1.5-5 species), except in autumn where it was considerably lower at the channel habitat type M (*ca* 2 species) than at any other habitat (*ca* 4.5-9 species; Fig. 5.1.3.1a). However, the mean number of species did not tend to be consistently greater at any particular habitat, thus helping to account for the significant interaction term detected for this dependent variable. For example, while the mean number of species was notably greater at C than any other habitat in autumn, it was greatest at F and J in winter and spring, respectively, and greatest at G and M in summer (Fig. 5.1.3.1a). The mean number of species was far lower in summer than in all other seasons at every habitat except M, at which the values recorded in summer and autumn were similarly low. In contrast, the greatest or second greatest mean number of species was found in winter at all habitats. Considerably lower values for this dependent variable were recorded in autumn relative to spring at habitats I, J and M, whereas the opposite was true at C and similar values were recorded in these two seasons at the remaining habitats (Fig. 5.1.3.1a).

The cause of the significant and relatively important site x season interaction for mean density was clearly attributable to the fact that, at all sites except those representing habitat A, at which values were lowest or close to the lowest in every season, there was little tendency for this dependent variable to exhibit consistent spatial or temporal trends (Fig. 5.1.3.1b). Thus, in summer, the greatest mean densities by far were recorded at sites representing habitat G, while in autumn, a pronounced peak was detected at C1. The highest densities were found at G1, J1 and both sites from habitat M in winter, and at sites from habitats G, I and M in spring. Despite the erratic trends in this dependent variable, the lowest values were recorded in either summer or autumn at all habitats (Fig. 5.1.3.1b).

Table 5.1.3.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for a habitat x season PERMANOVA on the number of benthic macroinvertebrate species, and site x season PERMANOVAs on the density and quantitative taxonomic distinctness of benthic macroinvertebrate assemblages recorded throughout the Swan Estuary during each season in 2005. df=degrees of freedom. Significant results are highlighted in bold.

	Number of Species					**Density**					**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects														
Habitat	6	**3.137**	**8.220**	**0.285**	**0.001**									
Season	3	**3.900**	**10.209**	**0.254**	**0.001**	3	**36.428**	**24.670**	**0.763**	**0.001**	**19.872**	**5.227**	**0.518**	**0.003**
Site						11	**15.264**	**10.337**	**0.830**	**0.001**	**10.288**	**2.706**	**0.569**	**0.004**
Two-way Interactions														
Habitat * Season	18	**1.042**	**2.730**	**0.279**	**0.002**									
Season * Site						33	**6.610**	**4.477**	**1.013**	**0.001**	5.300	1.393	0.547	0.101
Residual	212	0.382		0.618		192	1.48		1.215		3.802		1.950	

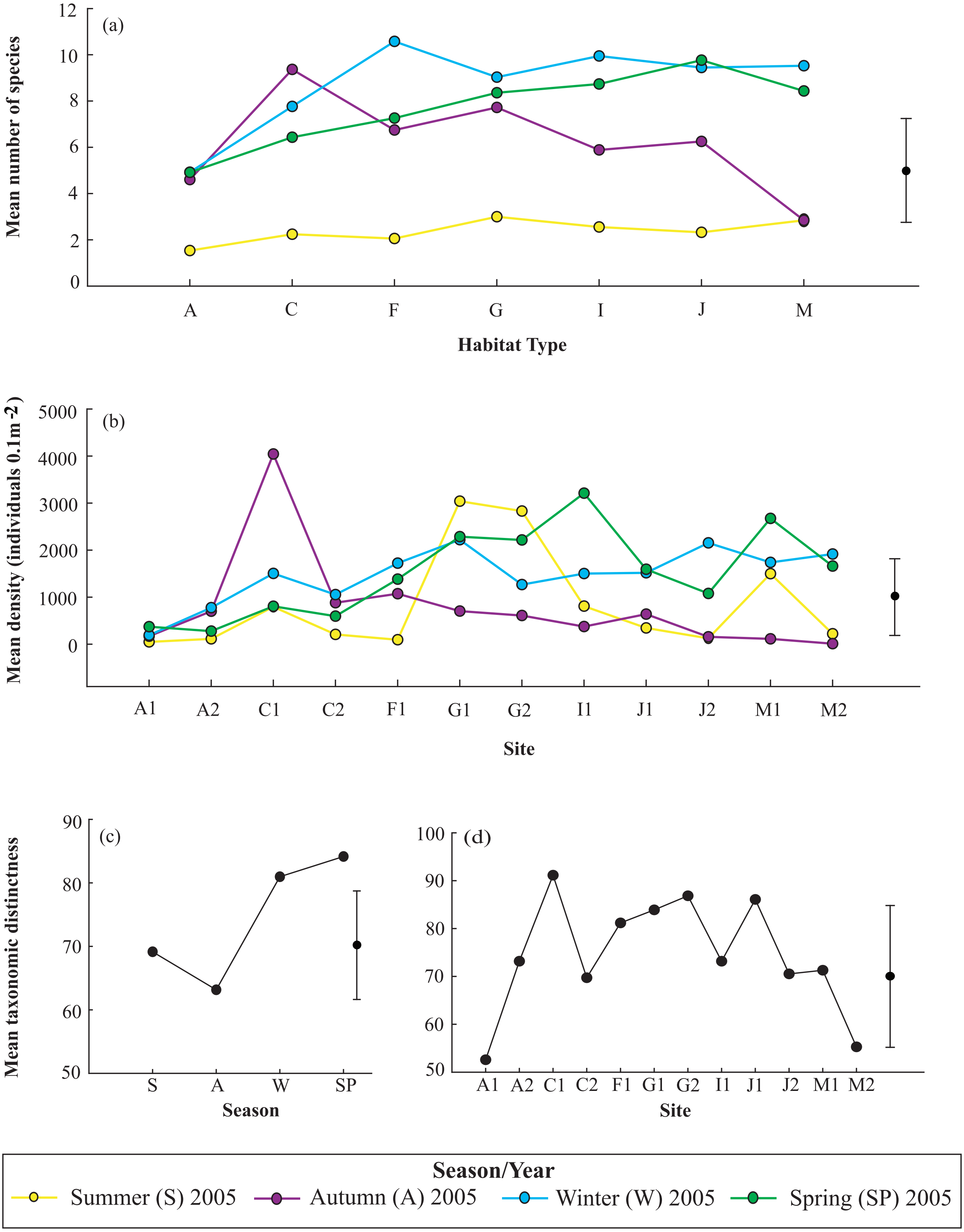


Figure 5.1.3.1: Mean (a) number of species, (b) density and (c-d) quantitative taxonomic distinctness of the benthic macroinvertebrate assemblage recorded at each site/habitat throughout the Swan Estuary in each season in 2005. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

The mean taxonomic distinctness of the benthic macroinvertebrate assemblage was greater in both winter and spring than in summer and particularly autumn (Fig. 5.1.3.1c). By far the least diverse assemblages were found at sites A1 and M2 at opposing ends of the estuary, while the greatest diversity was recorded at C1, F1, G1, G2 and J1 (Fig. 5.1.3.1d).

5.1.3.3 Composition of benthic macroinvertebrate assemblages among habitat types

An initial three-way PERMANOVA was used to ascertain whether the spatial differences in the composition of benthic macroinvertebrate assemblages recorded throughout the Swan Estuary in each season during 2005 were most appropriately examined at the broader habitat type or finer site level. This test showed that each term in the model was significant (p=0.001), but that the relative importance of habitat type was at least 1.5 times greater than that of site or the site x season interaction. Furthermore, one-way ANOSIM tests for site, carried out separately for the data recorded in each season in view of the above significant seasonal main effect and interaction, demonstrated that while there were significant differences between sites assigned to the same habitat type in several cases, the extent of those differences was almost always relatively low, *i.e.* pairwise R-statistics nearly always <0.500. In view of these results, it was considered appropriate in the following analyses to treat the replicate samples collected at each site as representative of their assigned habitat type.

One-way ANOSIM tests for habitat type, performed separately for the data collected in each season, showed that the compositions of the benthic macroinvertebrate assemblages differed significantly among habitat types in each case (p=0.1%) and that the overall extents of those differences were greatest in winter followed by spring (*i.e.* Global R=0.665 and 0.564, respectively) and least in summer (*i.e.* Global R=0.354). Significant differences were detected between almost all pairs of habitats in each season except summer (Table 5.1.3.3). The relative extents of the spatial differences in faunal composition in each season are also illustrated on the MDS ordination plots shown in Fig. 5.1.3.2 by the degree of separation of groups of samples representing different habitats, and the extent of sample dispersion within those groups.

During winter and spring, the composition of the benthic macroinvertebrate assemblages at the upper estuary habitats A and C differed markedly from those at all other habitats, as indicated by the fact that the relevant pairwise R-statistics were typically greater than 0.800 (Table 5.1.3.3c and d). While the compositions of the assemblages at A and C were also significantly different, the extent of those differences was only moderate in winter and low in spring, *i.e.* R=0.586 and 0.121, respectively. Such trends were illustrated on the MDS plots shown in Fig. 5.1.3.2c and d, in which all or the majority of samples from habitats A and C

Table 5.1.3.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the benthic macroinvertebrate composition among each habitat type sampled in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005. Insignificant pairwise comparisons are highlighted in grey.

(a) Summer 2005; p=0.1%, Global R=0.354

	A	C	F	G	I	J
C	0.083					
F	0.060	0.054				
G	0.799	0.464	0.882			
I	0.752	0.188	0.840	0.695		
J	0.188	0.066	0.064	0.488	0.524	
M	0.493	0.257	0.225	0.400	0.006	0.419

(b) Autumn 2005; p=0.1%, Global R=0.450

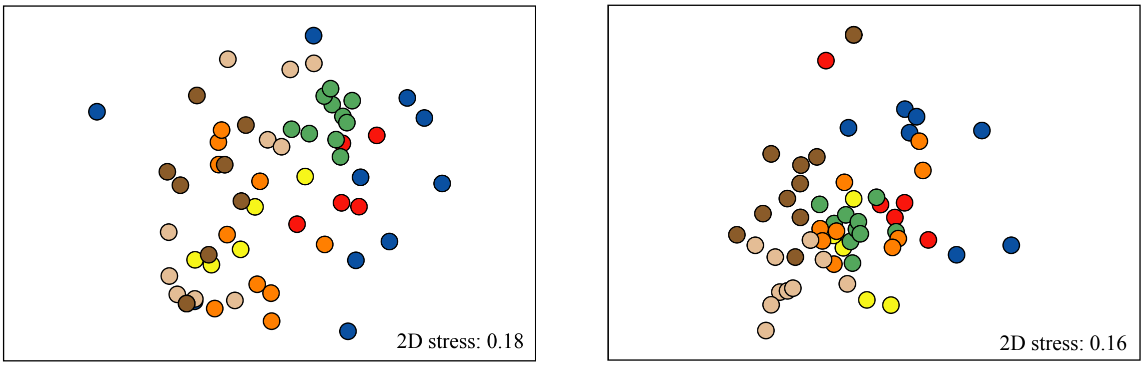
	A	C	F	G	I	J
C	0.425					
F	0.479	0.504				
G	0.602	0.609	0.351			
I	0.457	0.761	0.480	0.591		
J	0.252	0.392	0.203	0.297	0.121	
M	0.539	0.838	0.617	0.668	0.203	0.372

(c) Winter 2005; p=0.1%, Global R=0.665

	A	C	F	G	I	J
C	0.586					
F	0.873	0.966				
G	0.833	0.942	0.396			
I	0.846	1.000	0.588	0.812		
J	0.713	0.699	0.408	0.490	0.232	
M	0.900	0.941	0.515	0.660	0.225	0.264

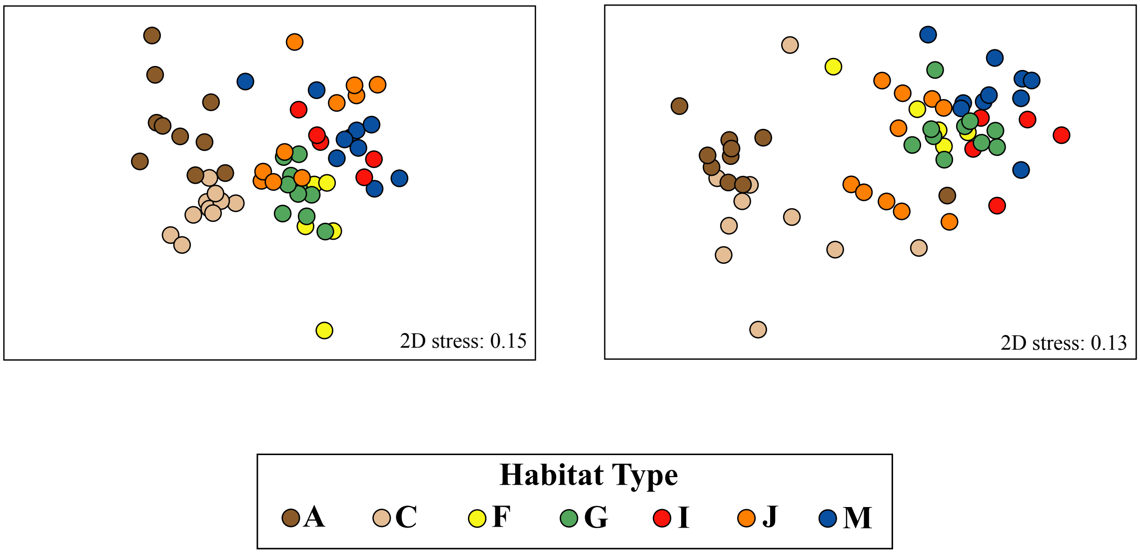
(d) Spring 2005; p=0.1%, Global R=0.564

	A	C	F	G	I	J
C	0.121					
F	0.754	0.684				
G	0.896	0.854	0.059			
I	0.930	0.863	0.360	0.271		
J	0.766	0.588	0.160	0.410	0.631	
M	0.947	0.926	0.364	0.395	0.312	0.560



(a) Summer 2005

(b) Autumn 2005



(c) Winter 2005

(d) Spring 2005

Figure 5.1.3.2: MDS ordination plots constructed from the benthic macroinvertebrate assemblage data recorded in each replicate sample at each habitat in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005.

formed groups that lay adjacent to each other, but were separated to the greatest extent from those for the remaining habitat types, and particularly those for the lower estuary habitats I and M which lay largely on the opposite side of the plots. Samples from habitat A were more dispersed than those from C in winter, while the reverse was true in spring.
SIMPER demonstrated that, in both of these seasons, the assemblages at habitat A were typified by *L. normalis, C. aequisetis* and *A. semen*, but that these species were often either found in higher abundances at other habitats, or were not important in distinguishing the assemblages at this habitat from that of others (Table 5.1.3.4c and d). The benthic invertebrate fauna at C was characterised by two of the above species in both winter and spring, but also by several others that are listed in Table 5.1.3.4 c and d, respectively. During winter, these included *P. excavatum* and *B. limnicola*, which were always found in greater densities at C than any other habitat.

During winter, the assemblages at the lower estuary habitats I and M did not differ significantly from each other, but were each notably distinct from those at the middle to upper basin habitats F and G (R=0.515-0.812; Table 5.1.3.3c), which was also reflected by the fact that samples representing the former two habitats lay adjacent to, but discrete from, those for the latter two on the MDS plot shown in Fig. 5.1.3.2c. Although the characteristic faunas at these four habitats shared several species in common, including *L. normalis, G. propodentata* and *S. biradiata*, the consistency of their occurrence differed and some of these habitats were characterised by species that were not prevalent at the others, *e.g. P. cirrifera* and *V. australis* at F, *A. semen* at G and *P. kempi* at I and M (Table 5.1.3.4c). The least significant difference in assemblage composition during winter surprisingly occurred between habitat J at the base of the Swan River *vs* I and M in the lower estuary (R <0.264), followed by those between habitat F *vs* G and J (R <0 .408). The similarities in assemblage composition within the above groups of habitats was further demonstrated by the fact that their representative samples intermingled considerably on the MDS plot shown in Fig. 5.1.3.2c, and that their characteristic faunas shared several species in common (Table 5.1.3.4c). In contrast, the assemblage at habitat J was notably distinct from those at I and M during spring (R=0.560-0.631; Table 5.1.3.3d), with samples from the former habitat lying between the groups of samples from habitats in the upper and lower estuary on the ordination plot shown in Fig. 5.1.3.2d. Although these three habitats were characterised by similar suites of species in this season, the relative importance of those species differed considerably between habitat J *vs* I and M. For instance, while *S. biradiata*, *P. kempi* and *C. minor* were markedly consistent at the two lower estuary habitats and almost always distinguished these faunas from those at other habitats, they were less consistent at J, while the reverse was true for *L. normalis* (Table 5.1.3.4d).

Table 5.1.3.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the benthic macroinvertebrate assemblages at each habitat in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of habitat types, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively (_i.e._ Sim:SD or Diss:SD; >1.5-4*, >4-6**, >6***).

(a) Summer 2005

	A	**C**	**F**	**G**	**I**	**J**	**M**
A	_C. aequisetis_ _L. normalis_ _A. semen_						
C	▨	_P. excavatum_ _C. capitata_ _C. aequisetis_ _L. normalis_ _A. semen_					
F	▨	▨	_C. aequisetis_* _C. capitata_				
G	_C. capitata_^{G} Oligochaete spp.^{G} Nematode spp.^{G} _C. aequisetis_^{G} _C. minor_^{G} _L. normalis_^{G} _S. biradiata_^{G} _P. kempi_^{G} _G. propodentata_^{G}* _A. semen_^{G}	_C. capitata_^{G} Oligochaete spp.^{G}* _C. aequisetis_^{G} Nematode spp.^{G} _C. minor_^{G} _A. semen_^{C} _L. normalis_^{G} _S. biradiata_^{G} _P. kempi_^{G} _G. propodentata_^{G}*	_C. capitata_^{G}* Oligochaete spp.^{G}* Nematode spp.^{G} _C. aequisetis_^{G}* _C. minor_^{G} _L. normalis_^{G} _S. biradiata_^{G} _P. kempi_^{G} _G. propodentata_^{G} _A. semen_^{G}	_C. capitata_* _C. aequisetis_* Oligochaete spp.* _G. propodentata_*			
I	_C. capitata_^{I}* _V. australis_^{I} Oligochaete spp.^{I}* _S. biradiata_^{I} _C. aequisetis_^{A} _L. normalis_^{A} Nematode spp.^{I}	▨	_C. capitata_^{I}* _V. australis_^{I}* Oligochaete spp.^{I}* _S. biradiata_^{I}* _C. aequisetis_^{F}* _P. kempi_^{I} Nematode spp.^{F} _L. normalis_^{I}	_C. aequisetis_^{G}* Nematode spp.^{G} Oligochaete spp.^{G} _V. australis_^{I}* _C. capitata_^{G} _C. minor_^{G} _L. normalis_^{G} _P. kempi_^{G} _S. biradiata_^{I}* _G. propodentata_^{G}* _A. semen_^{G}*	_C. capitata_** _V. australis_ _S. biradiata_* Oligochaete spp.**		

	A	C	F	G	I	J	M
J	*C. aequisetis*^{J} Paranthurid sp.2^{A} *L. normalis*^{A} Oligochaete spp.^{A}			*C. capitata*^{G}* Oligochaete spp.^{G}* Nematode spp.^{G} *C. aequisetis*^{G} *C. minor*^{G} *L. normalis*^{G} *P. kempi*^{G} *S. biradiata*^{G} *G. propodentata*^{G}* *A. semen*^{G}	*C. capitata*^{I}* *V. australis*^{I} *C. aequisetis*^{J} Oligochaete spp.^{I} *S. biradiata*^{I}* *P. kempi*^{I} *L. normalis*^{I} Nematode spp.^{I}	*C. aequisetis* Paranthurid sp. 1 *M. sanguinea* Oligochaete spp.	
M	*L. normalis*^{M} *Heteromastus* sp.^{M} *P. kempi*^{M}	*C. capitata*^{M} *L. normalis*^{M} *C. aequisetis*^{C} *Heteromastus* sp.^{M}		*C. capitata*^{G} *C. aequisetis*^{G}* Nematode spp.^{G} Oligochaete spp.^{G} *C. minor*^{G} *L. normalis*^{G} *P. kempi*^{G} *S. biradiata*^{G} *G. propodentata*^{G}* *Heteromastus* sp.^{M} *A. semen*^{G}		Oligochaete spp.^{M} *C. capitata*^{M} *L. normalis*^{M} *Heteromastus* sp.^{M} *P. kempi*^{M}	Oligochaete spp. *L. normalis* *Nassarius* sp. *Heteromastus* sp.

(b) Autumn 2005

	A	C	F	G	I	J	M
A	_L. normalis_ _C. aequisetis_ _A. semen_						
C	_P. excavatum_^{C} _A. semen_^{C} _C. aequisetis_^{C} _C. minor_^{C} _C. capitata_^{C} _B. limnicola_^{C} _L. normalis_^{A} _G. propodentata_^{C}*	_C. aequisetis*_ _L. normalis*_ _A. semen_ _P. excavatum_ _C. capitata_ _C. minor_ _G. propodentata*_					
F	_C. capitata_^{F}* _L. normalis_^{A}* _C. aequisetis_^{F} _C. minor_^{F} _A. semen_^{A} _S. biradiata_^{F} _G. propodentata_^{F}	_A. semen_^{C}* _P. excavatum_^{C} _C. capitata_^{F}* _B. limnicola_^{C} _C. minor_^{C} _C. aequisetis_^{C} _S. trigonella_^{C} _S. biradiata_^{F} _L. normalis_^{C}* _G. propodentata_^{C}	_C. capitata**_ _C. aequisetis**_ _L. normalis**_				
G	_C. capitata_^{G} _L. normalis_^{A}* _C. minor_^{G} _S. biradiata_^{G}* _A. semen_^{G} _C. aequisetis_^{G} _G. propodentata_^{G}	_P. excavatum_^{C} _A. semen_^{C}* _C. aequisetis_^{C} _L. normalis_^{C}* _B limnicola_^{C} _C. minor_^{C} _C. capitata_^{G} _S. biradiata_^{G}* _G. propodentata_^{C}	_C. capitata_^{F} _A. semen_^{G} _C. minor_^{G} _S. biradiata_^{G}* _C. aequisetis_^{F} _L. normalis_^{F} _G. propodentata_^{G}	_C. aequisetis*_ _C. capitata*_ _S. biradiata**_ _A. semen_ _L. normalis*_ _C. minor_ _G. propodentata_			
I	_C. capitata_^{I} _L. normalis_^{A} _A. ehlersii_^{I} _C. aequisetis_^{A} _P. kempi_^{I} _S. biradiata_^{I}	_P. excavatum_^{C} _A. semen_^{C}* _C. aequisetis_^{C} _A. ehlersii_^{I} _C. minor_^{C}* _C. capitata_^{I} _L. normalis_^{C} _B. limnicola_^{C} _G. propodenata_^{C}* _P. kempi_^{I} _S. biradiata_^{I}	_C. capitata_^{F} _A. ehlersii_^{I} _C. aequisetis_^{F} _C. minor_^{F} _P. kempi_^{I}* _S. biradiata_^{F} _G. propodenata_^{F} _A. semen_^{I}	_C. capitata_^{I} _A. ehlersii_^{I} _A. semen_^{G} _C. minor_^{G} _G. propodentata_^{G} _P. kempi_^{I} _S. biradiata_^{G}	_C. capitata_ _A. ehlersii_ _C. aequisetis_ _L. normalis_ _P. kempi_		

	A	C	F	G	I	J	M
J	*L. normalis*^{A} *C. aequisetis*^{A} *S. biradiata*^{J}* *C. capitata*^{J} *A. semen*^{A} *G. propodentata*^{J}	*P. excavatum*^{C} *A. semen*^{C} *C. aequisetis*^{C} *C. minor*^{C} *B. limnicola*^{C} *C. capitata*^{C} *S. biradiata*^{J} *G. propodentata*^{C}		*C. capitata*^{J} *C. aequisetis*^{G} *L. normalis*^{J} *A. semen*^{G} *A. ehlersii*^{J} *C. minor*^{G} *G. propodentata*^{G} *S. biradiata*^{J}		*L. normalis** *S. biradiata* *C. capitata* *C. aequisetis**	
M	*L. normalis*^{A}* *C. aequisetis*^{A} *A. semen*^{A}	*A. semen*^{C}* *C. aequisetis*^{C}* *P. excavatum*^{C} *L. normalis*^{C}* *C. minor*^{C}* *B. limnicola*^{C} *C. capitata*^{C} *G. propodentata*^{C}* *A. ehlersii*^{M}	*C. capitata*^{F}* *C. aequisetis*^{F}* *L. normalis*^{F}* *C. minor*^{F} *A. ehlersii*^{M} *G. propodentata*^{F} *S. biradiata*^{F}	*C. capitata*^{G} *C. aequisetis*^{G} *A. semen*^{G} *C. minor*^{G} *S. biradiata*^{G}* *L. normalis*^{G} *A. ehlersii*^{M} *G. propodentata*^{G}		*L. normalis*^{J}* *A. ehlersii*^{M} *C. aequisetis*^{J} *S. biradiata*^{J} *G. propodentata*^{M}	*A. ehlersii* *C. capitata* *C. aequisetis*

(c) Winter 2005

	A	C	F	G	I	J	M
A	*L. normalis** *C. aequisetis** *A. semen*						
C	*P. excavatum*^{C}* *C. aequisetis*^{C} *B. limnicola*^{C}* *A. semen*^{C} *C. capitata*^{C} *G. propodentata*^{C}* *L. normalis*^{A} *M. senhausia*^{A}	*C. aequisetis*** *P. excavatum** *L. normalis** *B. limnicola** *G. propodentata** *C. capitata*					
F	*C. capitata*^{F}** *P. cirrifera*^{F} *C. minor*^{F}* *S. biradiata*^{F} *G. propodentata*^{F}* *V. australis*^{F} *T. deltoidalis*^{F} *L. normalis*^{F} *C. aequisetis*^{F} *V. crenata*^{F} *A. semen*^{A}	*P. excavatum*^{C}* *C. capitata*^{F}* *P. cirrifera*^{F} *C. minor*^{F}* *V. australis*^{F} *T. deltoidalis*^{F} *B. limnicola*^{C}* *S. biradiata*^{F} *L. normalis*^{F} *V. crenata*^{F} *G. propodentata*^{F}* *A. semen*^{C} *C. aequisetis*^{C}*	*C. capitata**** *C. aequisetis*** *L. normalis** *C. minor** *G. propodentata* *P. cirrifera* *S. biradiata* *V. australis*				
G	*C. capitata*^{G}** *C. minor*^{G}* *G. propodentata*^{G}* *C. aequisetis*^{G} *S. biradiata*^{G}* *P. kempi*^{G} *L. normalis*^{A} *A. semen*^{G}	*P. excavatum*^{C}* *C. capitata*^{G}* *C. minor*^{G}* *B. limnicola*^{C}* *A. semen*^{C} *P. kempi*^{G} *G. propodentata*^{G} *L. normalis*^{G} *S. biradiata*^{G} *C. aequisetis*^{C}	*P. cirrifera*^{F} *V. australis*^{F} *T. deltoidalis*^{F} *L. normalis*^{F} *P. kempi*^{F} *V. crenata*^{F} *G. propodentata*^{G} *S. biradiata*^{F} *C. minor*^{G} *A. semen*^{G} *C. capitata*^{G} *C. aequisetis*^{G}	*C. capitata**** *C. aequisetis*** *C. minor** *G. propodentata** *L. normalis** *S. biradiata* *A. semen*			
I	*S. biradiata*^{I}** *P. kempi*^{I}* *C. capitata*^{I} *L. normalis*^{I} *C. aequisetis*^{A} *G. propodentata*^{I}* *A. semen*^{A} *A. elhersii*^{I} *C. minor*^{I}*	*S. biradiata*^{I}* *P. kempi*^{I}** *P. excavatum*^{C}* *C. capitata*^{I}* *C. aequisetis*^{C}* *L. normalis*^{I}* *B. limnicola*^{C}* *A. semen*^{C} *A. elhersii*^{I} *G. propodentata*^{C}	*S. biradiata*^{I}* *P. kempi*^{I}* *P. cirrifera*^{F} *C. capitata*^{F}* *C. minor*^{F}* *V. australis*^{F} *T. deltoidalis*^{F} *L. normalis*^{I}* *C. aequisetis*^{I}* *G. propodentata*^{F}* *V. crenata*^{F} *A. semen*^{F} *A. elhersii*^{I}	*S. biradiata*^{I}* *P. kempi*^{I}* *C. capitata*^{G}* *C. minor*^{G}* *L. normalis*^{I} *C. aequisetis*^{G}* *G. propodentata*^{G} *A. semen*^{G} *A. elhersii*^{I}	*S. biradiata*** *L. normalis*** *P. kempi** *C. aequisetis** *G. propodentata**		

	A	C	F	G	I	J	M
J	*P. kempi*^{J}* *G. propodentata*^{J}* *S. biradiata*^{J}* *A. ehlersii*^{J} *C. aequisetis*^{J} *L. normalis*^{J} *A. semen*^{A}	*P. excavatum*^{C}* *P. kempi*^{J}* *L. normalis*^{J}* *A. ehlersii*^{J} *C. aequisetis*^{J} *S. biradiata*^{J} *G. propodentata*^{J}* *A. semen*^{C} *B. limnicola*^{C} *C. capitata*^{C}	*C. capitata*^{F}* *P. cirrifera*^{F} *P. kempi*^{J} *A. ehlersii*^{J} *L. normalis*^{J} *V. australis*^{F} *C. aequisetis*^{F}* *C. minor*^{F}* *T. deltoidalis*^{F} *S. biradiata*^{J} *V. crenata*^{F} *G. propodentata*^{J} *A. semen*^{F}	*C. capitata*^{G}* *L. normalis*^{J}* *C. minor*^{G}* *P. kempi*^{J} *A. ehlersii*^{J} *C. aequisetis*^{G} *S. biradiata*^{J} *A. semen*^{G} *G. propodentata*^{J}*	*S. biradiata*^{I}* *C. capitata*^{I} *G. propodentata*^{J}* *C. aequisetis*^{J} *A. ehlersii*^{J} *P. kempi*^{I}* *L. normalis*^{J} *A. semen*^{I}	*L. normalis** *G. propodentata**** *P. kempi** *S. biradiata**	
M	*P. kempi*^{M}* *S. biradiata*^{M}* *C. capitata*^{M}* *G. propodentata*^{M}* *L. normalis*^{M} *C. aequisetis*^{M} *C. minor*^{M}* *A. semen*^{A} *T. dulongii*^{M} *C. victoriensis*^{M}	*P. kempi*^{M}* *P. excavatum*^{C}* *S. biradiata*^{M}* *C. aequisetis*^{C} *L. normalis*^{M} *A. semen*^{C} *B. limnicola*^{C}* *C. minor*^{M}* *C. capitata*^{M}* *G. propodentata*^{M} *T. dulongii*^{M} *C. victoriensis*^{M}	*P. kempi*^{M}* *P. cirrifera*^{F} *S. biradiata*^{M} *C. capitata*^{F} *C. aequisetis*^{F} *L. normalis*^{M} *V. australis*^{F} *T. deltoidalis*^{F} *G. propodentata*^{M} *C. minor*^{F} *V. crenata*^{F} *A. semen*^{F} *C. victoriensis*^{M} *T. dulongii*^{M}	*P. kempi*^{M}* *S. biradiata*^{M}* *C. aequisetis*^{G} *C. capitata*^{G} *L. normalis*^{M} *A. semen*^{G}* *C. minor*^{G} *G. propodentata*^{M} *A. ehlersii*^{M} *C. victoriensis*^{M} *T. dulongii*^{M}		*P. kempi*^{M}* *S. biradiata*^{M} *C. aequisetis*^{J} *A. ehlersii*^{J} *C. capitata*^{M}* *L. normalis*^{J} *G. propodentata*^{J} *C. victoriensis*^{M} *C. minor*^{M} *T. dulongii*^{M}	*P. kempi** *L. normalis** *C. capitata** *S. biradiata* *G. propodentata** *C. minor**

(d) Spring 2005

	A	C	F	G	I	J	M
A	*C. aequisetis** *L. normalis** *A. semen*						
C	*M. senhausia*^{C} *B. limnicola*^{C} *S. biradiata*^{C} *A. semen*^{C} *G. propodentata*^{C} *L. normalis*^{A} *C. aequisetis*^{C}	*C. aequisetis** *A. semen* *M. senhausia*					
F	*C. capitata*^{F}** *S. biradiata*^{F}* *L. normalis*^{F}* *P. kempi*^{F}* *G. propodentata*^{F}* *C. minor*^{F} *C. aequisetis*^{F}* *A. semen*^{A}	*C. capitata*^{F}** *L. normalis*^{F}* *S. biradiata*^{F}* *P. kempi*^{F}* *G. propodentata*^{F}* *A. semen*^{C} *C. minor*^{F} *C. aequisetis*^{F}*	*L. normalis*** *C. capitata**** *C. aequisetis** *S. biradiata* *P. kempi* *G. propodentata*				
G	*G. propodentata*^{G}* *S. biradiata*^{G}* *C. capitata*^{G}* *P. kempi*^{G}* *C. minor*^{G}* *L. normalis*^{G}* *C. aequisetis*^{G} *A. semen*$^{-}$ *M. senhousia*^{A}	*G. propodentata*^{G}* *C. capitata*^{G}* *S. biradiata*^{G}* *P. kempi*^{G}* *L. normalis*^{G}* *C. minor*^{G}* *C. aequisetis*^{G} *A. semen*^{C}		*G. propodentata*** *L. normalis*** *S. biradiata** *C. aequisetis** *C. capitata** *P. kempi** *C. minor*			
I	*S. biradiata*^{I}* *G. propodentata*^{I}* *P. kempi*^{I}* *C. capitata*^{I}* *L. normalis*^{I}* *C. minor*^{I}* *C. aequisetis*^{I} *A. semen*^{A}* *A. elhersii*^{I}*	*S. biradiata*^{I}* *G. propodentata*^{I}* *C. capitata*^{I}* *P. kempi*^{I}* *L. normalis*^{I} *A. semen*^{C}* *C. minor*^{I}* *C. aequisetis*^{I} *A. elhersii*^{I}*	*S. biradiata*^{I} *G. propodentata*^{I} *C. capitata*^{I}* *L. normalis*^{I} *P. kempi*^{I}* *C. aequisetis*^{I} *C. minor*^{I}* *A. semen*^{F} *A. elhersii*^{I}	*S. biradiata*^{I}* *C. capitata*^{I} *L. normalis*^{I} *C. aequisetis*^{G} *P. kempi*^{I}* *G. propodentata*^{I} *C. minor*^{G} *A. semen*^{G} *A. elhersii*^{I}	*S. biradiata*** *G. propodentata** *P. kempi** *C. capitata* *C. aequisetis*** *L. normalis* *C. minor***		

	A	C	F	G	I	J	M
J	_G. propodentata_^{J}* _S. biradiata_^{J}* _P. kempi_^{J} _L. normalis_^{J}* _C. minor_^{J} _A. semen_^{J} _B. limnicola_^{J} _C. aequisetis_^{J} _C. capitata_^{J} _M. senhousia_^{A}	_L. normalis_^{J}* _P. kempi_^{J} _G. propodentata_^{J}* _S. biradiata_^{J}* _C. minor_^{J} _A. semen_^{C}* _B. limnicola_^{C} _C. aequisetis_^{J} _C. capitata_^{J}		_C. capitata_^{G}* _G. propodentata_^{G} _P. kempi_^{G} _S. biradiata_^{G}* _C. aequisetis_^{G} _C. minor_^{G} _A. semen_^{J} _B. limnicola_^{J}* _L. normalis_^{G}	_S. biradiata_^{I}* _C. capitata_^{I}* _P. kempi_^{I}* _G. propodentata_^{I}* _L. normalis_^{I} _C. aequisetis_^{I} _A. semen_^{J} _B. limnicola_^{J}* _C. minor_^{I} _A. elhersii_^{I}	_L. normalis_** _C. aequisetis_* _S. biradiata_* _G. propodentata_* _A. semen_ _C. minor_ _B. limnicola_	
M	_P. kempi_^{M}* _S. biradiata_^{M}* _G. propodentata_^{M}* _C. minor_^{M}* _C. capitata_^{M}* _L. normalis_^{M}* _A. semen_^{A}* _C. aequisetis_^{A} _M. senhousia_^{A}	_P. kempi_^{M}* _S. biradiata_^{M}* _G. propodentata_^{M}* _C. minor_^{M}* _L. normalis_^{M}* _C. capitata_^{M}* _A. semen_^{C}* _C. aequisetis_^{C}	_P. kempi_^{M}* _G. propodentata_^{M} _S. biradiata_^{M} _C. minor_^{M} _C. aequisetis_^{F} _C. capitata_^{F}* _L. normalis_^{F} _A. semen_^{F}	_P. kempi_^{M}* _C. aequisetis_^{G} _C. capitata_^{G}* _G. propodentata_^{G} _S. biradiata_^{M} _C. minor_^{M} _A. semen_^{G} _L. normalis_^{G}	_C. capitata_^{I}* _P. kempi_^{M} _S. biradiata_^{I}* _L. normalis_^{I} _C. aequisetis_^{I} _G. propodentata_^{I} _C. minor_^{M} _A. elhersii_^{I}	_P. kempi_^{M}* _S. biradiata_^{M}* _C. aequisetis_^{J} _A. semen_^{J} _G. propodentata_^{M} _C. minor_ ^{M} _C. capitata_^{M} _B. limnicola_^{J}* _L. normalis_^{J}	_P. kempi_** _S. biradiata_** _L. normalis_* _G. propodentata_* _C. minor_* _C. capitata_

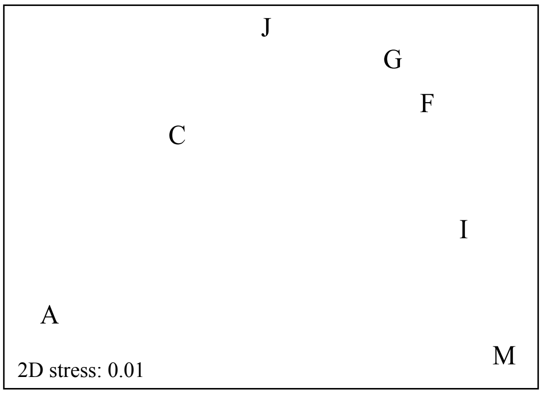
During summer and, to a lesser extent, autumn, the differences in assemblage composition among habitats were far less pronounced than in winter and spring (Table 5.1.3.3a and b). Thus, although most of the samples from habitats A and C in the first two seasons were, as in latter two seasons, located on the opposite side of the ordination plot from those representing I and M (Fig. 5.1.3.2a and b), the degree of separation was far less and/or the level of sample dispersion within those habitats was far greater. During summer, the assemblages at the basin habitats G and I were the most distinct, as reflected by the large pairwise ANOSIM R-statistics detected between each of these habitats *vs* A, F and each other (R=0.695-0.882; Table 5.1.3.3a) and the fact that, on the ordination plot shown in Fig. 5.1.3.2a, samples from these two habitats formed relatively tight groups that were largely discrete from each other and those for the other habitats listed above. SIMPER demonstrated that, while the assemblages at habitats G and I were characterised by several species that also typified the faunas at various other habitats in this season (*e.g. C. capitata*, Oligochaete spp. and, in the case of G, also *C. aequisetis*), they were the only two habitats at which these and other species occurred with any notable consistency, with the minor exception of one of the species that characterised habitat F (Table 5.1.3.4a). These species were also always in greater abundances at habitats G and I than at other habitats. Furthermore, these two habitats were each typified by other species that were exclusive to that habitat in this season, *e.g. G. propodentata* at G and *V. australis* and *S. biradiata* at I (Table 5.1.3.4a).

During autumn, the composition of the benthic macroinvertebrate fauna at the upper estuary habitat C was moderately to markedly different from those at all other habitats except A and J (*i.e.* R=0.504-0.838), while the differences between the uppermost habitat A and all other habitats were generally less than in winter and spring and, in the case of A *vs* G and I, also summer (*i.e.* R=0.252-0.602; Table 5.1.3.3b). These results were also reflected by the distribution of the samples representing A and C on the ordination plot shown in Fig. 5.1.3.2b, in which those for the latter habitat formed a much less dispersed group than those for the former habitat. The assemblages at A in this season were typified only by *L. normalis, C. aequisetis* and *A. semen*, none of which occurred with any notable consistency. However, the first of these species was always recorded in higher densities at A than any other habitat in this season, while the latter two species were only more abundant at A than at J and the lower estuary habitats I and M in most cases (Table 5.1.3.4b). Habitat C, on the other hand, was typified by each of the above species in addition to several others in autumn, the first two of which and *G. propodentata* occurred consistently. Of this suite of characteristic species, *C. aequisetis*, *A. semen, P. excavatum,* and *C. minor* always occurred in greater densities at C than any other habitat in this season (Table 5.1.3.4b). Notable differences also occurred between the composition of the fauna at habitat G *vs* I and M and F *vs* M in autumn (R=0.591-0.668), with samples for the first of these habitats forming a particularly tight group in the middle of the ordination plot that intermingled with those from habitats J and F (Fig. 5.1.3.2b). Several of the species that characterised the basin habitats G and F also characterised I and/or M, *e.g. C. capitata, C. aequisetis* and *L. normalis.* However, each of these species were highly consistent in their occurrence at the former two habitats, whereas they were not particularly consistent at the latter two and were almost always less abundant (Table 5.1.3.4b). Moreover, habitat G was characterised by several species that did not typify the assemblages at either I or M, *i.e. S. biradiata, C. minor* and *G. propodendata*, while the opposite was true for *P. kempi* and *A. ehlersii* (Table 5.1.3.4b).

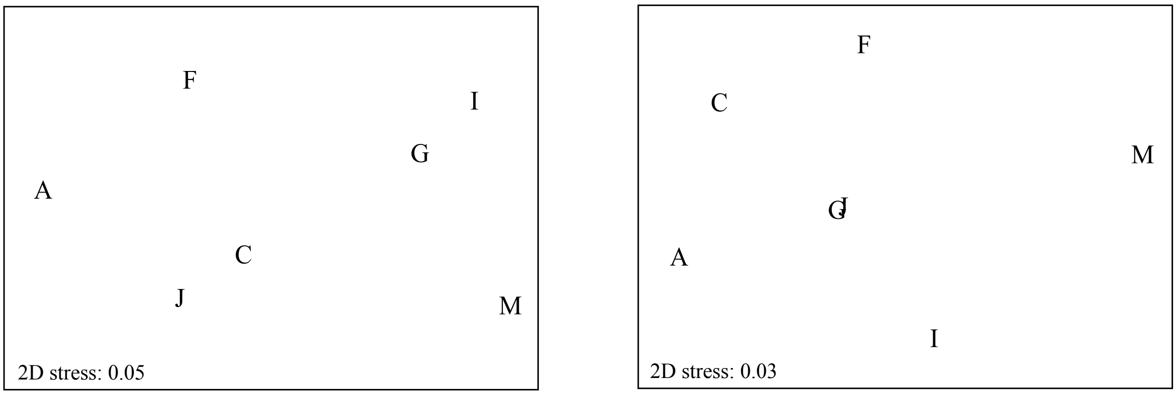
5.1.3.4 Matching spatial patterns between the environmental and benthic macroinvertebrate characteristics of habitats

The RELATE procedure showed that the arrangement of the rank order of resemblances in matrices constructed from the average of the benthic macroinvertebrate assemblage data recorded at each habitat in summer, autumn, winter and spring were each significantly correlated with that derived from the average of the enduring environmental variables used to define those habitats, *i.e.* p=0.1-0.3%. Moreover, the extent of that correlation was moderately high in the first three seasons (*i.e.* ρ=0.545, 0.501 and 0.664, respectively) and high in the latter (*i.e.* ρ=0.745), indicating that the relative spatial differences in the enduring environmental characteristics of the habitats in the Swan Estuary provided, in each season, a good surrogate for those exhibited by the benthic macroinvertebrate fauna. Such results are illustrated by the similarities in the distribution of samples representing each habitat on the MDS plots shown in Fig. 5.1.3.3 that are constructed from the average (a) enduring environmental data at each habitat and (b-e) faunal composition data recorded at the various habitats in each season. In contrast, when RELATE was used to test the correlation between each of the above faunal matrices and complementary matrices derived from data for the suite of non-enduring (i) water quality variables (*i.e.* salinity, temperature and dissolved oxygen) and (ii) sediment characteristics (*i.e.* mean grain size, sedimentary chlorophyll concentration, organic matter content and transition zone depth), significant correlations were obtained only for winter and spring in the first set of tests (p=0.2 and 2.5%, ρ=0.681 and 0.514, respectively), and only for spring in the latter set (p=1.2%, ρ=0.571). Moreover, the extents of those significant correlations were, in

(a) Enduring environmental data



(b) Summer 2005; p=1.1%, ρ=0.545 **(c) Autumn 2005; p=3.4%, ρ=0.504**



(d) Winter 2005; p=0.4%, ρ=0.664 **(e) Spring 2005; p=0.2%, ρ=0.745**

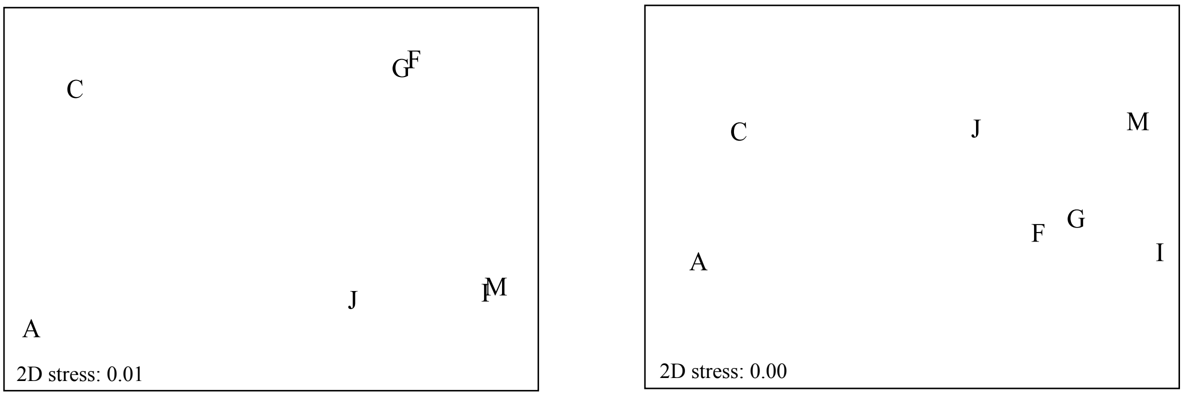


Figure 5.1.3.3: MDS ordination plots constructed from the averages at each habitat type in the Swan Estuary of their (a) enduring environmental measurements and (b-e) benthic macroinvertebrate composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the above benthic macroinvertebrate data are also provided for each season.

almost all cases, weaker than the comparable analyses obtained above when the faunal and enduring environmental data were matched.

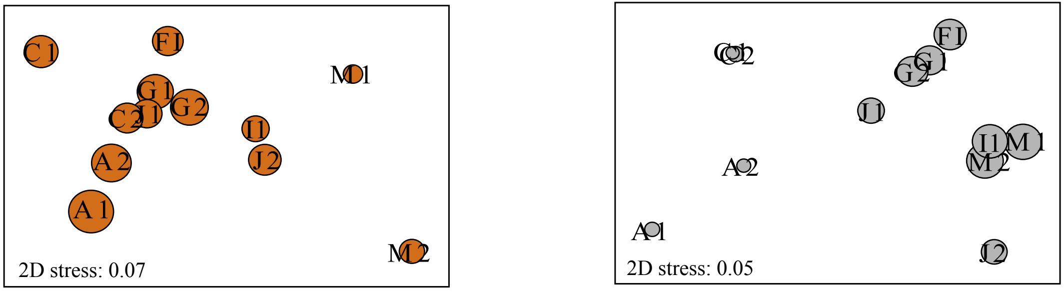
BIOENV was then employed to determine whether a greater correlation could be achieved between the complementary faunal and non-enduring environmental matrices by only using a subset of water or sediment variables, rather than the full suites. Note that these analyses were performed on the averages of data recorded at each site rather than habitat type, in order to maximise the number of samples in the reference (faunal) matrices and thus minimise the likelihood of BIOENV finding a subset of water or sediment quality variables that provided a good match with those references by chance. For comparability purposes, it should also be noted that, when the RELATE routine was used to match the complementary benthic macroinvertebrate and water/sediment quality matrices constructed from the averages recorded at each site, the results were very similar to those obtained above when habitat averages were employed, except for the correlation between the faunal and sediment data during winter, *i.e.* p=1%, ρ=0.340 at the site level *vs* p=18.6%, ρ=0.210 at the habitat level.

In the case of the water quality variables, significant BIOENV results were obtained only in winter and spring (p=1%), but the correlation with the spatial patterns in the complementary faunal matrices was improved considerably in both cases when data for only salinity and/or temperature were employed (*i.e.* ρ=0.732 and 0.874 for winter and spring, respectively). Significant results were obtained in autumn, winter and spring when BIOENV was used to match the complementary faunal and sediment quality matrices (p=1-5%), which were each associated with reasonable improvements in the extent of the correlations, *i.e.* ρ=0.513, 0.467 and 0.644, respectively. During autumn, the improved match was obtained when data for only sedimentary chlorophyll concentration was employed, and that for both of the latter seasons resulted from using data for only mean grain size and organic matter content.

The spatial relationships between the composition of the benthic macroinvertebrate assemblages and the magnitude of the water and/or sediment parameters selected by the BIOENV procedure are illustrated, for each season in which significant results were obtained, by the MDS and associated bubble plots shown in Fig. 5.1.3.4. In both winter and spring, the marked difference in the average species composition of sites representing the upper estuary habitats A and C compared to those for the remaining sites, and particularly those at sites representing the lower estuary habitats I and M, were well reflected by spatial differences in salinity. Thus, in both of these seasons, markedly lower salinities were recorded at sites from the first two habitats than any other, while the greatest salinities were recorded at sites from the latter two habitats (Fig. 5.1.3.4b and f). Furthermore, in winter, water temperatures at the faunally-

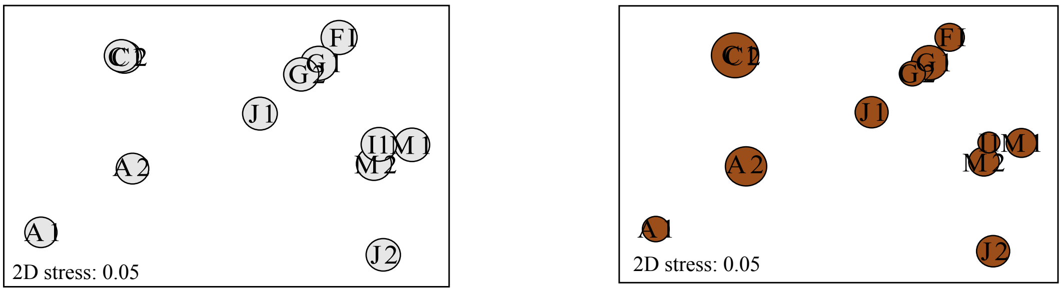
(a) Autumn 2005; p=5%, ρ=0.513

(b) Winter 2005; p=1%, ρ=0.732



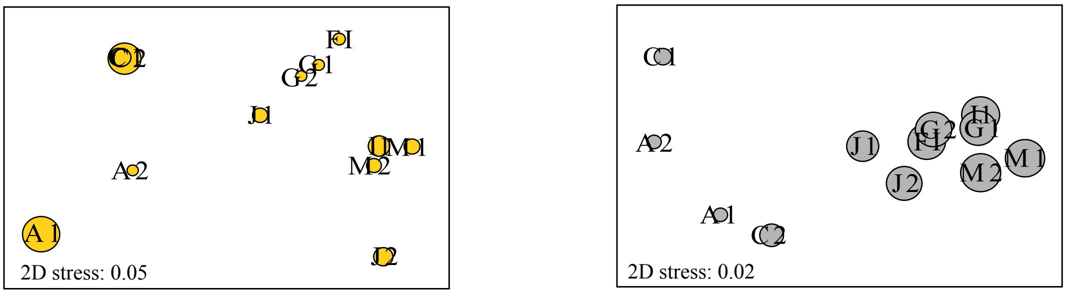
(c) Winter 2005; p=1%, ρ=0.732

(d) Winter 2005; p=4%, ρ=0.467



(e) Winter 2005; p=4%, ρ =0.467

(f) Spring 2005; p=1%, ρ=0.874



(g) Spring 2005; p=1%, ρ=0.644

(h) Spring 2005; p=1%, ρ=0.644

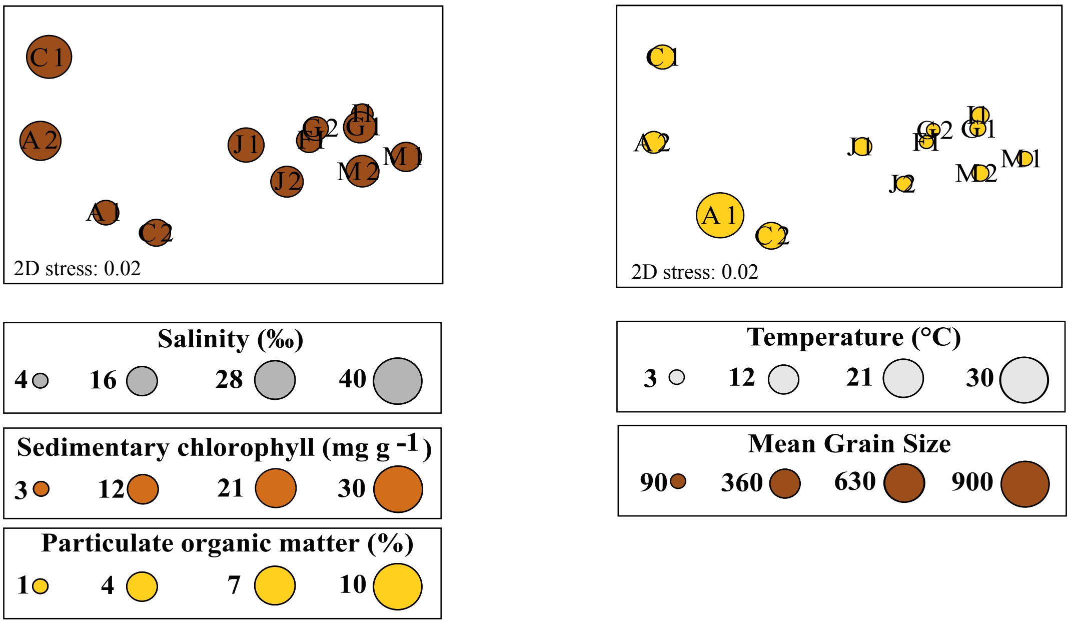


Figure 5.1.3.4: MDS ordination plots derived from the average benthic macroinvertebrate composition recorded at each site in the Swan Estuary in a particular sampling season. The magnitude of those water quality or sediment variables selected by the BIOENV routine when one of the matrices constructed from the above faunal data was matched with that constructed from the complementary water quality or sediment data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

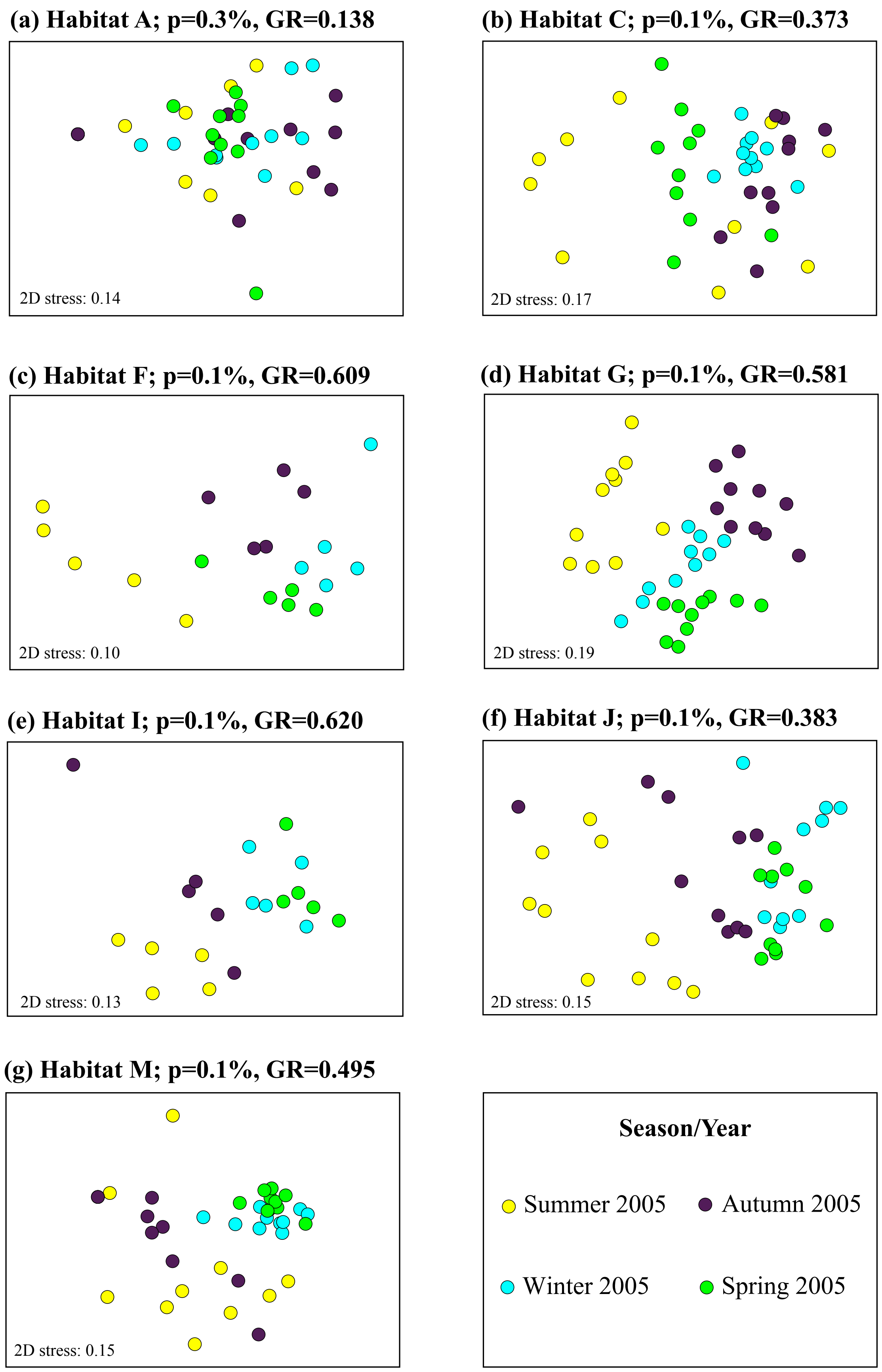
distinct sites from habitat A were notably lower than those recorded at any other site throughout the estuary (Fig. 5.1.3.4c).

Examination of the spatial relationships between the species composition data and the various sediment parameters selected by BIOENV in autumn, winter and spring demonstrated that, in the first of these seasons, the marked differences between the faunal composition at sites from habitat M and those of the remaining habitats reflected the considerably lower concentrations of sedimentary chlorophyll recorded at that channel habitat (Fig. 5.1.3.4a). During both winter and spring, the mean grain size and sedimentary organic matter content was notably greater at particular sites representing habitats A and C than at all other sites (Fig. 5.1.3.4d, e, g and h). However, there was also considerable spatial variation exhibited by the faunal assemblages that was not well explained by the above selected sediment parameters in each season. For example, while there were notable faunal differences between sites from the middle to upper basin habitats F, G and J and those from the lower estuary habitats I and M in winter, there were no clear differences in mean grain size among these two groups of sites (Fig. 5.1.3.4d).

5.1.3.5 Composition of benthic macroinvertebrate assemblages among seasons

One-way ANOSIM tests, carried out separately for the species composition data recorded at each habitat type, showed that the benthic macroinvertebrate assemblages differed significantly among seasons in each case (p=0.1-0.3%). The greatest seasonal differences occurred at the main basin habitats I, F and G (Global R=0.581-0.620), whereas the weakest by far were recorded at habitat A (Global R=0.138). All pairwise comparisons between seasons were significant at each habitat except A, at which no significant differences were detected between winter *vs* autumn and spring, and J, where the winter *vs* summer comparison was not significant. The extents of the seasonal differences in species composition at each habitat are illustrated by the MDS plots and associated global ANOSIM results presented in Fig. 5.1.3.5.

At the basin habitats F, G, I and J, pronounced seasonal differences in benthic macroinvertebrate composition occurred between summer and each of the other seasons, as reflected by the high ANOSIM R-statistics that were obtained for these comparisons (*i.e.* 0.709-0.964), with the exception of those for summer *vs* winter at habitat G and summer *vs* autumn at habitats I and J (R=0.263-0.464). Such trends were illustrated by the fact that samples representing summer formed a group on one side of the MDS plots shown in Fig. 5.1.3.5c-f, that was typically the most distinct from those representing the other three seasons. Marked differences were also detected between autumn *vs* spring at habitat G (R=0.846), which was


(a) Habitat A; p=0.3%, GR=0.138

(b) Habitat C; p=0.1%, GR=0.373

(c) Habitat F; p=0.1%, GR=0.609

(d) Habitat G; p=0.1%, GR=0.581

(e) Habitat I; p=0.1%, GR=0.620

(f) Habitat J; p=0.1%, GR=0.383

(g) Habitat M; p=0.1%, GR=0.495

Figure 5.1.3.5: MDS ordination plots constructed from the benthic macroinvertebrate assemblage data recorded in each replicate sample in each sampling season at habitat (a) A, (b) C, (c) F, (d) G, (e) I, (f) J and (g) M in the Swan Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

reflected by the tight and discrete groups of samples representing each of these seasons on the MDS plot shown in Fig. 5.1.3.5d, and autumn *vs* winter and spring at habitat I (R=0.516-0.652), as illustrated by the fact that most samples from the first season formed a discrete group that lay adjacent to that containing samples from the two latter seasons on the ordination plot shown in Fig. 5.1.3.5e. The distinctiveness of the faunal samples collected in summer at habitat F was due largely to their depauperate composition, compared to those recorded in other seasons. Thus, the faunal assemblage of these samples was characterised by only two species, namely *C. aequisetis* and *C. capitata*, which were each present in relatively low numbers. In contrast, relatively large numbers of both of the above species, together with others such as *L. normalis, C. minor, S. biradiata* and *G. propodentata*, also typified the assemblages at this habitat in each of the remaining seasons, and some species further characterised the faunas of only one of those seasons, *e.g. P. cirrifera* and *V. australis* in winter. At habitat G, however, the distinctiveness of the faunal composition in summer was usually attributable to relatively large numbers of Oligochaete spp., *C. capitata*, Nematode sp. and *C. aequisetis*, while that at I was consistently distinguished by a prevalence of the first of these species and *V. australis*. In contrast, species such as *G. propodentata, S. biradiata, L. normalis, P. kempi, C. minor* and *A. semen* were often recorded in higher numbers in seasons other than summer at both of these main basin habitats. The large difference between the faunal compositions in autumn *vs* spring at habitat G was due mainly to the far greater prevalence of *G. propodentata, P. kempi, S. biradiata, L. normalis, C. capitata, C. aequisetis* and *C. minor* in the latter season. Almost all of these species were also mainly responsible for distinguishing the fauna in autumn from that in both winter and spring at habitat type I, where they were notably less abundant in the former season than the latter two. In contrast, *A. elhersii* was consistently more abundant in autumn than either winter or spring at this habitat. At habitat type J, the notable differences in faunal composition between summer *vs* winter and spring were due mainly to comparatively lower densities of *L. normalis, P. kempi, G. propodentata*, C. *aequisetis* and *S. biradiata* in the first of those seasons.

In contrast to the above basin habitats, the greatest seasonal differences at habitat C were detected between spring *vs* autumn and winter (R=0.506-0.632; Fig. 5.1.3.5b) and between autumn *vs* winter and spring at the channel habitat M (R=0.764-0.836; Fig. 5.1.3.5g), while the R-statistics for comparisons involving summer at these two habitats never exceeded 0.371 and 0.570, respectively. All pairwise seasonal comparisons at habitat A had low R-statistic values, *i.e.* ≤0.267, which is also reflected by the high degree of intermingling of samples from different seasons on the MDS plot shown in Fig. 5.1.3.5a. SIMPER showed that the faunal differences between spring *vs* autumn and winter at habitat C were commonly due to far lower densities of

P. excavatum, C. capitata, L. normalis, C. aequisetis, B. limnicola and *G. propodentata* in the first of those seasons, while the opposite was true for *S. biradiata*. At the lower estuary habitat M, the pronounced differences in composition for autumn *vs* winter and spring were largely attributable to the assemblages in the latter two seasons both being typified by considerably higher densities of *P. kempi, L. normalis, C. capitata, S. biradiata, G. propodentata*, *C. minor* and *C. aequisetis*, whereas those in autumn contained low and relatively inconsistent numbers of even its typifying species, *i.e. A. elhersii, C. capitata* and C. *aequisetis*. The greatest seasonal differences at habitat type A, *i.e.* summer *vs* winter, were driven mainly by greater densities of *L. normalis, C. aequisetis* and *A. semen* in the latter season.

5.1.4 Nematode assemblages

5.1.4.1 Species mean density at each habitat type

A total of 61 nematode species and 149 260 individuals (*i.e.* after the number of nematodes in each sample had been adjusted to that in 10 cm^2 and summed) were found in sediment samples collected from seven habitat types throughout the Swan Estuary in each season during 2005 (Table 5.1.4.1). The most speciose habitats were M, located in the estuary channel, and G, located in the middle to upper reaches of the main basin, *i.e.* 50 and 42 species, respectively. Similar numbers of species were recorded at all other habitats (25-27) except for F, at which a slightly greater number of species was found (32; Table 5.1.4.1). The greatest mean densities of nematodes were recorded at the lower estuary habitats M and I (972 and 931 individuals 10 cm^{-2}, respectively), followed by that at the basin habitats G and F (875 and 795 individuals 10 cm^{-2}, respectively). Far lower mean densities were recorded at the remaining habitats (208-497 nematodes 10 cm^{-2}), and particularly at the upper estuary habitat C (Table 5.1.4.1).

The dominant nematode species differed considerably among habitats. Thus, the assemblages at the upper estuary habitats A and C were both dominated by *Theristus* sp.1, which also ranked first at habitat J located in the small basin at the foot of the Swan River. However, the percentage contribution (*ca* 60%) and mean density of this species at habitat A was about two and four times, respectively, that at both C and J. *Metalinhomeous* sp. also ranked within the top three most abundant species at habitats A and C, but the remaining species that were abundant at A (*i.e.* those contributing more than 5% to the total density of nematodes) were not abundant at C, and vice versa (see highlighted species in Table 5.1.4.1). Two of the abundant species at C were also abundant at J, namely *Pierrickia* sp. and *Dichromadora* sp., with the latter making a greater contribution to the nematofauna at J. However, the assemblages at that latter

Table 5.1.4.1: Mean density (M), standard deviation (SD), percentage contribution to the overall mean density (%) and rank by density (R) of each nematode species recorded at each habitat type sampled in the Swan Estuary in each season in 2005. Abundant species at each habitat (*i.e.* those that contribute >5% to the overall mean density) are highlighted in grey. The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of nematodes in each sample had been adjusted to that in 10 cm^2 and summed) are given for each habitat type.

	Habitat type A				Habitat type C				Habitat type F				Habitat type G			
Species name	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Theristus sp.1	299.50	377.40	60.21	1	64.05	100.61	30.73	1	3.20	9.50	0.40	17	13.10	24.74	1.50	13
Metalinhomeous sp.	39.80	44.87	8.00	2	19.43	50.44	9.32	3	10.90	33.91	1.37	15	0.20	0.76	0.02	35
Nannolaimoides decoratus	32.05	32.65	6.44	3	2.33	4.86	1.12	14	31.30	51.91	3.94	9	48.10	95.02	5.50	6
Parodontophora aurata	25.40	29.55	5.11	4	5.93	9.17	2.85	9	0.10	0.45	0.01	31				
Pierrickia sp.	24.55	27.83	4.94	5	18.85	21.22	9.05	4	11.10	11.14	1.40	14	2.75	9.55	0.31	21
Metadesmolaimus sp.2	24.00	24.45	4.82	6	25.73	57.77	12.35	2					6.35	11.84	0.73	17
Dichromadora sp.	12.90	12.34	2.59	7	11.00	18.77	5.28	6	84.40	160.37	10.62	2	191.95	442.55	21.94	1
Parascolaimus breviseta	10.85	14.65	2.18	8	5.00	9.47	2.40	11					0.20	1.26	0.02	35
Halichoanolaimus duodecimpapillatus	7.45	7.62	1.50	9	2.25	3.79	1.08	15	33.50	20.95	4.21	8	36.45	33.1	4.17	9
Pontonema sp.1	4.95	6.84	1.00	10	7.55	10.77	3.62	8	47.70	40.94	6.00	5	35.75	39.5	4.09	10
Terschillingia sp.1	4.90	7.88	0.99	11	5.23	6.74	2.51	10	52.40	52.30	6.59	4	17.20	21.38	1.97	12
Viscosia glabra	4.05	5.56	0.81	12	18.55	28.32	8.90	5	36.10	46.84	4.54	7	74.10	126.32	8.47	4
Oncholaimus domesticus	1.85	7.07	0.37	13	1.25	4.45	0.60	17					0.30	1.07	0.03	32
Chromadorina sp.	1.30	3.67	0.26	14	2.90	5.16	1.39	13	15.30	26.94	1.93	13	28.55	82.73	3.26	11
Comesoma arenae	1.10	3.73	0.22	15	1.20	5.51	0.58	18	26.10	34.75	3.28	10	41.35	59.03	4.73	7
Spirinia parasitifera	1.05	3.10	0.21	16	10.60	33.22	5.09	7	270.70	205.15	34.06	1	142.15	198.98	16.25	2
Linhomeous sp.	0.40	1.98	0.08	17	0.10	0.63	0.05	20	0.40	1.79	0.05	25	0.30	1.40	0.03	32
Enoploides sp.1	0.30	1.40	0.06	18												
Gen Nov.1 sp.1	0.20	1.26	0.04	19	0.05	0.32	0.02	25					0.45	1.78	0.05	29
Neochromadora sp.1	0.20	0.88	0.04	19									1.60	4.86	0.18	24
Paracomesoma sipho	0.20	1.26	0.04	19					0.40	1.23	0.05	25	8.00	17.84	0.91	14
Bathylaimus australis	0.15	0.70	0.03	22	3.70	10.09	1.78	12	1.40	3.95	0.18	22	7.55	23.79	0.86	16
Camacholaimus sp.	0.10	0.63	0.02	23	0.05	0.32	0.02	25	0.20	0.89	0.03	29	0.90	3.07	0.10	28
Bolbonema spiralis	0.10	0.63	0.02	23					0.20	0.89	0.03	29	0.40	1.52	0.05	29
Quadricoma sp.	0.10	0.63	0.02	23												
Theristus sp.2					2.00	9.06	0.96	16	67.30	58.44	8.47	3	92.55	72.07	10.58	3
Metadesmolaimus sp.1					0.20	0.88	0.10	19	46.40	76.22	5.84	6	56.55	84.42	6.46	5

Species name	Habitat type A				Habitat type C				Habitat type F				Habitat type G			
	M	SD	%	R	M	SD	%	R	M	SD	%	R	M	SD	%	R
Eubostrichus otti					0.10	0.63	0.05	20	1.00	2.55	0.13	23	1.40	3.33	0.16	25
Prooncholaimus sp.					0.10	0.63	0.05	20	0.40	1.79	0.05	25				
Subsphaerolaimus sp.					0.10	0.63	0.05	20	16.10	16.32	2.03	12				
Trefusia sp.					0.10	0.44	0.05	20					0.40	2.53	0.05	29
Epacanthion georgei					0.05	0.32	0.02	25	0.10	0.45	0.01	31	5.80	14.74	0.66	18
Gomphionema typicum									20.40	23.47	2.57	11	7.65	15.87	0.87	15
Choniolaimus papillatus									7.30	19.72	0.92	16	3.45	6.85	0.39	20
Halaphanalaimus sp.									2.80	4.51	0.35	18	1.20	3.03	0.14	26
Pseudochromadora cazca									2.60	7.37	0.33	19	36.65	44.67	4.19	8
Daptonema sp.									2.40	5.26	0.30	20	1.20	3.41	0.14	26
Gammanema aff. *smithi*									1.60	4.19	0.20	21				
Cytolaimium sp.									0.60	2.68	0.08	24				
Leptolaimus sp.									0.40	1.79	0.05	25				
Neochromadora sp.2													4.80	18.12	0.55	19
Halichoanolaimus aff. *chordiurus*													2.75	5.81	0.31	21
Halalaimus bayensis													1.75	3.71	0.20	23
Gen Nov.1 sp. 2													0.30	1.40	0.03	32
Neochromadora sp.3													0.20	1.26	0.02	35
Paralinhomeous sp.													0.20	1.26	0.02	35
Cephalanticoma sp.													0.10	0.63	0.01	39
Metacyatholaimus sp.													0.10	0.63	0.01	39
Pomponema sp.2													0.10	0.63	0.01	39
Setosabatieria sp.													0.10	0.63	0.01	39
Number of species		**25**				**27**				**32**				**42**		
Total mean density		**497**				**208**				**795**				**875**		
Number of samples		**40**				**40**				**20**				**40**		
Total number of nematodes		**19 898**				**8 335**				**15 896**				**34 998**		

Species name	Habitat type I				Habitat type J				Habitat type M			
	M	SD	%	R	M	SD	%	R	M	SD	%	R
Theristus sp.1	10.00	18.56	1.07	11	84.60	74.49	26.75	1	2.60	7.61	0.27	23
Metalinhomeous sp.	0.20	0.89	0.02	21	4.30	13.36	1.36	15	10.85	22.96	1.12	13
Nannolaimoides decoratus	116.40	263.89	12.50	3	1.80	2.59	0.57	16	15.65	26.82	1.61	12
Parodontophora aurata					6.40	13.95	2.02	10				
Pierrickia sp.					18.85	38.71	5.96	5	0.10	0.63	0.01	48
Metadesmolaimus sp.2					4.45	9.43	1.41	14				
Dichromadora sp.	46.40	72.13	4.98	6	27.30	32.07	8.63	3	59.90	130.31	6.17	5
Parascolaimus breviseta	0.20	0.89	0.02	21	0.20	0.88	0.06	24				
Halichoanolaimus duodecimpapillatus	50.20	39.63	5.39	5	1.30	3.31	0.41	17	22.80	22.72	2.35	10
Pontonema sp.1	0.40	1.23	0.04	20	16.85	22.51	5.33	6	1.55	2.81	0.16	27
Terschillingia sp.1	33.40	32.84	3.59	8	1.15	2.35	0.36	18	16.25	22.84	1.67	11
Viscosia glabra	23.80	16.34	2.56	9	5.20	16.22	1.64	13	25.25	70.38	2.60	8
Oncholaimus domesticus	1.00	3.64	0.11	15	5.55	9.41	1.75	12	4.40	11.41	0.45	19
Chromadorina sp.	21.20	43.28	2.28	10	5.90	7.92	1.87	11	111.50	214.20	11.48	2
Comesoma arenae	0.20	0.89	0.02	21	0.80	2.07	0.25	19	79.95	67.83	8.23	4
Spirinia parasitifera	326.80	215.44	35.10	1	14.70	24.33	4.65	8	363.10	418.63	37.38	1
Linhomeous sp.									1.95	4.65	0.20	26
Enoploides sp.1												
Gen Nov.1 sp.1									0.05	0.32	0.01	48
Neochromadora sp.1	0.20	0.89	0.02	21					23.30	71.63	2.40	9
Paracomesoma sipho	1.20	3.21	0.13	14	0.05	0.32	0.02	26	3.60	15.36	0.37	20
Bathylaimus australis	106.40	235.44	11.43	4	65.10	121.26	20.58	2	35.60	80.70	3.66	7
Camacholaimus sp.					0.30	1.07	0.09	21	8.60	12.50	0.89	15
Bolbonema spiralis	0.40	1.79	0.04	17					0.60	2.80	0.06	34
Quadricoma sp.												
Theristus sp.2	151.00	133.52	16.22	2	10.70	16.21	3.38	9	94.45	160.62	9.72	3
Metadesmolaimus sp.1	36.20	30.11	3.89	7	22.80	27.58	7.21	4	40.80	61.49	4.20	6
Eubostrichus otti									2.80	6.16	0.29	22
Prooncholaimus sp.	0.40	1.79	0.04	17					0.30	1.40	0.03	40
Subsphaerolaimus sp.	0.40	1.79	0.04	17	0.05	0.32	0.02	26				
Trefusia sp.									0.35	1.42	0.04	38
Epacanthion georgei									3.25	5.37	0.33	21
Gomphionema typicum	1.40	2.98	0.15	12	16.85	28.07	5.33	6	0.20	1.26	0.02	44
Choniolaimus papillatus									0.30	1.40	0.03	40

Species name	Habitat type I				Habitat type J				Habitat type M			
	M	SD	%	R	M	SD	%	R	M	SD	%	R
Halaphanalaimus sp.	1.40	2.35	0.15	12					0.60	2.13	0.06	34
Pseudochromadora cazca									1.40	4.01	0.14	29
Daptonema sp.	0.20	0.89	0.02	21					2.65	5.89	0.27	23
Gammanema aff. *smithi*	0.20	0.89	0.02	21					0.95	3.07	0.10	30
Cytolaimium sp.												
Leptolaimus sp.												
Neochromadora sp.2	1.00	2.20	0.11	15					0.20	1.26	0.02	44
Halichoanolaimus aff. *chordiurus*												
Halalaimus bayensis	0.20	0.89	0.02	21					2.20	6.34	0.23	25
Gen Nov.1 sp.2									0.05	0.32	0.01	48
Neochromadora sp.3									0.75	2.71	0.08	31
Paralinhomeous sp.									0.30	1.40	0.03	40
Cephalanticoma sp.									0.45	2.00	0.05	37
Metacyatholaimus sp.									0.20	1.26	0.02	44
Pomponema sp.2									5.40	17.20	0.56	18
Setosabatieria sp.	0.20	0.89	0.02	21					0.80	3.97	0.08	31
Pomponema sp.1					0.40	2.53	0.13	20	5.65	11.84	0.58	17
Monhysteridae sp.					0.30	0.97	0.09	21				
Spilophorella aff. *euxina*					0.25	1.30	0.08	23				
Onyx cephalispiculum					0.15	0.95	0.05	25	9.10	22.43	0.94	14
Mesacanthion sp.									7.05	18.07	0.73	16
Paramesonchium sp.									1.60	5.51	0.16	27
Oncholaimus sp.2									0.70	2.20	0.07	33
Chromadoridae sp.									0.60	2.32	0.06	34
Odontophora serrata									0.35	1.92	0.04	38
Subsphaerolaimus sp.1									0.30	1.90	0.03	40
Endelophus sp.									0.15	0.70	0.02	44
Number of species		**27**				**27**				**50**		
Total mean density		**931**				**316**				**972**		
Number of samples		**20**				**40**				**40**		
Total number of nematodes		**18 620**				**12 652**				**38 860**		

habitat were also dominated by several other species that were either not present or abundant at A or C, *i.e. Bathylaimus australis, Metadesmolaimus* sp.1, *Pontonema* sp.1 and *Gomphionema typicum* (Table 5.1.4.1). Moreover, 12 nematode species were recorded at either C or J that were never found at A, while the opposite was true for four other species.

The nematode assemblages at habitats F, G and I, located in different regions of the main basin, were each dominated by *Spirinia parasitifera*, which ranked either first or second in terms of abundance. However, the percentage contribution and mean density of this species at F and I was about twice that at G. *Theristus* sp.2 was also abundant at all three of these habitats, ranking second at I (*ca* 16%) and third at both F and G (8-11%). *Dichromadora* sp. ranked within the top two species at habitats F and G, but its contribution to the nematofauna at the latter habitat (*i.e. ca* 22%) was more than twice that at the former, while *Metadesmolaimus* sp.1 was abundant and made similar contributions to both of these habitats. In contrast, neither of these species was abundant at habitat I. *Nannolaimoides decoratus* was abundant at both G and I, but was far more prevalent at the latter habitat. The remaining species that were abundant at either F, G or I were not abundant at the other two of those habitats, *i.e. Terschillingia* sp.1 and *Pontonema* sp.1 at F, *Viscosia glabra* at G and *B. australis* and *Halichoanolaimus duodecimpapillatus* at I. Eighteen species were recorded at one or more of these main basin habitats that were never recorded at either A or C in the upper estuary.

Like the above basin habitats, the nematofauna at the channel habitat M was dominated by *S. parasitifera*, which comprised *ca* 37% of the total density of individuals at that habitat (Table 5.1.4.1), and *Theristus* sp.2 was also abundant (*ca* 10%). The percentage contribution and mean density of the first of these species at M was slightly greater than that at I and far greater than that at G, whereas the contribution of the second species at M was less than at I and similar to that at G. Like habitats F and G, *Dichromadora* sp. was also abundant at M, but it made a far lower contribution to this channel habitat than either of those basin habitats, and particularly G, *i.e. ca* 6% *vs* 22%. However, *Chromodorina* sp. and *Comesoma arenae*, which were abundant and ranked second and fourth, respectively, at M, were not abundant at any other habitat. Furthermore, seven species were recorded at M that were not found at any other habitat (Table 5.1.4.1).

5.1.4.2 Spatial and temporal differences in mean species richness, density and taxonomic diversity

The replicate data for number of nematode species, density and taxonomic distinctness recorded seasonally throughout the Swan Estuary were each subjected to a preliminary three-way PERMANOVA to test whether their spatial differences were most appropriately analysed at the finer site or broader habitat level. These tests detected significant site and/or site x season effects in the case of number of species and taxonomic distinctness, but not of density. In view of these results, the replicate data for the first two dependent variables were then subjected to a site x season PERMANOVA, while that for the latter dependent variable was subjected to a habitat x season PERMANOVA, to better elucidate the nature and extent of their spatial differences.

The mean number of species differed significantly among sites and the site x season interaction, but the relative importance of the first of these effects was greater, as shown by the difference in their associated components of variation (Table 5.1.4.2). In contrast, mean taxonomic distinctness differed among all terms in the model, with the relative influence of the site x season interaction being the greatest, followed by that of site. Mean density of nematodes also differed among both main effects and the interaction, but the influence of habitat alone was far greater than that for either season or the habitat x season interaction (Table 5.1.4.2).

The mean number of nematode species was lowest at sites representing each of the upper estuary habitats A and C and also sites I1 and J2 during every season except winter, where the lowest values were recorded at sites C2, J2 and M1. These values typically ranged between seven and 11 species (Fig. 5.1.4.1a). In contrast, the highest mean values, or those close to the highest, were recorded at basin sites F1 and G2 in every season (*ca* 12-17 species) except for summer, at which the most speciose site was clearly M1 (*ca* 21 species). The values recorded at this site and the other channel site M2, were also relatively high in all other seasons except winter and summer, respectively. The significant site x season interaction detected for this dependent variable was due to the differences between sites in the range and rank order among seasons. For example, whereas the mean number of species at M1 ranged between *ca* eight species in winter to 21 species in summer, it ranged only between *ca* nine and 11 species throughout the year at C1. Differences in the seasonal rank order among sites were well exemplified by the fact that the greatest mean number of species were found in winter at sites A1, A2 and C1, whereas the least species were recorded in this season at F1, G2, J2 and M1 (Fig. 5.1.4.1a).

The mean density of nematodes was relatively low at the upper estuary habitats A and C and also J in the small upper basin in every season, with the exception of summer at habitat A (Fig. 5.1.4.1b). Particularly high mean densities were recorded at the basin habitats F, G and I in spring, while the values recorded at the channel habitat M during winter were notably higher than at any other habitat in that season. The greatest mean densities were recorded during spring at every habitat except A and M, at which densities were second highest in this season, while the

Table 5.1.4.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for site x season PERMANOVAs on the number of species and quantitative taxonomic distinctness of nematode assemblages and a habitat x season PERMANOVA on the density of nematodes recorded throughout the Swan Estuary during each season in 2005. df = degrees of freedom. Significant results are highlighted in bold.

	Number of Species					**Density**					**Quantitative Taxonomic Distinctness**				
	df	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p
Main Effects															
Habitat						6	**2427.600**	**32.036**	**8.331**	**0.001**					
Season	3	197.300	1.752	1.188	0.117	3	**730.810**	**9.644**	**3.469**	**0.001**	3	**345.420**	**22.657**	**2.346**	**0.001**
Site	11	**1404.600**	**12.469**	**8.037**	**0.001**						11	**233.970**	**15.346**	**3.307**	**0.001**
Two-way Interactions															
Habitat * Season						18	**201.390**	**2.658**	**3.851**	**0.001**					
Season * Site	33	**337.360**	**2.995**	**6.704**	**0.001**						33	**130.600**	**8.566**	**4.803**	**0.001**
Residual	192	112.650		10.613		212	75.776		8.705		192	15.246		3.905	

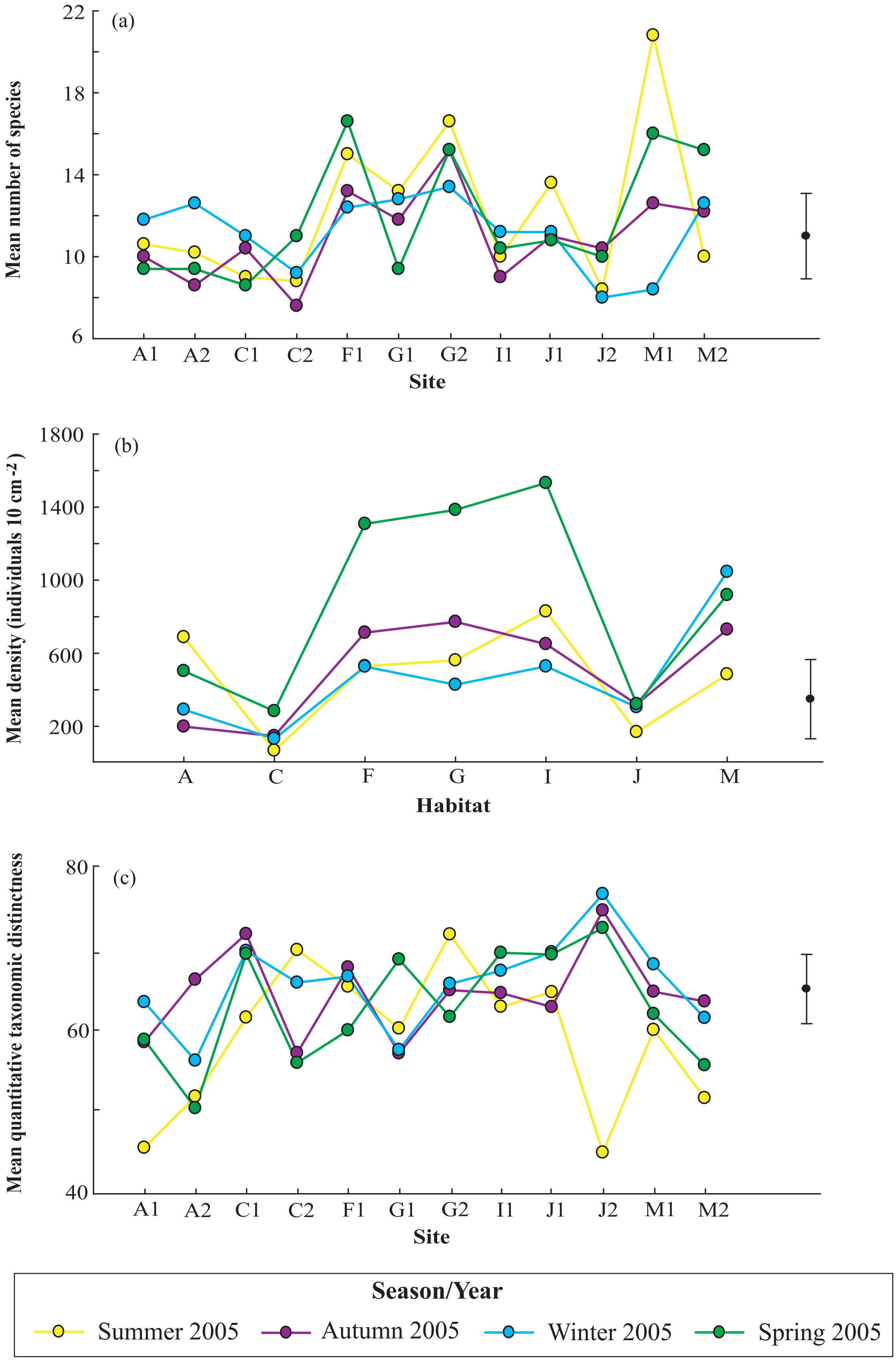


Figure 5.1.4.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the nematode assemblages recorded at each site/habitat in the Swan Estuary in each season in 2005. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

lowest or second lowest densities were found during winter at all habitats except M, at which they were the greatest in this season (Fig. 5.1.4.1b). Differences among habitats in the pattern and range of seasonal differences further contributed to the significant habitat x season interaction for this dependent variable. For example, whereas densities at habitat I ranged between *ca* 1550 individuals 10 cm^{-2} during spring to *ca* 550 individuals 10 cm^{-2} in winter, the seasonal range at habitat J was only *ca* 350-170 individuals 10 cm^{-2} in spring/autumn and summer, respectively (Fig. 5.1.4.1b).

The highly inconsistent seasonal trend in the magnitude of mean taxonomic distinctness among sites was clearly responsible for the relatively important site x season interaction detected for this dependent variable (Fig. 5.1.4.1c). Thus, there was little tendency for this diversity measure to be consistently greater or lower during any particular season among the various sites. Notably lower mean taxonomic distinctness values were recorded at sites A1 and J2 during summer than for any other site or season. However, the greatest values were recorded at that latter site in all other seasons, and relatively high values were also recorded at C1 during autumn, winter and spring (Fig. 5.1.4.1c).

5.1.4.3 Composition of nematode assemblages among habitats

A three-way PERMANOVA test was used initially to determine whether habitats, or their representative sites, were most appropriate for examining spatial differences in the composition of the nematofauna collected seasonally throughout the Swan Estuary. This test detected significant differences for all terms in the model, but the associated components of variation demonstrated that the influence of habitat was up to twice that of site or the site x season interaction. Furthermore, one-way ANOSIM tests for site, carried out separately for the data collected in each season in view of the above significant seasonal main effect and interaction, demonstrated that, while nearly all pairwise comparisons between sites were significant, the average extent of the differences between sites assigned to the same site (*i.e.* R=0.588) was far less than that between sites belonging to different habitats (R=0.900). Given the lesser importance of intra-habitat differences in nematode composition compared to the large differences between habitats, the following analyses to more thoroughly examine spatial differences in the nematofauna throughout the Swan Estuary were carried out at the habitat rather than site level. They were also performed separately for the data collected in each season, given the results of the above PERMANOVA test.

One-way ANOSIM tests for habitat type, carried out separately for the replicate data recorded in each season, demonstrated that nematofaunal compositions differed significantly in each case (p=0.1%), and that the overall extents of those differences were large (Global R=0.687-0.795). Although the extent of those spatial differences did not vary substantially among seasons, the greatest differences were detected in spring while the least occurred in winter (Table 5.1.4.3). All pairwise comparisons between habitats were significant in each season, except for the lower basin habitat I *vs* the channel habitat M in winter and spring and G *vs* F and I in summer. Furthermore, the R-statistics for the large majority of the significant pairwise comparisons typically ranged between 0.700 and 1.000, thus demonstrating that there were marked differences in nematode composition between most habitats (Table 5.1.4.3). The largest differences in species composition (*i.e.* those cases in which R >0.900), most commonly occurred between the uppermost habitat A and all other habitats except C and, to a lesser extent, J. Those cases in which R did not exceed 0.700 were typically for pairwise comparisons between the channel habitat M and the basin habitats F, G and I, and between other adjacent habitats, *e.g.* A *vs* C, C *vs* J and F *vs* G (Table 5.1.4.3).

The MDS ordination plots shown in Fig. 5.1.4.2 clearly illustrate that, in each season, groups of samples representing each habitat often exhibited a pronounced tendency to form distinct groups. Moreover, during summer and autumn, samples representing the upper estuary habitats A and C and the adjacent habitat J clearly tended to occupy one side of the plot, while those from the remaining basin habitats and the channel habitat were located on the opposite side (Fig. 5.1.4.2a and b). This trend was still largely true for winter and spring, except for the samples from habitat J, which occupied the region between the two main groups of samples from the upper *vs* middle to lower estuary (Fig. 5.1.4.2c and d).

In each season, samples representing habitat A formed a tight group on the MDS plots shown in Fig. 5.1.4.2, but this was particularly marked in summer and winter. Samples representing C and J were more widely dispersed in each season, and exhibited some tendency to intermingle with each other and/or A. SIMPER demonstrated that, in each season, the assemblage at habitat A was characterised exclusively by some nematode species (*e.g. Parodontophora aurata* and *Metalinhomeous* sp. in summer, winter and spring and *N. decoratus* and *Dichromadora* sp. in autumn), as well as by others that also typified the nematofaunas only at habitats C and/or J, *e.g. Theristus* sp.1 in each season, *Metadesmolaimus* sp.2 in summer and spring, *Pierrickia* sp. in autumn and spring and *Parascolaimus breviseta* in winter (Table 5.1.4.4). Moreover, in those cases in which the latter species were important in distinguishing the nematofauna at A from those at C and/or J, their abundances were always greater at the former habitat. While the species that characterised C and J exhibited some overlap in each season, they always contained some that were typical of one of these habitats but not the

Table 5.1.4.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the nematode composition among habitat types in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005. Insignificant pairwise comparisons are highlighted in grey.

(a) Summer 2005; p=0.1%, Global R=0.694

	A	C	F	G	I	J
C	0.654					
F	1.000	0.765				
G	0.918	0.791	0.037			
I	1.000	0.943	0.832	0.161		
J	0.570	0.243	0.828	0.873	0.997	
M	0.949	0.934	0.402	0.606	0.410	0.976

(b) Autumn 2005; p=0.1%, Global R=0.729

	A	C	F	G	I	J
C	0.310					
F	0.976	0.804				
G	0.973	0.906	0.327			
I	0.986	0.882	0.904	0.473		
J	0.819	0.544	0.934	0.873	0.921	
M	0.957	0.932	0.497	0.394	0.279	0.868

(c) Winter 2005; p=0.1%, Global R=0.687

	A	C	F	G	I	J
C	0.289					
F	1.000	0.737				
G	0.991	0.795	0.370			
I	1.000	0.716	0.700	0.501		
J	0.833	0.558	0.724	0.804	0.702	
M	0.966	0.888	0.373	0.390	0.313	0.729

(d) Spring 2005; p=0.1%, Global R=0.795

	A	C	F	G	I	J
C	0.178					
F	0.985	0.861				
G	0.998	0.950	0.345			
I	1.000	0.980	0.856	0.549		
J	0.946	0.789	0.996	0.928	1.000	
M	0.995	0.975	0.359	0.708	0.236	0.984

Table 5.1.4.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the nematode assemblages at each habitat in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Summer 2005

	A	C	F	G	I	J	M
A	*P. aurata* *Theristus* sp.1 *Metadesmolaimus* sp.2 *Metalinhomeous* sp.						
C	*P. aurata*^{A} *Theristus* sp.1^{A} *Metalinhomeous* sp.^{A} *Metadesmolaimus* sp.2^{A}	*Theristus* sp.1 *Metadesmolaimus* sp.2 *Pierrickia* sp. *Pontonema* sp.1					
F	*Theristus* sp.1^{A} *P. aurata*^{A} *Metadesmolaimus* sp.2^{A} *Theristus* sp.2^{F} *G. typicum*^{F} *S. parasitifera*^{F} *Pontonema* sp.1^{F} *Terschillingia* sp.1^{F} *H. duodecimpapillatus*^{F} *V. glabra*^{F} *Subsphaerolaimus* sp.^{F}	*Theristus* sp.2^{F} *H. duodecimpapillatus*^{F} *G. typicum*^{F} *S. parasitifera*^{F} *Pontonema* sp.1^{F} *Terschillingia* sp.1^{F} *V. glabra*^{F} *Dichromadora* sp.^{F} *Subsphaerolaimus* sp.^{F} *Theristus* sp.1^{C} *N. decoratus*^{F}	*Theristus* sp.2 *H. duodecimpapillatus* *S. parasitifera* *Terschillingia* sp.1 *G. typicum* *Pontonema* sp.1 *V. glabra* *Dichromadora* sp.				
G	*P. aurata*^{A} *Theristus* sp.1^{A} *Theristus* sp.2^{G} *Metalinhomeous* sp.^{A} *V. glabra*^{G}	*Theristus* sp.2^{G} *V. glabra*^{G} *Theristus* sp.1^{C}	▨	*Theristus* sp.2 *H. duodecimpapillatus*			
I	*P. aurata*^{A} *Theristus* sp.1^{A} *Theristus* sp.2^{I} *H. duodecimpapillatus*^{I} *S. parasitifera*^{I} *Metadesmolaimus* sp.2^{A} *Metalinhomeous* sp.^{A} *V. glabra*^{I}	*H. duodecimpapillatus*^{I} *Theristus* sp.2^{I} *S. parasitifera*^{I} *N. decoratus*^{I} *Theristus* sp.1^{C}	*Pontonema* sp.1^{F} *H. duodecimpapillatus*^{I} *G. typicum*^{F} *Subsphaerolaimus* sp.^{F} *S. parasitifera*^{I}	▨	*H. duodecimpapillatus* *Theristus* sp.2 *S. parasitifera* *N. decoratus* *V. glabra*		

	A	C	F	G	I	J	M
J	*P. aurata*^{A} *Theristus* sp.1^{A} *G. typicum*^{J} *Metadesmolaimus* sp.2^{A}	*Pierrickia* sp.^{J} *G. typicum*^{J}	*Theristus* sp.2^{F} *H. duodecimpapillatus*^{F} *S. parasitifera*^{F} *Terschillingia* sp.1^{F} *Metadesmolaimus* sp.2^{J} *Theristus* sp.1^{J} *V. glabra*^{F} *Subsphaerolaimus* sp.^{F}	*Theristus* sp.2^{G} *Theristus* sp.1^{J}	*H. duodecimpapillatus*^{I} *Theristus* sp.2^{I} *S. parasitifera*^{I} *N. decoratus*^{I} *Metadesmolaimus* sp.2^{J} *Theristus* sp.1^{J} *V. glabra*^{I}	*Metadesmolaimus* sp.2 *Theristus* sp.1 *G. typicum*	
M	*P. aurata*^{A} *Theristus* sp.1^{A} *Metadesmolaimus* sp.2^{A} *H. duodecimpapillatus*^{M}	*Theristus* sp.1^{C}	*G. typicum*^{F} *Theristus* sp.2^{F} *Terschillingia* sp.1^{F} *Dichromadora* sp.^{F} *Subsphaerolaimus* sp.^{F}	*Theristus* sp.2^{G}	*Theristus* sp.2^{I} *S. parasitifera*^{I}	*G. typicum*^{J} *Metadesmolaimus* sp.2^{J} *Theristus* sp.1^{J}	*C. arenae* *O. cephalispiculum*

(b) Autumn 2005

	A	C	F	G	I	J	M
A	*Theristus* sp.1 *H. duodecimpapillatus* *N. decoratus* *Pierrickia* sp. *Dichromadora* sp.						
C	*N. decoratus*^{A}	*Theristus* sp.1 *Pierrickia* sp. *Pontonema* sp.1 *Metadesmolaimus* sp.2 *P. aurata*					
F	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *Terschillingia* sp.1^{F} *S. parasitifera*^{F} *H. duodecimpapillatus*^{F} *Theristus* sp.1^{A} *Metadesmolaimus* sp.1^{F} *Theristus* sp.2^{F} *V. glabra*^{F} *Dichromadora* sp.^{A}	*Pontonema* sp.1^{F} *H. duodecimpapillatus*^{F} *Subsphaerolaimus* sp.^{F} *Terschillingia* sp.1^{F} *S. parasitifera*^{F} *Metadesmolaimus* sp.1^{F} *Theristus* sp.1^{C} *Metadesmolaimus* sp.2^{C} *Theristus* sp.2^{F}	*Pontonema* sp.1 *H. duodecimpapillatus* *Subsphaerolaimus* sp. *Terschillingia* sp.1 *S. parasitifera* *Metadesmolaimus* sp.1 *Theristus* sp.2				
G	*P. cazca*^{G} *Metadesmolaimus* sp.1^{G} *H. duodecimpapillatus*^{G} *C. arenae*^{G} *Theristus* sp.2^{G} *Theristus* sp.1^{A} *C. papillatus*^{G} *N. decoratus*^{A} *Dichromadora* sp.^{A}	*H. duodecimpapillatus*^{G} *P. cazca*^{G} *Metadesmolaimus* sp.1^{G} *C. arenae*^{G} *Theristus* sp.2^{G} *C. papillatus*^{G} *Theristus* sp.1^{C}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *P. cazca*^{G} *S. parasitifera*^{F} *Pierrickia* sp.^{F}	*H. duodecimpapillatus* *P. cazca* *Theristus* sp.2 *C. arenae* *Terschillingia* sp.1 *C. papillatus*			
I	*S. parasitifera*^{I} *H. duodecimpapillatus*^{I} *Terschillingia* sp.1^{I} *Theristus* sp.1^{A} *Pierrickia* sp.^{A} *Metadesmolaimus* sp.1^{I} *V. glabra*^{I} *Dichromadora* sp.^{A}	*S. parasitifera*^{I} *H. duodecimpapillatus*^{I} *Terschillingia* sp.1^{I} *Pierrickia* sp. nov.^{C} *Metadesmolaimus* sp.1^{I} *Theristus* sp.1^{C} *Metadesmolaimus* sp.2^{C}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *Pierrickia* sp.^{F} *Terschillingia* sp.1^{F}	*P. cazca*^{G} *C. arenae*^{G} *S. parasitifera*^{I} *C. papillatus*^{G}	*S. parasitifera* *H. duodecimpapillatus* *Terschillingia* sp.1 *Metadesmolaimus* sp.1		
J	*B. australis*^{J} *N. decoratus*^{A} *Metadesmolaimus* sp.1^{J} *Theristus* sp.2^{J} *H. duodecimpapillatus*^{A} *Dichromadora* sp.^{A} *Chromadorina* sp.^{J}	*B. australis*^{J} *Pierrickia* sp.^{C} *Metadesmolaimus* sp.1^{J} *Metadesmolaimus* sp.2^{C} *Theristus* sp.2^{J}	*Pontonema* sp.1^{F} *H. duodecimpapillatus*^{F} *Terschillingia* sp.1^{F} *Subsphaerolaimus* sp.^{F} *S. parasitifera*^{F} *Theristus* sp.1^{J} *Chromadorina* sp.^{J}	*H. duodecimpapillatus*^{G} *P. cazca*^{G} *Metadesmolaimus* sp.1^{G} *C. arenae*^{G} *Terschillingia* sp.1^{G} *C. papillatus*^{G} *Theristus* sp.1^{J}	*H. duodecimpapillatus*^{I} *Terschillingia* sp.1^{I} *S. parasitifera*^{I} *Theristus* sp.1^{J} *V. glabra*^{I} *Chromadorina* sp.^{J} *N. decoratus*^{I}	*Theristus* sp.1 *B. australis* *Metadesmolaimus* sp.1 *Theristus* sp.2 *Chromadorina* sp. *S. parasitifera*	

	A	C	F	G	I	J	M
M	*C. arenae*^{M} *S. parasitifera*^{M} *Theristus* sp.1^{A} *Theristus* sp.2^{M} *Pierrickia* sp.^{A} *N. decoratus*^{A} *Terschillingia* sp.1^{M} *Dichromadora* sp.^{A}	*C. arenae*^{M} *S. parasitifera*^{M} *Pierrickia* sp.^{C} *Theristus* sp.2^{M} *Theristus* sp.1^{C}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *C. arenae*^{M} *S. parasitifera*^{M} *Pierrickia* sp.^{F} *Metadesmolaimus* sp.1^{M}	*P. cazca*^{G} *C. papillatus*^{G} *Theristus* sp.2^{M}		*C. arenae*^{M} *Theristus* sp.1^{J} *Metadesmolaimus* sp.1^{M} *Theristus* sp.2^{M} *Chromadorina* sp.^{J}	*C. arenae* *S. parasitifera* *H. duodecimpapillatus* *Theristus* sp.2

(c) Winter 2005

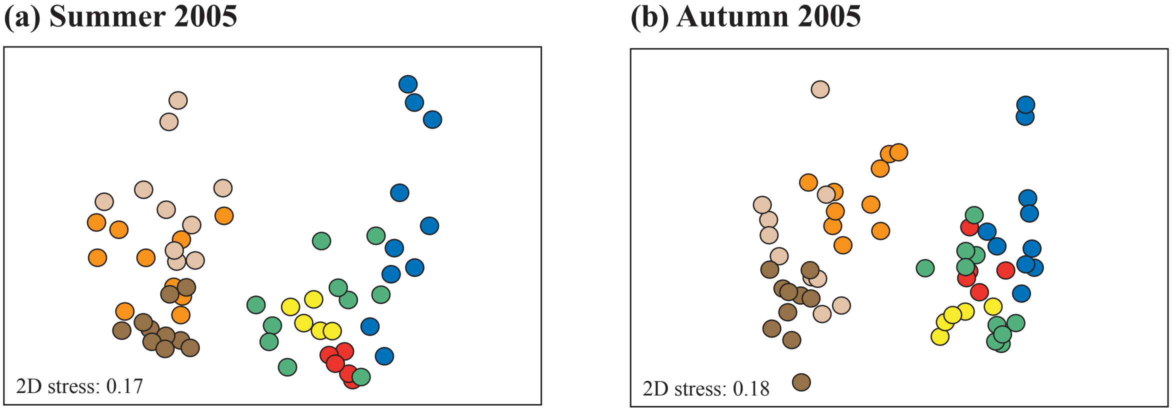
	A	C	F	G	I	J	M
A	*P. breviseta* *Theristus* sp.1 *P. aurata* *H. duodecimpapillatus* *Metalinhomeous* sp. *Pontonema* sp.1						
C	*P. breviseta*^{A} *Pontonema* sp.1^{A}	*Theristus* sp.1 *P. breviseta* *V. glabra* *Pierrickia* sp. *Metadesmolaimus* sp.2 *Dichromadora* sp.					
F	*P. breviseta*^{A} *Metadesmolaimus* sp.1^{F} *Theristus* sp.1^{A} *S. parasitifera*^{F} *Subsphaerolaimus* sp.^{F} *P. aurata* sp. nov.^{A} *Theristus* sp.2^{F} *Metalinhomeous* sp.^{A} *H. duodecimpapillatus*^{F}	*Pontonema* sp.1^{F} *Metadesmolaimus* sp.1^{F} *Subsphaerolaimus* sp.^{F} *S. parasitifera*^{F} *Theristus* sp.2^{F} *H. duodecimpapillatus*^{F} *Pierrickia* sp.^{C} *Theristus* sp.1^{C} *Metadesmolaimus* sp.2^{C}	*Pontonema* sp.1 *Metadesmolaimus* sp.1 *S. parasitifera* *Theristus* sp.2 *V. glabra* *Dichromadora* sp.				
G	*P. breviseta*^{A} *Theristus* sp.2^{G} *Metadesmolaimus* sp.1^{G} *P. cazca*^{G} *P. aurata*^{A} *C. arenae*^{G} *Theristus* sp.1^{A} *Metalinhomeous* sp.^{A} *H. duodecimpapillatus*^{G}	*Theristus* sp.2^{G} *Metadesmolaimus* sp.1^{G} *P. cazca*^{G} *C. arenae*^{G} *H. duodecimpapillatus*^{G} *V. glabra*^{G}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *P. cazca*^{G} *C. arenae*^{G} *Dichromadora* sp.$^{-}$ *Theristus* sp.2^{G}	*Theristus* sp.2 *Metadesmolaimus* sp.1 *P. cazca* *H. duodecimpapillatus* *C. arenae* *V. glabra* *Chromadorina* sp.			
I	*P. breviseta*^{A} *S. parasitifera*^{I} *Metadesmolaimus* sp.1^{I} *Theristus* sp.2^{I} *Pierrickia* sp.^{A} *P. aurata*^{A} *Theristus* sp.1^{A} *Metalinhomeous* sp.^{A} *Pontonema* sp.1^{A} *Halaphanalaimus* sp.^{I}	*S. parasitifera*^{I} *Metadesmolaimus* sp.1^{I} *Theristus* sp.2^{I} *H. duodecimpapillatus*^{I} *Halaphanalaimus* sp.^{I} *Metadesmolaimus* sp.2^{C} *V. glabra*^{C} *Dichromadora* sp.^{C}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *Terschillingia* sp.1^{F} *N. decoratus*^{I}	*P. cazca*^{G} *C. arenae*^{G} *Halaphanalaimus* sp.^{I}	*H. duodecimpapillatus* *Metadesmolaimus* sp.1 *S. parasitifera* *Theristus* sp.2 *V. glabra*		

	A	C	F	G	I	J	M
J	*P. breviseta*^{A} *P. aurata*^{A} *Metadesmolaimus* sp.1^{J} *Metalinhomeous* sp.^{A} *H. duodecimpapillatus*^{A} *Theristus* sp.1^{A} *Terschillingia* sp.1^{A}	*B. australis*^{J} *Metadesmolaimus* sp.1^{J} *S. parasitifera*^{J}	*Subsphaerolaimus* sp.^{F} *Terschillingia* sp.1^{F} *S. parasitifera*^{F} *O. domesticus*^{J} *Theristus* sp.1^{J} *H. duodecimpapillatus*^{F} *Theristus* sp.2^{F} *Pierrickia* sp.^{F} *V. glabra*^{F} *Chromadorina* sp.^{F}	*P. cazca*^{G} *H. duodecimpapillatus*^{G} *Theristus* sp.2^{G} *C. arenae*^{G} *V. glabra*^{G} *Dichromadora* sp.^{J}	*H. duodecimpapillatus*^{I} *S. parasitifera*^{I} *Theristus* sp.2^{I} *V. glabra*^{I} *Halaphanalaimus* sp.^{I} *Dichromadora* sp.^{J} *Chromadorina* sp.^{I}	*B. australis* *O. domesticus* *Theristus* sp.1 *Dichromadora* sp. *Metadesmolaimus* sp.1 *Pontonema* sp.1	
M	*P. breviseta*^{A} *S. parasitifera*^{M} *Theristus* sp.1^{A} *C. arenae*^{M} *Pierrickia* sp.^{A} *P. aurata* sp.^{A} *Dichromadora* sp.^{M} *Metalinhomeous* sp.^{A} *Pontonema* sp.1^{A} *H. duodecimpapillatus*^{M}	*Chromadorina* sp.^{M} *S. parasitifera*^{M} *C. arenae*^{M} *H. duodecimpapillatus*^{M} *Dichromadora* sp.^{M}	*Pontonema* sp.1^{F} *Subsphaerolaimus* sp.^{F} *Theristus* sp.2^{M} *S. parasitifera*^{M} *Dichromadora* sp.^{M} *C. arenae*^{M}	*S. parasitifera*^{M} *Theristus* sp.2^{G} *P. cazca*^{G} *C. arenae*^{M}	*Chromadorina* sp.^{M} *Theristus* sp.2^{M} *C. arenae*^{M} *Halaphanalaimus* sp.^{I}	*Chromadorina* sp.^{M} *S. parasitifera*^{M} *C. arenae*^{M} *H. duodecimpapillatus*^{M} *Dichromadora* sp.^{M}	*Chromadorina* sp. *S. parasitifera* *H. duodecimpapillatus* *C. arenae*

(d) Spring 2005

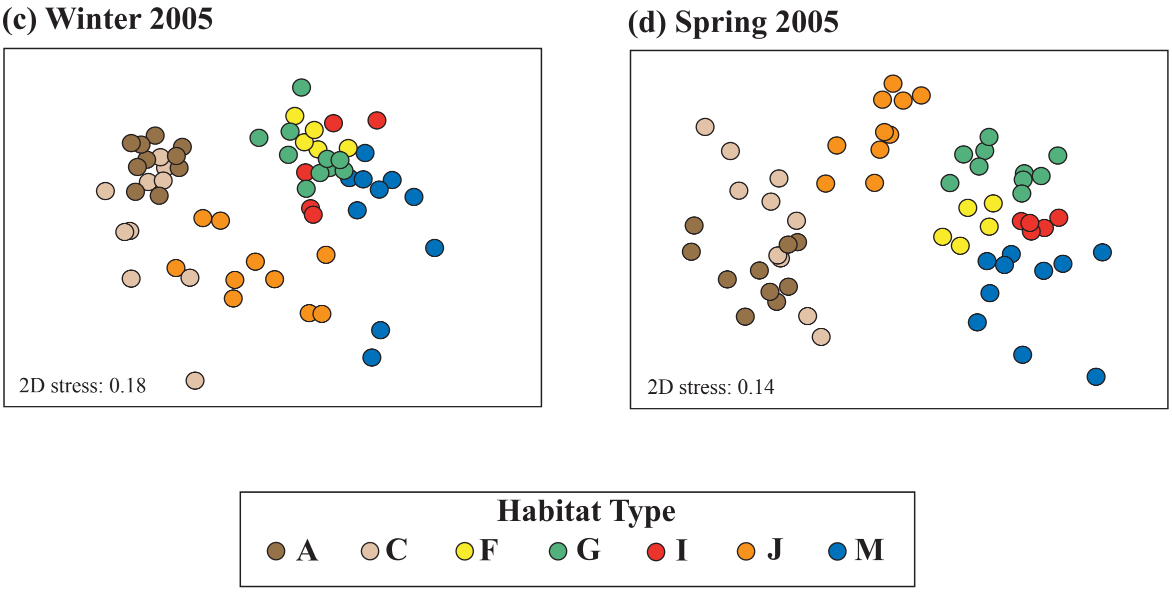
	A	C	F	G	I	J	M
A	*Theristus* sp.1 *Metalinhomeous* sp. *Metadesmolaimus* sp.2 *P. aurata* *Pierrickia* *N. decoratus*						
C	*Theristus* sp.1^{A} *Metalinhomeous* sp.^{A} *P. aurata*^{A} *N. decoratus*^{A}	*Pierrickia* sp. *Pontonema* sp.1 *Metadesmolaimus* sp.2 *Theristus* sp.1 *P. breviseta* sp. *Dichromadora* sp.					
F	*Dichromadora* sp.^{F} *Theristus* sp.1^{A} *S. parasitifera*^{F} *C. arenae*^{F} *G. typicum*^{F} *Terschillingia* sp.1^{F} *P. aurata*^{A} *Pontonema* sp.1^{F} *V. glabra*^{F} *Metadesmolaimus* sp.2^{A} *H. duodecimpapillatus*^{F} *Chromadorina* sp.^{F} *Metalinhomeous* sp.^{A} *Metadesmolaimus* sp.1^{F} *Theristus* sp.2^{F}	*N. decoratus*^{F} *Dichromadora* sp.^{F} *S. parasitifera*^{F} *G. typicum*^{F} *C. arenae*^{F} *Terschillingia* sp.1^{F} *H. duodecimpapillatus*^{F} *V. glabra*^{F} *Chromadorina* sp.^{F} *Theristus* sp.2^{F} *Metadesmolaimus* sp.1^{F}	*N. decoratus* *Dichromadora* sp. *Pontonema* sp.1 *H. duodecimpapillatus* *C. arenae* *S. parasitifera* *G. typicum* *Chromadorina* sp. *Theristus* sp.2 *Metadesmolaimus* sp.1				
G	*Dichromadora* sp.^{G} *Pontonema* sp.1^{G} *Theristus* sp.1^{A} *V. glabra*^{G} *Metalinhomeous* sp.^{A} *P. aurata*^{A} *N. decoratus*^{G} *Pierrickia*^{A} *Metadesmolaimus* sp.2^{A} *Metadesmolaimus* sp.1^{G} *S. parasitifera*^{G}	*Dichromadora* sp.^{G} *Pontonema* sp.1^{G} *N. decoratus*^{G} *V. glabra*^{G} *Metadesmolaimus* sp.1^{G}	*Dichromadora* sp.^{G} *G. typicum*^{F} *N. decoratus*^{G}	*Pontonema* sp.1 *Dichromadora* sp. *V. glabra* *N. decoratus* *Metadesmolaimus* sp.1 *S. parasitifera* *Chromadorina* sp.			

	A	C	F	G	I	J	M
I	*B. australis*^{I} *N. decoratus*^{I} *Theristus* sp.1^{A} *Theristus* sp.2^{I} *Dichromadora* sp.^{I} *Metadesmolaimus* sp.1^{I} *Metalinhomeous* sp.^{A} *P. aurata*^{A} *H. duodecimpapillatus*^{I} *S. parasitifera*^{I} *Chromadorina* sp.^{I} *Pierrickia* sp.^{A} *Metadesmolaimus* sp.2^{A} *V. glabra*^{I}	*N. decoratus*^{I} *B. australis*^{I} *Theristus* sp.2^{I} *Dichromadora* sp.^{I} *H. duodecimpapillatus*^{I} *Metadesmolaimus* sp.1^{I} *Chromadorina* sp.^{I} *Pierrickia* sp.^{C} *S. parasitifera*^{I} *Pontonema* sp.1^{C} *Theristus* sp.1^{C}	*B. australis*^{I} *Pontonema* sp.1^{F} *C. arenae*^{F} *G. typicum*^{F} *Dichromadora* sp.^{F} *Terschillingia* sp.1^{F} *Theristus* sp.2^{I} *Metadesmolaimus* sp.1^{I}	*Pontonema* sp.1^{G} *B. australis*^{I} *S. parasitifera*^{I}	*N. decoratus* *B. australis* *Dichromadora* sp. *Theristus* sp.2 *H. duodecimpapillatus* *Metadesmolaimus* sp.1 *S. parasitifera* *V. glabra* *Chromadorina* sp.		
J	*Pontonema* sp.1^{J} *Metalinhomeous* sp.^{A} *Metadesmolaimus* sp.2^{A} *Pierrickia* sp.^{A} *Metadesmolaimus* sp.1^{J} *P. aurata*^{A} *O. domesticus*^{J} *N. decoratus*^{A} *Dichromadora* sp.^{J} *B. australis*^{J}	*Pontonema* sp.1^{J} *Metadesmolaimus* sp.2^{C} *O. domesticus*^{J} *Metadesmolaimus* sp.1^{J} *Theristus* sp.1^{C} *B. australis*^{J}	*N. decoratus*^{F} *Terschillingia* sp.1^{F} *S. parasitifera*^{F} *C. arenae*^{F} *H. duodecimpapillatus*^{F} *V. glabra*^{F} *Dichromadora* sp.^{F} *G. typicum*^{F} *O. domesticus*^{J} *Chromadorina* sp.^{F} *Theristus* sp.1^{J} *Theristus* sp.2^{F} *B. australis*^{J}	*Dichromadora* sp.^{G} *V. glabra*^{G} *N. decoratus*^{J} *Theristus* sp.1^{J} *O. domesticus*^{J} *Theristus* sp.2^{G} *S. parasitifera*^{G} *Metadesmolaimus* sp.1^{G}	*N. decoratus*^{I} *Pontonema* sp.1^{J} *B. australis*^{I} *H. duodecimpapillatus*^{I} *Theristus* sp.2^{I} *Terschillingia* sp.1^{I} *S. parasitifera*^{I} *Theristus* sp.1^{J} *V. glabra*^{I} *Chromadorina* sp.^{I} *O. domesticus*^{J} *Dichromadora* sp.^{I}	*Pontonema* sp.1 *Dichromadora* sp. *Theristus* sp.1 *Metadesmolaimus* sp.1 *O. domesticus* *B. australis*	
M	*Theristus* sp.1^{A} *Chromadorina* sp.^{M} *C. arenae*^{M} *S. parasitifera*^{M} *P. aurata*^{A} *Pierrickia* sp.^{A} *Metadesmolaimus* sp.2^{A} *Metalinhomeous* sp.^{A} *Theristus* sp.2^{M} *Metadesmolaimus* sp.1^{M}	*Chromadorina* sp.^{M} *C. arenae*^{M} *S. parasitifera*^{M} *Pierrickia* sp.^{C} *Theristus* sp.1^{C} *Theristus* sp.2^{M} *Metadesmolaimus* sp.1^{M}	*Pontonema* sp.1^{F} *G. typicum*^{F} *Terschillingia* sp.1^{F} *V. glabra*^{F}	*Pontonema* sp.1^{G} *Dichromadora* sp.^{G} *V. glabra*^{G} *C. arenae*^{M}		*Pontonema* sp.1^{J} *Chromadorina* sp.^{M} *C. arenae*^{M} *S. parasitifera*^{M} *Theristus* sp.1^{J} *Theristus* sp.2^{M} *V. glabra*^{M}	*C. arenae* *Chromadorina* sp. *S. parasitifera* *Dichromadora* sp. *V. glabra* *Theristus* sp.2



(a) Summer 2005

(b) Autumn 2005



(c) Winter 2005

(d) Spring 2005

Figure 5.1.4.2: MDS ordination plots constructed from the nematode assemblage data recorded in each replicate sample at each habitat in the Swan Estuary during (a) summer, (b) autumn, (c) winter and (d) spring 2005.

other. Examples of species that were characteristic of the faunas at C but not those at J included *Pierrickia* sp. in each season, *Pontonema* sp.1 in summer and autumn and *V. glabra* in winter, while the opposite was true for *Gomphionema typicum* in summer, *B. australis* in autumn, winter and spring and *Oncholaimus domesticus* in winter and spring (Table 5.1.4.4).

Samples from the channel habitat M tended, in every season, to be located furthest from those representing the upper estuary habitats on the ordination plots shown in Fig. 5.1.4.2, and were typically the most distinct of the habitats in the middle to lower estuary. However, they were also among the most dispersed in each case, and particularly during summer and winter (Fig. 5.1.4.2a and c). Samples from the basin habitats F, G and I each formed relatively tight groups on the MDS plots that were either discrete yet lay relatively close to each other (which was often the case with those from F and I), or tended to intermingle with each other, which was typically the case with those from G (Fig. 5.1.4.2). The nematofauna at habitat M was typified by only two species in summer*, C. arenae* and *Onyx cephalispiculum*, neither of which was important in distinguishing it from that at other habitats in this season (Table 5.1.4.4a). In contrast, the first of these species was also among those that characterised the nematofaunas at M in each of the remaining seasons, and it was often important in distinguishing the assemblages at this habitat from those at most others (Table 5.1.4.4b-d). The same was also true of *S. parasitifera*, *Theristus* sp.2 and *Chromadorina* sp. in at least two of those seasons. The assemblages at the basin habitats F, G and I shared several common characteristic species in each season, such as *H. duodecimpapillatus*, *Theristus* sp.2 and *S. parasitifera* in all or most cases (Table 5.1.4.4). However, the suite of characteristic species at each of these habitats frequently contained some that were not typical of those at either of the other two basin habitats. For example, F was the only main basin habitat to be characterised by *Pontonema* sp.1 in every season, with the minor exception that it also typified the fauna at habitat G in spring, *Pseudochromadora cazca* was only prevalent at G in autumn and winter and *B. australis* was characteristic of the nematofauna only at I in spring (Table 5.1.4.4).

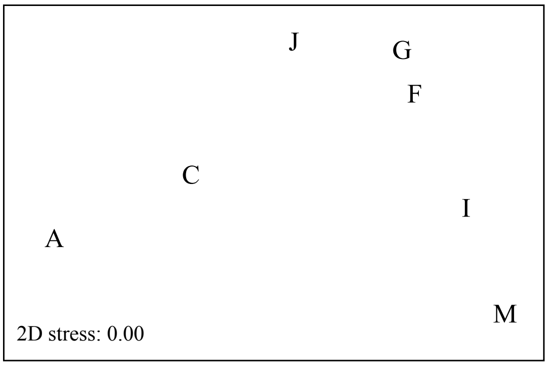
5.1.4.4 Matching spatial patterns between the environmental and nematode assemblage characteristics of habitats

RELATE demonstrated that, in all sampling seasons, the spatial pattern among habitats, as defined by their enduring environmental characteristics, significantly matched that exhibited by the composition of their nematode faunas (p=0.1-0.4%). The extent of that correlation was high in autumn, winter and spring (ρ=0.700-0.788) and moderate in summer (ρ=0.581), thus indicating that, in each season, the relative spatial differences in the enduring environmental characteristics of habitat types provided a reliable surrogate for those in the composition of the nematofauna. These results are illustrated by the similarities in the spatial distribution of points representing the various habitats on the MDS plots shown in Fig. 5.1.4.3 of the average (a) enduring environmental composition at each habitat type and (b-e) nematode species composition at each habitat type in each season.

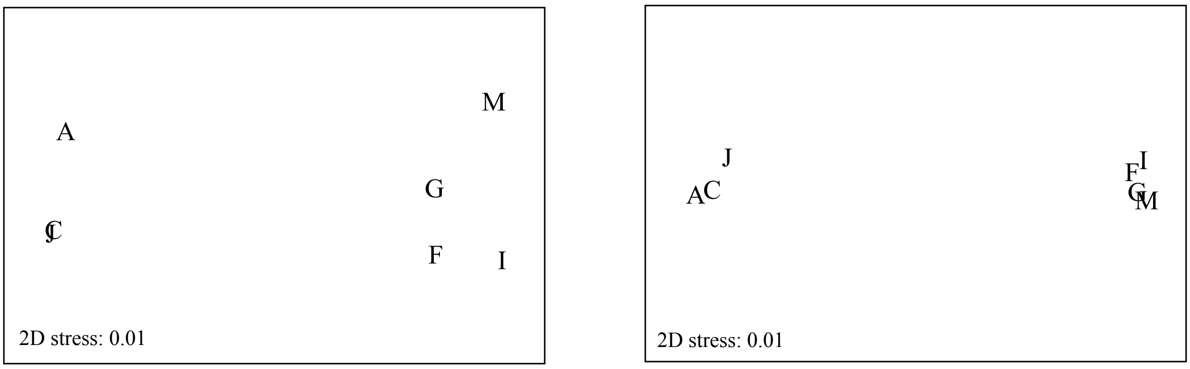
Each of the matrices constructed from the average species abundances at each habitat in each individual season were then matched with the complementary matrices constructed from the suite of non-enduring (i) water quality parameters (*i.e.* salinity, temperature and dissolved oxygen) and (ii) sediment parameters (*i.e.* mean grain size, sedimentary chlorophyll concentration, organic matter content and transition zone depth). Significant correlations were detected in all cases (p=0.1-2.9%), except for in summer. The extent of the correlations between the complementary faunal and water quality matrices in autumn, winter and spring (*i.e.* ρ=0.709, 0.844 and 0.744, respectively) were largely similar to those obtained for the comparable analyses between the faunal and enduring environmental matrices. However, those between the complementary faunal and sediment quality matrices were, in all seasons except summer, considerably lower than those detected in the comparable analyses between the faunal and enduring matrices, *i.e.* ρ=0.518, 0.566, 0.457 and 0.529 for summer, autumn, winter and spring 2005, respectively.

The BIOENV routine was then used to ascertain whether the correlation between the complementary nematofaunal and non-enduring environmental matrices could be improved by using only a subset of water or sediment variables, rather than the full suites. Note that these analyses were performed on the averages of data recorded at each site rather than habitat type, in order to maximise the number of samples in the reference (faunal) matrices and thus minimise the likelihood of BIOENV finding a subset of water or sediment quality variables that provided a good match with those references by chance. Prior to undertaking these BIOENV tests, RELATE was used to match the complementary nematode and water/sediment quality matrices constructed from the averages recorded at each site to determine whether the resulting correlations in each season were comparable with those obtained previously using habitat averages. Similar results were obtained for the matches between the faunal and water quality matrices in summer and spring, but the correlations obtained using site averages in autumn and winter (*i.e.* ρ=0.570 and 0.713, respectively) were lower than those obtained previously using habitat averages (*i.e.* ρ=0.709 and 0.844, respectively). The matches between the faunal and sediment quality matrices in each season were lower than those obtained using habitat averages, *i.e.* ρ=0.244, 0.151, 0.192 and 0.441, in summer, autumn, winter and spring 2005, respectively.

(a) Enduring environmental data



(b) Summer 2005; p=0.4%, ρ=0.581 **(c) Autumn 2005; p=0.2%, ρ=0.788**



(d) Winter 2005; p=0.2%, ρ=0.700 **(e) Spring 2005; p=0.1%, ρ=0.757**

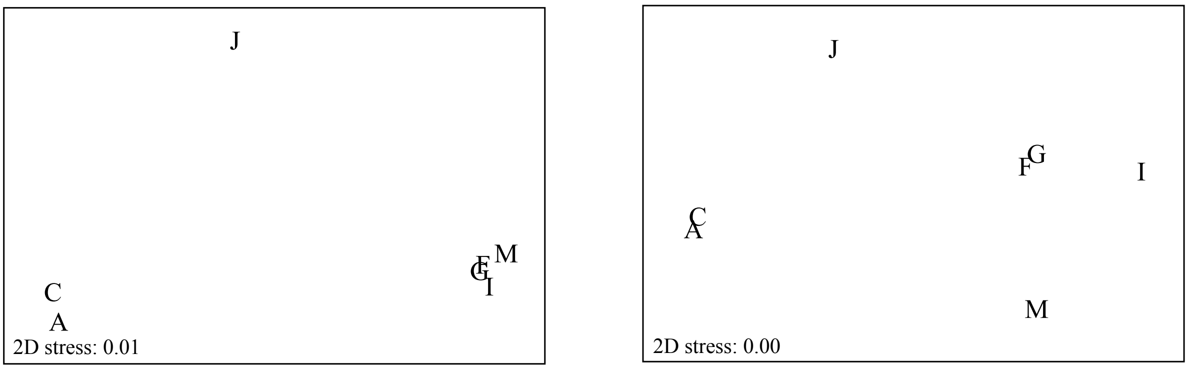


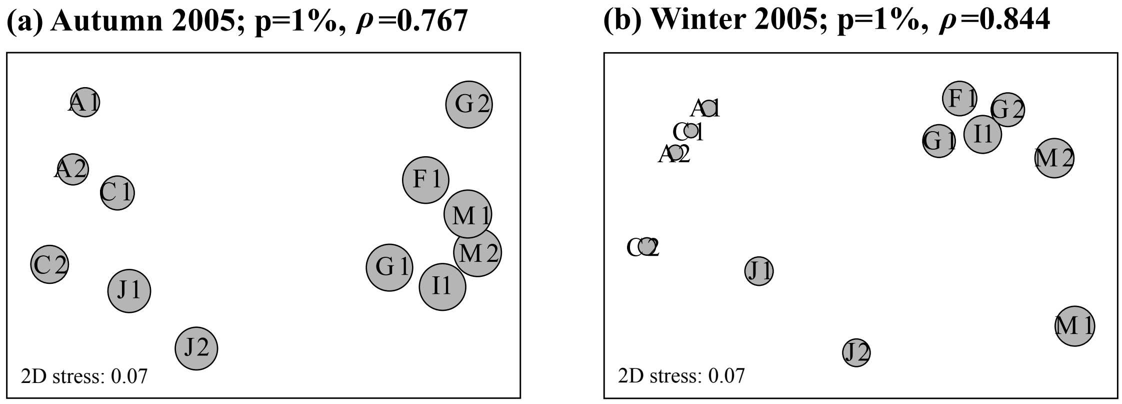
Figure 5.1.4.3: MDS ordination plots constructed from the averages at each habitat type in the Swan Estuary of their (a) enduring environmental measurements and (b-e) nematode composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the above nematode assemblage data are also provided for each season.

BIOENV detected significant and improved matches between the faunal and water quality matrices in autumn, winter and spring when data for only salinity were employed, *i.e.* p=1%, ρ=0.767, 0.844 and 0.830, respectively. Significant and slightly improved results were detected between the faunal and sediment parameter matrices only during spring when data for both organic matter content and chlorophyll concentration were employed (p=1%, ρ=0.478). The relationships between the spatial differences in the composition of the nematode assemblages and the magnitude of the non-enduring environmental parameters selected by the BIOENV procedure are illustrated, for each season in which significant results were obtained, by the MDS and associated bubble plots shown in Fig. 5.1.4.4. In autumn, winter and spring, but particularly the latter two seasons, the pronounced difference in the average species composition of sites representing habitats A, C and, to a lesser extent, J *vs* those from the remaining habitats, were well reflected by the lower salinities recorded at those first three habitats (Fig. 5.1.4.4a-c). Furthermore, the above spatial differences in the average species assemblages recorded during spring were, to a moderate extent, also reflected by the lower sedimentary chlorophyll concentrations recorded at sites from J and the greater organic matter content found at sites from habitats A and C (Fig. 5.1.4.4d and e).

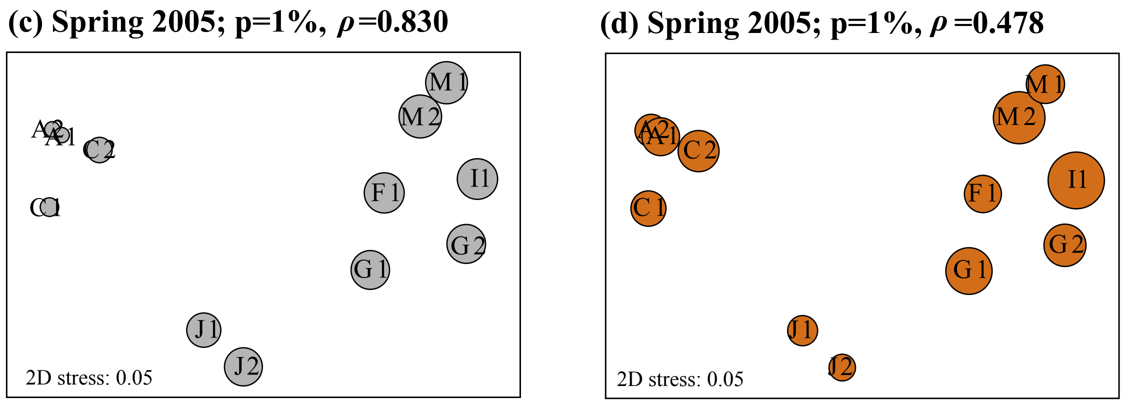
5.1.4.5 Composition of nematode assemblages among seasons

The composition of the nematofauna was shown by ANOSIM to differ significantly among seasons at each individual habitat (p=0.1%). The overall extent of those seasonal differences was far greater at each of the basin habitats F, G, I and J (Global R=0.511-0.705) than at the two upper estuary habitats A and C and the channel habitat M (Global R=0.173-0.322). All pairwise comparisons between seasons were significant at every habitat, except for summer *vs* autumn and winter *vs* spring at habitat C. The extents of the seasonal differences in nematofaunal composition at each habitat are illustrated by the MDS ordination plots and associated global ANOSIM results presented in Fig. 5.1.4.5.

The species compositions recorded during spring at the main basin habitats F, G and I tended to be most distinct from those recorded in each of the other seasons, *i.e.* R=0.660-0.752 at F, R=0.572-0.751 at G and R=0.812-0.928 at I. This was also illustrated by the fact that samples representing spring on the MDS plots of the nematofaunal data recorded at each of these three habitats tended to form a group to one side of those plots that was essentially discrete from samples representing each of the other seasons (Fig. 5.1.4.5c-e). Considerable differences in nematode composition were also detected for summer *vs* autumn at F (R=0.880) and for summer *vs* autumn and winter at I (R=0.528-0.652), which is also reflected by the degree of separation


(a) Autumn 2005; p=1%, ρ=0.767

(b) Winter 2005; p=1%, ρ=0.844


(c) Spring 2005; p=1%, ρ=0.830

(d) Spring 2005; p=1%, ρ=0.478

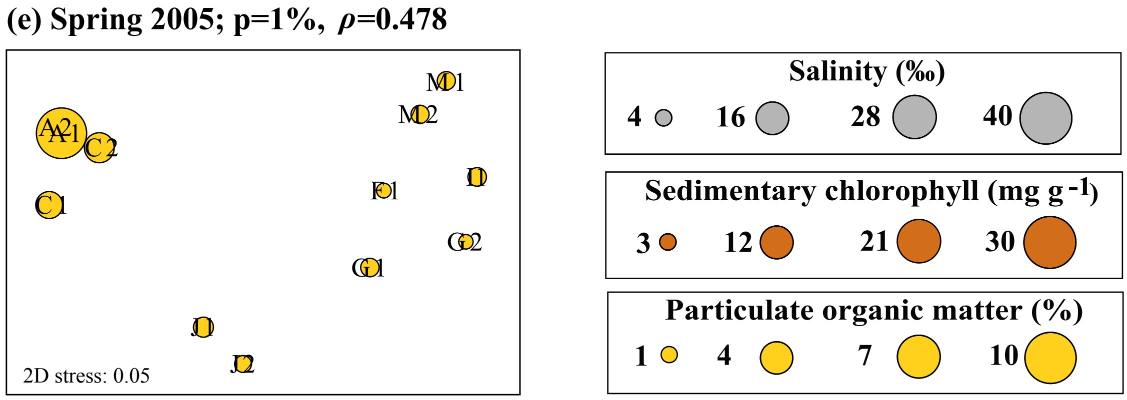
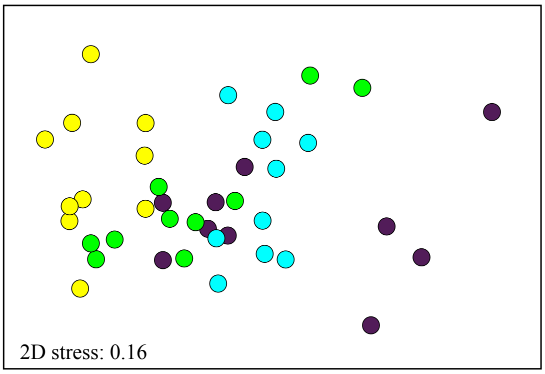
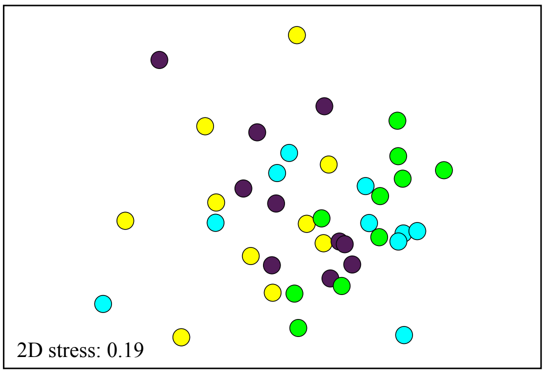

(e) Spring 2005; p=1%, ρ=0.478

Figure 5.1.4.4: MDS ordination plots derived from the average nematode composition recorded at each site in the Swan Estuary in a particular sampling season. The magnitude of those water quality or sediment variables selected by the BIOENV routine when one of the matrices constructed from the above faunal data was matched with that constructed from the complementary water quality or sediment data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

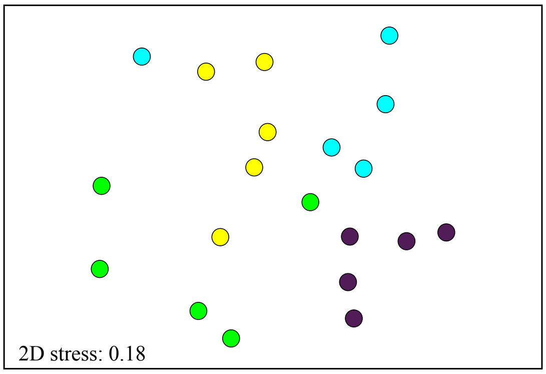
(a) Habitat A; p=0.1%, GR=0.322



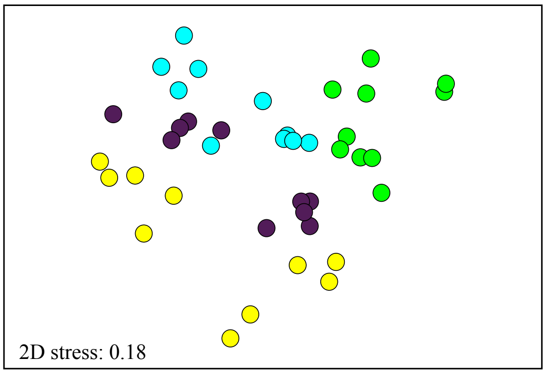
(b) Habitat C; p=0.1%, GR=0.173



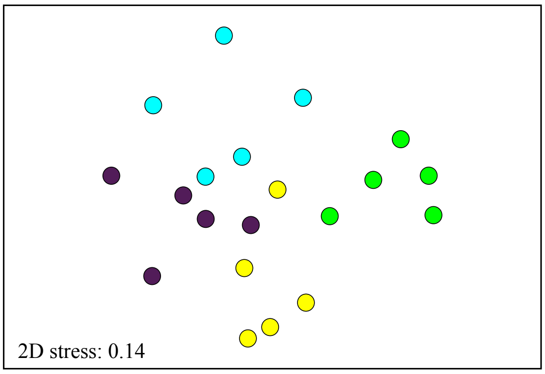
(c) Habitat F; p=0.1%, GR=0.644



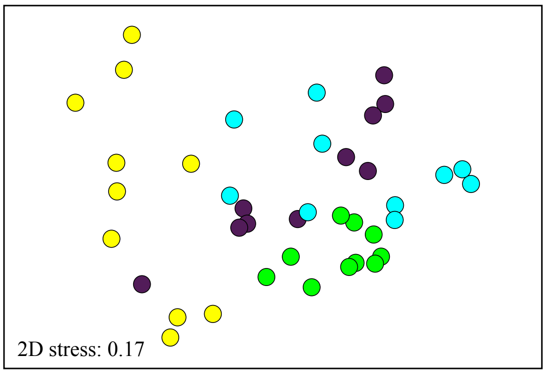
(d) Habitat G; p=0.1%, GR=0.518



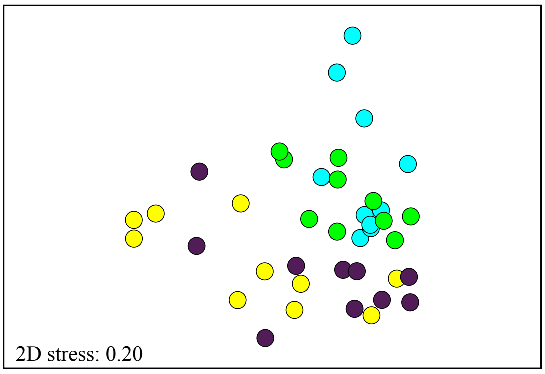
(e) Habitat I; p=0.1%, GR=0.705



(f) Habitat J; p=0.1%, GR=0.511



(g) Habitat M; p=0.1%, GR=0.323



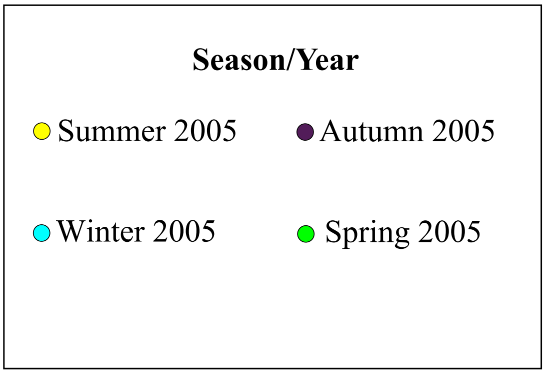


Figure 5.1.4.5: MDS ordination plots constructed from the nematode assemblage data recorded in each replicate sample in each sampling season at habitat (a) A, (b) C, (c) F, (d) G, (e) I, (f), J and (g) M in the Swan Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

and discreteness of the groups of samples representing those seasons on the MDS plots shown in Fig. 5.1.4.5c and e, respectively.

SIMPER demonstrated that the nematode assemblages in spring at habitat F were best distinguished from those in each of the other seasons by greater and more consistent numbers of *N. decoratus, Dichromodora* sp*., V. glabra*, *C. arenae* and *Chromadorina* sp.. Furthermore, the greater prevalence of *Theristus* sp.2 in summer and *Pontonema* sp.1 and *Halichoanolaimus chordiurus* in autumn also helped to distinguish the nematofaunas in these seasons from those found in spring. The first three of the above species were also more abundant in spring than in each of the other seasons at habitat G, as was *Pontonema* sp.1 and, compared to summer and winter, *Metadesmolaimus* sp.1 and *C. arenae*, respectively. Conversely, *Choanolaimus papillatus* and *P. cazca* were more prevalent in autumn and winter, respectively, than in spring at this habitat. Several of the above species that were most abundant in spring at habitats F and G were also most prevalent during this season at habitat I, namely *N. decoratus*, *Dichromadora* sp. and *Chromadorina* sp.. However, *B. australis*, *Theristus* sp.2 and *Metadesmolaimus* sp.1 were also consistently more abundant in spring than at least two of the other seasons at this habitat. In contrast, *S. parasitifera* and *Halaphanalaimus* sp. were more prevalent in winter than spring, and thus further contributed to the differences in species composition between these seasons at habitat I. The relatively large differences in the nematode assemblages recorded in summer *vs* autumn at habitat F were mainly attributable to the greater and more consistent numbers of *Pontonema* sp.1, *Subsphaerolaimus* sp., *H. chordiurus* and *Pierrickia* sp. in the latter season, while the reverse was true for *Theristus* sp.2 , *Dichromadora* sp. and *N. decoratus*. Moreover, the notable differences in assemblage composition for summer *vs* both autumn and winter at habitat I were due largely to the greater prevalence of *Theristus* sp.2 and *H. chordiurus* in summer, *Terschillingia* sp.1 and *Metadesmolaimus* sp.1 in autumn and the latter species in addition to *Halaphanalaimus* sp. and *Chromadorina* sp. in winter.

The most pronounced seasonal differences in nematofaunal composition at habitat J occurred between summer and each of the other seasons (R=0.635-0.763), which was also reflected by the fact that samples representing this season tended to form a group, albeit relatively dispersed, to one side of the MDS plot that was largely discrete from those representing other seasons (Fig. 5.1.4.5f). The distinctiveness of the nematofauna in summer at this habitat was due mainly to its depauperate composition, and that most distinguishing species, with the exception of *Pierrickia* sp. and *Metadesmolaimus* sp.2, were in greater abundances in other seasons. At the uppermost habitat A, the most distinct seasonal differences occurred between summer and winter (R=0.842), while the remaining pairwise seasonal comparisons reflected low to moderate differences in species composition (R=0.114-0.423). The groups of samples representing these two seasons lay adjacent to each other, but were entirely discrete, on the MDS plot shown in Fig. 5.1.4.5a, whereas samples representing autumn and spring were highly dispersed and/or intermingled with those from all other seasons. *Parascolaimus brevista* and *Pontonema* sp.1 were considerably more abundant in winter than summer at this habitat, whereas the opposite was true for *P. aurata* and *Metadesmolaimus* sp.2. The greatest seasonal differences at the other upper estuary habitat C, were detected between summer and spring (R=0.316), and the modest extent of that difference reflected the weak seasonality in nematode composition that was detected at this habitat overall. Such results were also illustrated on the MDS plot shown in Fig. 5.1.4.5b by the large degree of overlap of groups of samples from all seasons and the dispersed nature of all groups except that representing spring. The compositional differences between summer and spring at this habitat were largely driven by larger, but not particularly consistent, numbers of each of the above four species in the latter season.

At the channel habitat M, the greatest seasonal differences in nematofaunal composition were detected for summer *vs* winter and for spring and autumn *vs* spring (R=0.400-0.491). Samples from summer and autumn intermingled extensively on the MDS plot shown in Fig. 5.1.4.5g but tended to occupy one side of that plot, while those from winter and spring, which also intermingled extensively, occupied the other side. However, these two groups of samples were not well separated, thus contributing to the moderate seasonal differences that were detected for this habitat. The composition of summer samples was best distinguished from those collected in winter and spring by their lower abundances of several species, namely *Chromadorina* sp. and *S. parasitifera* compared to winter and *Chromadorina* sp., *Dichromadora* sp. and *Theristus* sp.2 compared to spring. However, greater, but not particularly consistent, numbers of *Daptonema* sp. and *C. arenae* were recorded in summer than in winter and spring, respectively. The nematode assemblages in autumn nematofaunas were mainly separated from those recorded in spring by greater numbers *C. arenae*, *Mesacanthion* sp. and *Metadesmolaimus* sp.1 in the former season and of *Chromadorina* sp., *Dichromadora* sp. and *V. glabra* in the latter. However, as for the previous seasonal comparisons at this channel habitat, these differences in species composition were not particularly consistent.

5.1.5 Hyperbenthic faunal assemblages

5.1.5.1 Species mean density at each habitat type

Sampling of the hyperbenthic faunal assemblages at eight habitat types throughout the Swan Estuary in both winter 2005 and summer 2006 yielded 5601 individuals, after the number of hyperbenthos in each replicate sample had been adjusted to that in 1 m^3 and summed. These fauna represented 92 species and 10 phyla, namely Annelida, Arthropoda, Chaetognatha, Chordata, Cnidaria, Ctenophora, Echinodermata, Mollusca, Nematoda and Platyhelminthes. The Crustacea were by far the most speciose class (44 species), followed by the Polychaeta (14 species; Table 5.1.5.1).

The greatest number of species was recorded at habitat type G in the middle reaches of the estuary (50), followed by that at habitats E and M (46), which were both located in the channel. Habitats A and C in the upper reaches of the estuary, and habitat J in the small basin at the foot of the Swan River, each contained similar numbers of species (38-43), while habitats F and I in the main basin of the system contained slightly fewer species (35). The mean density of hyperbenthic fauna was also greatest at habitat G, followed closely by that at F and then E, *i.e.* 122-82 individuals m^{-3}. These mean densities were far higher than those recorded at the remaining habitats, particularly in the case of A, *i.e.* 54-17 individuals m^{-3} (Table 5.1.5.1).

The hyperbenthic fauna at habitat A was dominated by the bivalve *Musculista senhousia*, which comprised nearly 60% of the total number of individuals, and the copepod harpacticoid sp.1, which comprised nearly 6% (Table 5.1.5.1). In contrast, that at the other upper estuary habitat, C, was dominated by the copepods calanoid spp. 2 and 4 and Mysidellinid sp. (86.3%), the first two of which comprised only *ca* 0.1% of the total hyperbenthic fauna at A, and the latter of which was not even present at that uppermost habitat. Furthermore, 21 species recorded at habitat C were not found at A, while six species found at habitat A were not recorded at any other habitat in the Swan Estuary (Table 5.1.5.1).

Considerable differences were also detected in the characteristics of the species assemblages among habitats located in various regions of the middle estuary, *i.e.* F, G, I and J. Thus, while cyclopoid sp.1, harpacticoid sp.1, ostracod sp.3 and harpacticoid sp.7 ranked first, second or third and fourth, respectively, at both habitats F and G, Spirorbid sp. was also abundant at F but was never recorded at G, while the opposite was true for the mite Halacarid sp.1 (Table 5.1.5.1). Furthermore, nine other species found at F were never recorded at G, while the reverse applied to 24 other species. Habitat type I, located in the lower reaches of the main basin, was also largely dominated by cyclopoid sp.1 (*i.e. ca* 54% of the total number of individuals), but other copepod species were also abundant at this habitat that were not abundant at either F or G, *i.e.* calanoid spp. 2 and 4. Moreover, the mean density of cyclopoid sp.1 at I was less than half that at F or G. Habitat J was dominated by a completely different suite of species than those at F and G and, in the case of some species, also to I, *i.e.* calanoid spp. 2, 4 and 3 and

Table 5.1.5.1: Mean density (M), standard deviation (SD), percentage contribution to the overall mean density (%) and rank by density (R) of each hyperbenthic faunal species recorded at each habitat type sampled in the Swan Estuary during winter 2005 and summer 2006. Abundant species at each habitat type (*i.e.* those that contribute >5% to the overall mean density) are highlighted in grey. Each taxon has been assigned to its respective phyla (P) and class (C) (*i.e.* A-Arthropoda, An-Annelida, Ch-Chordata, Cha-Chaetognatha, Cn-Cnidaria, Ct-Ctenophora, E-Echinodermata, M-Mollusca, N-Nematoda, Pl-Platyhelminthes, Ac-Ascidiacea, Ad-Adenophorea, Ap-Appenicularia, As-Asteroidea, Az- Anthozoa, B-Bivalvia, C-Crustacea, Cl-Chelicerata, G-Gastropoda, O-Osteichthyes, P-Polychaeta, S-Scyphozoa, Sa-Sagittoidea, T-Turbellaria, U-Uniramia). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of hyperbenthic fauna in each sample had been adjusted to that in 1 m^3 and summed) are given for each habitat type.

		Habitat type A				Habitat type C				Habitat type E				Habitat type F			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Musculista senhousia	M/B	9.65	18.43	58.45	1	0.45	1.19	0.84	7	1.73	4.80	2.11	11				
harpacticoid sp.1	A/C	0.97	1.84	5.88	2	0.10	0.27	0.19	16	7.39	9.95	9.01	4	18.51	50.14	16.49	2
Sabellid sp.	An/P	0.75	1.71	4.54	3												
harpacticoid sp.7	A/C	0.65	1.40	3.94	4	0.42	0.82	0.78	9	8.05	11.09	9.82	3	8.64	23.36	7.70	4
Hyalid sp.2	A/C	0.52	1.57	3.15	5					0.73	1.99	0.89	17	0.20	0.63	0.18	20
Capitellid sp.	An/P	0.47	1.08	2.85	6	0.62	2.08	1.15	6	0.17	0.42	0.21	36	0.03	0.11	0.03	33
Mullid sp.	Ch/O	0.40	0.82	2.42	7												
Phyllodoce sp.	An/P	0.30	0.73	1.82	8												
Arthritica semen	M/B	0.28	0.75	1.70	9	0.17	0.35	0.32	14					0.07	0.14	0.06	30
Tanypodin sp.	A/U	0.25	0.76	1.51	10												
Littorinid sp.1	M/G	0.25	1.12	1.51	10												
Serpulid sp.	An/P	0.15	0.35	0.91	12	0.02	0.08	0.04	29	1.00	3.18	1.22	15	0.10	0.23	0.09	23
Austrolestes sp.	A/U	0.15	0.37	0.91	12												
Ischyrocerid sp.1	A/C	0.12	0.45	0.73	14	0.42	0.94	0.78	9	2.40	5.23	2.93	8				
Daphnia sp.	A/C	0.10	0.31	0.61	15	1.32	2.22	2.46	5								
crab sp.	A/C	0.10	0.31	0.61	15					0.10	0.32	0.12	38				
Palaemonetes australis	A/C	0.10	0.31	0.61	15	0.35	1.35	0.65	11	10.00	7.50	12.20	2	0.50	0.71	0.45	12
Australonereis elhersii	An/P	0.10	0.45	0.61	15	0.45	2.01	0.84	7					0.33	0.72	0.29	14
Ceratonereis aquisetis	An/P	0.10	0.31	0.61	15					0.23	0.42	0.28	29	0.90	2.51	0.80	10
Exoedicerotid sp.	A/C	0.10	0.31	0.61	15												
cyclopoid sp.4	A/C	0.08	0.31	0.48	21					0.03	0.11	0.04	45				
ostracod sp.3	A/C	0.08	0.24	0.48	21	0.10	0.33	0.19	16	1.33	3.99	1.62	13	13.95	31.74	12.43	3

		Habitat type A				Habitat type C				Habitat type E				Habitat type F			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Ischyrocerid sp.2	A/C	0.07	0.23	0.42	23												
calanoid sp.1	A/C	0.07	0.17	0.42	23					0.03	0.11	0.04	45	0.10	0.23	0.09	23
calanoid sp.12	A/C	0.07	0.17	0.42	23	1.47	3.01	2.73	4	0.23	0.39	0.28	29				
cyclopoid sp.1	A/C	0.07	0.30	0.42	23	0.03	0.10	0.06	26	5.19	10.63	6.33	6	46.26	125.93	41.22	1
nematode spp.	N/Ad	0.07	0.23	0.42	23	0.34	1.35	0.63	12	0.23	0.23	0.28	29	0.30	0.64	0.27	15
Corophium minor	A/C	0.05	0.22	0.30	28	0.02	0.08	0.04	29	1.60	4.06	1.95	12				
Corixid sp.	A/U	0.05	0.22	0.30	28	0.05	0.22	0.09	18								
flabelliferan sp.1	A/C	0.05	0.22	0.30	28												
Halacarid sp.1	A/Cl	0.05	0.16	0.30	28	0.02	0.07	0.04	29								
cyclopoid sp.3	A/C	0.03	0.10	0.18	32												
Oribatid sp.	A/Cl	0.03	0.10	0.18	32												
Caraziella sp.	An/P	0.03	0.10	0.18	32												
syllid sp.2	An/P	0.03	0.15	0.18	32												
syllid sp.1	An/P	0.03	0.10	0.18	32	0.02	0.07	0.04	29	0.13	0.32	0.16	37	0.07	0.14	0.06	30
calanoid sp.4	A/C	0.02	0.07	0.12	37	16.00	26.42	29.76	2	20.20	23.88	24.64	1	3.75	4.51	3.34	6
calanoid sp.2	A/C	0.02	0.08	0.12	37	21.96	77.25	40.85	1	4.15	5.71	5.06	7	3.29	2.79	2.93	7
harpacticoid sp.8	A/C	0.02	0.07	0.12	37												
Halacarid sp.2	A/Cl	0.02	0.08	0.12	37												
ostracod sp.1	A/C	0.02	0.08	0.12	37	0.02	0.07	0.04	29	0.20	0.45	0.24	33	0.03	0.11	0.03	33
syllid sp.4	An/P	0.02	0.07	0.12	37	0.05	0.12	0.09	18	0.33	0.42	0.40	23	0.10	0.23	0.09	23
Tanais dulongii	A/C	0.02	0.07	0.12	37					0.40	0.54	0.49	22	0.63	1.59	0.56	11
Mysidellinid sp.	A/C					8.45	30.63	15.72	3	0.30	0.48	0.37	24	0.10	0.32	0.09	23
Cirripedia nauplii	A/C					0.33	1.03	0.61	13								
Grandidierella propodentata	A/C					0.12	0.25	0.22	15	0.23	0.63	0.28	29	0.10	0.32	0.09	23
Leucothoid sp.2	A/C					0.05	0.22	0.09	18	0.20	0.63	0.24	33				
caprellid sp.1	A/C					0.05	0.22	0.09	18	1.77	3.61	2.16	10	2.33	6.59	2.08	8
Ephydrid sp.	A/U					0.05	0.22	0.09	18								
Nassarius nigellus	M/G					0.05	0.22	0.09	18	0.60	1.58	0.73	18	0.30	0.95	0.27	15
spionid sp.1	An/P					0.05	0.22	0.09	18								
spionid sp.2	An/P					0.05	0.22	0.09	18								
calanoid sp.3	A/C					0.03	0.15	0.06	26								
Penilia avirostris	A/C					0.03	0.15	0.06	26								
Hyalid sp.1	A/C					0.02	0.07	0.04	29	0.07	0.14	0.09	44	0.07	0.14	0.06	30
Ampithoid sp.	A/C					0.02	0.07	0.04	29	0.50	1.16	0.61	19	0.30	0.95	0.27	15

		Habitat type A				Habitat type C				Habitat type E				Habitat type F			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
calanoid sp.5	A/C					0.02	0.07	0.04	29	0.27	0.59	0.33	28	1.80	4.41	1.60	9
flabelliferan sp.2	A/C					0.02	0.07	0.04	29								
Oikopleura sp.	Ch/Ap					0.02	0.08	0.04	29	0.50	1.25	0.61	19	0.03	0.11	0.03	33
ctenophore sp.	Ct/Ct									5.60	10.73	6.83	5				
Spirorbid sp.	An/P									1.83	5.35	2.23	9	7.83	19.03	6.98	5
Gobiid sp.3	Ch/O									1.20	3.12	1.46	14				
Phyllorhiza punctata	Cn/S									1.00	2.54	1.22	15	0.30	0.67	0.27	15
Actinia tenebrosa	Cn/Az									0.47	0.96	0.57	21	0.40	1.26	0.36	13
caprellid sp.3	A/C									0.30	0.67	0.37	24				
Favartia planilirata	M/G									0.30	0.67	0.37	24				
Torquigener pleurogramma	Ch/O									0.30	0.67	0.37	24				
Diogenid sp.1	A/C									0.20	0.63	0.24	33				
Podon sp.	A/C									0.10	0.32	0.12	38				
Asteroid sp.2	E/As									0.10	0.32	0.12	38				
Apogon sp.	Ch/O									0.10	0.32	0.12	38	0.20	0.42	0.18	20
Metapenaeus dalli	A/C									0.10	0.32	0.12	38				
Velacumantus australis	M/G									0.10	0.32	0.12	38	0.20	0.42	0.18	20
Polyclad sp.2	P/T													0.30	0.95	0.27	15
Atherinid sp.	Ch/O													0.10	0.32	0.09	23
caprellid sp.5	A/C													0.10	0.32	0.09	23
Number of species			**43**				**38**				**46**				**35**		
Total mean density			**17**				**54**				**82**				**112**		
Number of samples			**20**				**20**				**10**				**10**		
Total number of hyperbenthos			**497**				**507**				**580**				**1 193**		

		Habitat type G				Habitat type I				Habitat type J				Habitat type M			
	P/C	M	SD	%	R	M	SD	%	R	M	SD	%	R	M	SD	%	R
Musculista senhousia	M/B	0.20	0.62	0.16	21	0.80	2.20	2.31	6	0.15	0.37	0.33	21				
harpacticoid sp.1	A/C	6.95	18.32	5.69	3	2.10	5.05	6.07	4	0.28	0.72	0.61	16	1.25	2.31	4.41	5
Sabellid sp.	An/P									0.05	0.16	0.11	31				
harpacticoid sp.7	A/C	6.64	15.75	5.43	4	0.60	1.44	1.74	7	0.30	0.59	0.66	14	0.67	1.07	2.36	7
Hyalid sp.2	A/C	0.40	1.57	0.33	14					0.03	0.10	0.07	37	0.18	0.43	0.64	17
Capitellid sp.	An/P	0.22	0.52	0.18	20	0.87	2.64	2.52	5	0.30	0.56	0.66	14	0.23	0.83	0.81	12
Mullid sp.	Ch/O													0.05	0.22	0.18	27
Phyllodoce sp.	An/P	0.15	0.67	0.12	22					0.05	0.22	0.11	31				
Arthritica semen	M/B	0.12	0.37	0.10	28	0.54	1.27	1.56	10	2.42	6.71	5.30	4	0.18	0.43	0.64	17
Tanypodin sp.	A/U																
Littorinid sp.1	M/G																
Serpulid sp.	An/P									0.07	0.23	0.15	30	0.15	0.37	0.53	21
Austrolestes sp.	A/U													0.02	0.08	0.07	38
Ischyrocerid sp.1	A/C	0.38	1.08	0.31	16	0.60	1.02	1.74	7	0.60	1.19	1.31	10	0.25	0.64	0.88	11
Daphnia sp.	A/C													0.03	0.10	0.11	36
crab sp.	A/C																
Palaemonetes australis	A/C	1.00	1.92	0.82	10	0.10	0.32	0.29	23	0.40	1.10	0.88	13	4.35	11.33	15.35	2
Australonereis elhersii	An/P									0.60	2.68	1.31	10				
Ceratonereis aquisetis	An/P	0.73	1.88	0.60	12	0.07	0.14	0.20	28	0.12	0.27	0.26	24				
Exoedicerotid sp.	A/C	0.05	0.22	0.04	36												
cyclopoid sp.4	A/C	0.02	0.07	0.02	43	0.03	0.11	0.09	30	0.12	0.37	0.26	24	0.02	0.08	0.07	38
ostracod sp.3	A/C	25.88	92.89	21.17	2	0.17	0.32	0.49	19	0.12	0.31	0.26	24	0.17	0.25	0.60	20
Ischyrocerid sp.2	A/C																
calanoid sp.1	A/C									0.03	0.15	0.07	37				
calanoid sp.12	A/C	0.03	0.10	0.02	43	0.23	0.42	0.67	18	0.94	3.27	2.06	7	0.08	0.21	0.28	25
cyclopoid sp.1	A/C	58.66	127.51	47.99	1	18.69	21.08	54.06	1	0.75	2.10	1.64	9	10.67	20.28	37.66	1
nematode spp.	N/Ad	0.12	0.33	0.10	28	0.50	1.13	1.45	11	0.17	0.47	0.37	19	0.22	0.44	0.78	13
Corophium minor	A/C	0.57	1.83	0.47	13	0.03	0.11	0.09	30	0.05	0.16	0.11	31	0.22	0.52	0.78	13
Corixid sp.	A/U																
flabelliferan sp.1	A/C																
Halacarid sp.1	A/Cl	6.55	26.60	5.36	5	0.13	0.28	0.38	21					0.02	0.08	0.07	38
cyclopoid sp.3	A/C																
Oribatid sp.	A/Cl	0.15	0.67	0.12	22					0.05	0.16	0.11	31	0.02	0.07	0.07	38

		Habitat type G				Habitat type I				Habitat type J				Habitat type M			
	P/C	M	SD	%	R	M	SD	%	R	M	SD	%	R	M	SD	%	R
Caraziella sp.	An/P																
syllid sp.2	An/P																
syllid sp.1	An/P	0.03	0.15	0.02	43	0.03	0.11	0.09	30	0.03	0.10	0.07	37	0.02	0.08	0.07	38
calanoid sp.4	A/C	3.55	6.81	2.90	6	2.81	3.37	8.13	2	9.34	16.02	20.44	2	3.25	3.40	11.47	3
calanoid sp.2	A/C	2.58	4.63	2.11	7	2.61	2.59	7.55	3	20.27	30.16	44.35	1	2.61	2.53	9.21	4
harpacticoid sp.8	A/C													0.02	0.07	0.07	38
Halacarid sp.2	A/Cl	0.02	0.07	0.02	43												
ostracod sp.1	A/C					0.03	0.11	0.09	30	0.08	0.18	0.18	28	0.05	0.16	0.18	27
syllid sp.4	An/P	0.13	0.43	0.11	26	0.37	0.62	1.07	15	0.55	0.91	1.20	12	0.18	0.47	0.64	17
Tanais dulongii	A/C	0.08	0.30	0.07	34												
Mysidellinid sp.	A/C					0.10	0.32	0.29	23	0.15	0.37	0.33	21	0.05	0.22	0.18	27
Cirripedia nauplii	A/C									1.05	3.19	2.30	6				
Grandidierella propodentata	A/C	0.05	0.22	0.04	36	0.07	0.21	0.20	28	0.08	0.24	0.18	28				
Leucothoid sp.2	A/C	0.10	0.45	0.08	30					0.20	0.89	0.44	17				
caprellid sp.1	A/C	0.05	0.22	0.04	36	0.40	1.26	1.16	12					0.57	1.39	2.01	8
Ephydrid sp.	A/U																
Nassarius nigellus	M/G	0.10	0.45	0.08	30	0.40	0.70	1.16	12	0.10	0.45	0.22	27	0.05	0.22	0.18	27
spionid sp.1	An/P																
spionid sp.2	An/P					0.03	0.11	0.09	30								
calanoid sp.3	A/C									2.78	7.79	6.08	3				
Penilia avirostris	A/C									0.02	0.07	0.04	41	0.03	0.10	0.11	36
Hyalid sp.1	A/C									0.03	0.10	0.07	37				
Ampithoid sp.	A/C	0.25	0.72	0.20	17	0.17	0.32	0.49	19	0.15	0.30	0.33	21	0.27	0.69	0.95	10
calanoid sp.5	A/C	0.13	0.31	0.11	26	0.13	0.32	0.38	21	0.94	1.59	2.06	7	0.84	1.77	2.97	6
flabelliferan sp.2	A/C	0.07	0.30	0.06	35												
Oikopleura sp.	Ch/Ap									1.86	6.46	4.07	5	0.02	0.07	0.07	38
ctenophore sp.	Ct/Ct																
Spirorbid sp.	An/P					0.40	0.70	1.16	12					0.48	1.34	1.69	9
Gobiid sp.3	Ch/O	0.25	0.79	0.20	17					0.17	0.67	0.37	19				
Phyllorhiza punctata	Cn/S	0.10	0.31	0.08	30					0.05	0.22	0.11	31	0.05	0.22	0.18	27
Actinia tenebrosa	Cn/Az	0.25	0.91	0.20	17									0.05	0.22	0.18	27
caprellid sp.3	A/C					0.30	0.95	0.87	17								
Favartia planilirata	M/G	0.05	0.22	0.04	36	0.10	0.32	0.29	23								
Torquigener pleurogramma	Ch/O																

		Habitat type G				Habitat type I				Habitat type J				Habitat type M			
	P/C	M	SD	%	R	M	SD	%	R	M	SD	%	R	M	SD	%	R
Diogenid sp.1	A/C					0.10	0.32	0.29	23								
Podon sp.	A/C																
Asteroid sp.2	E/As																
Apogon sp.	Ch/O	0.05	0.22	0.04	36					0.05	0.22	0.11	31	0.10	0.45	0.35	23
Metapenaeus dalli	A/C	0.10	0.45	0.08	30												
Velacumantus australis	M/G	0.15	0.37	0.12	22	0.60	1.58	1.74	7					0.15	0.67	0.53	21
Polyclad sp.2	P/T	1.48	5.53	1.21	9									0.10	0.31	0.35	23
Atherinid sp.	Ch/O																
caprellid sp.5	A/C																
Leucothoid sp.1	A/C	2.35	9.58	1.92	8									0.07	0.23	0.25	26
Blenniid sp.	Ch/O	0.75	3.35	0.61	11												
Tanaid sp.	A/C	0.40	1.05	0.33	14	0.33	0.72	0.95	16					0.20	0.70	0.71	15
Aplysiid sp. (juv.)	M/G	0.15	0.67	0.12	22												
Atherinosoma elongata	Ch/O	0.05	0.22	0.04	36									0.02	0.07	0.07	38
Polyclad sp.1	P/T	0.05	0.22	0.04	36												
ostracod sp.2	A/C	0.03	0.15	0.02	43												
Scalibregmatid sp.	An/P	0.03	0.15	0.02	43												
Asteroid sp.1	E/As	0.02	0.07	0.02	43												
ostracod sp.4	A/C	0.02	0.07	0.02	43					0.02	0.07	0.04	41	0.05	0.22	0.18	27
Odacid sp.	Ch/O					0.10	0.32	0.29	23								
cyclopoid sp.2	A/C					0.03	0.11	0.09	30								
calanoid sp.11	A/C									0.18	0.75	0.39	18	0.20	0.90	0.71	15
Littorinid sp.2	M/G													0.05	0.16	0.18	27
Sagitta sp.	Cha/Sa													0.05	0.22	0.18	27
Ascidian sp.	Ch/Ac													0.02	0.07	0.07	38
Number of species			**50**				**35**				**42**				**46**		
Total mean density			**122**				**35**				**46**				**28**		
Number of samples			**20**				**10**				**20**				**20**		
Total number of hyperbenthos			**1 144**				**267**				**517**				**896**		

the bivalve *Arthritica semen*. Furthermore, five species found at J were never recorded at any of the other basin habitats (Table 5.1.5.1).

Similar dominant species were detected at the channel habitats E and M. Thus, the four most abundant species at M, *i.e.* cyclopoid sp.1, the decapod *Palaemonetes australis* and the calanoid spp. 2 and 4, which represented nearly 70% of the total hyperbenthic fauna at that habitat, were all abundant at E. However, the rank order of those dominant species differed considerably. For example, whereas cyclopoid sp.1 ranked first and represented *ca* 38% of the individuals at M, it ranked sixth and comprised *ca* 6% of the hyperbenthic fauna at E. Moreover, the top ranking species at E, *i.e.* calanoid sp.4 (24.64%), ranked third and represented only 11.47% of the individuals at M. In addition to these differences, three other species, namely harpacticoid spp. 1 and 7 and the ctenophore sp., were also abundant at habitat E but not at M. Habitats E and M each contained three hyperbenthic species that were not recorded at any other habitat in the Swan Estuary (Table 5.1.5.1).

5.1.5.2 Spatial and temporal differences in mean number of species, density and taxonomic diversity

Preliminary three-way PERMANOVA tests were employed to determine whether habitats, or their representative sites, were the most appropriate for examining spatial differences in the number of species, overall density and taxonomic distinctness of the hyperbenthic fauna recorded in the Swan Estuary during winter 2005 and summer 2006. Significant differences between sites assigned to the same habitat type were not detected for number of species, but were detected in the case of overall density and taxonomic distinctness. As a result, the replicate data for the first of these dependent variables was subsequently subjected to a habitat x season PERMANOVA, while that for the latter two variables were subjected to a site x season PERMANOVA.

The above analyses showed that the mean number of species differed significantly among habitat types and the habitat x season interaction, the latter of which explained the greatest proportion of variation in this dependent variable (Table 5.1.5.2). Mean density and taxonomic distinctness of hyperbenthic fauna differed significantly among sites and the site x season interaction and, in the case of density, also season. The site x season interaction exerted the greatest influence on both of these dependent variables and, in the case of the former, the influence of site was considerably greater than that of season (Table 5.1.5.2).

The mean number of species at habitat types A and C was greater during winter 2005 than summer 2006, with this difference being particularly marked at the first of these habitats

Table 5.1.5.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for a habitat x season PERMANOVA on the number of hyperbenthic faunal species and site x season PERMANOVAs on the density and quantitative taxonomic distinctness of hyperbenthic faunal assemblages recorded throughout the Swan Estuary during winter 2005 and summer 2006. df = degrees of freedom. Significant results are highlighted in bold.

	Number of Species					**Density**					**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main effects														
Habitat	7	**201.95**	**6.95**	**3.28**	**0.001**									
Season	1	21.82	0.75	-0.35	0.404	1	**2390.30**	**11.11**	**5.78**	**0.001**	87.53	0.56	-1.03	0.637
Site						12	**1104.60**	**5.14**	**10.72**	**0.002**	**469.76**	**2.99**	**5.59**	**0.001**
Two-way Interactions														
Habitat * Season	7	**266.68**	**9.17**	**5.44**	**0.001**									
Season * Site						12	**1328.80**	**6.18**	**14.92**	**0.001**	**556.13**	**3.54**	**8.93**	**0.001**
Residual	114	29.07		5.39		104	215.10		14.67		157.07		12.53	

(Fig. 5.1.5.1a). However, the opposite was true at all remaining habitats except E, which thus made a substantial contribution to the significant interaction detected for this dependent variable. The greatest mean number of species was detected at the channel habitat E in both seasons (*ca* 15 species), which was particularly marked during winter. The lowest mean number of species in this season was recorded at the basin habitat G (*ca* 6), which was only slightly lower than that recorded at habitat types C, F, I, J and M (*ca* 8 species). However, in summer, the mean number of species was substantially lower at the upper estuary habitats A and C (*ca* 3 and 5, respectively) than at the remaining habitats, at which a minimum of 10 species were recorded (Fig. 5.1.5.1a).

The mean density of hyperbenthos was greater in summer 2006 than winter 2005 at the majority of sites. However, the opposite was true at A1, C1 and M1, thus contributing to the significant site x season interaction detected for this dependent variable (Fig. 5.1.5.1b). During winter, mean densities of hyperbenthos were greatest at sites A1 and M1, and were also relatively high at C2, E2, J1 and M2. The densities in this season were lowest at site G2, followed by J2, A2 and I1. In summer, the mean densities of hyperbenthic fauna were far lower at sites representing habitat A than at all other sites except C1, while the densities were greatest at sites C2, E2 and F1 (Fig. 5.1.5.1b).

Mean taxonomic distinctness did not exhibit any consistent tendency among sites to be greater in either winter 2005 or summer 2006, thus contributing to the significant site x season interaction detected for this dependent variable (Fig. 5.1.5.1c). However, the greatest, or close to the greatest, values of this diversity index were recorded at sites representing habitat A in both seasons. In winter, relatively high levels of taxonomic distinctness were also recorded at sites G2 and I1, while the least were found at M1, J1 and G1. During summer, high mean values of this diversity index were also recorded at C1 and J1, but that at J2 was far lower than at any other site in this season (Fig. 5.1.5.1c).

5.1.5.3 Composition of hyperbenthic faunal assemblages among habitat types

An initial three-way PERMANOVA test undertaken on the replicate species abundance data recorded at each site representing each habitat type in winter 2005 and summer 2006 was used to ascertain whether spatial differences in hyperbenthic faunal composition were most appropriately analysed at the site or broader habitat level. This test detected significant differences in species composition for all main effects and the site x season interaction (p=0.001-0.040), but the components of variation attributable to site and the interaction term were considerably less than that for habitat type. Furthermore, one-way ANOSIM tests, carried out

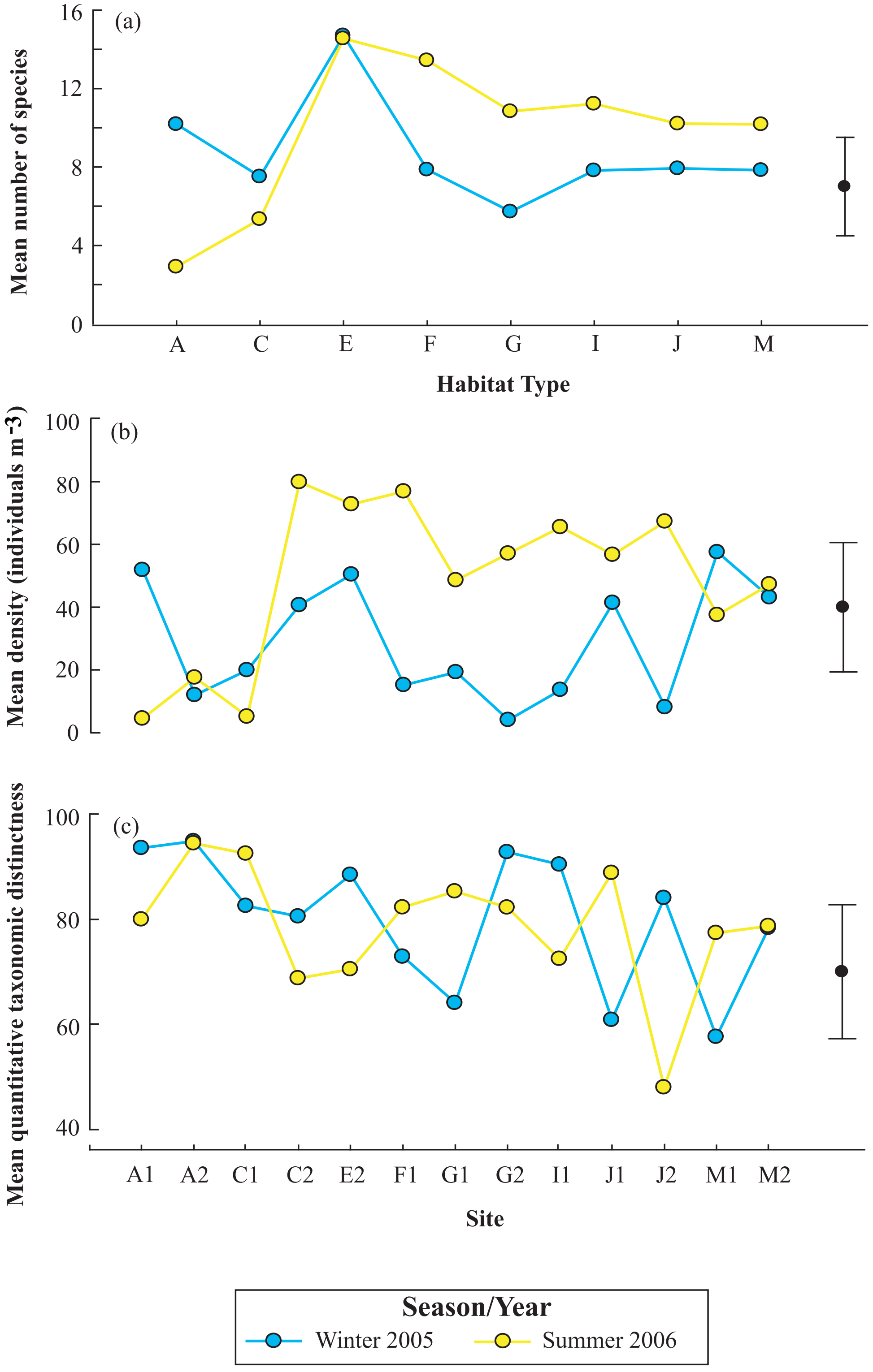


Figure 5.1.5.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the hyperbenthic faunal assemblages recorded at each habitat/site in the Swan Estuary during winter 2005 and summer 2006. For the sake of clarity, the average ±95% confidence intervals have been presented for each of these plots.

separately for the data recorded in each individual season, detected significant differences in hyperbenthic faunal composition between sites assigned to the same habitat type in only four of the 10 comparisons and, in almost all of those cases, the associated R-statistic did not exceed 0.500. Given the relatively small intra-habitat differences in hyperbenthic composition overall, the following analyses aimed at more thoroughly examining spatial differences in this faunal assemblage were carried out at the habitat rather than site level. They were also performed separately for the data recorded in each individual season, given the significant seasonal effects detected by the above test.

One-way ANOSIM tests showed that the compositions of the hyperbenthic faunal assemblages differed significantly among habitat types in both winter 2005 and summer 2006 (p=0.1%), but that in both cases, the overall extent of those differences was moderately low, *i.e.* Global R-statistic=0.331 and 0.386, respectively (Table 5.1.5.3). During winter, significant differences in composition were detected between habitats A, C and E and all other habitats, except for E *vs* I (p=0.1-0.8%; Table 5.1.5.3a). The differences were greatest between the upper estuary habitat C and the lower and middle estuary habitats E and F, respectively, *i.e.* R=0.647-0.745. However, there were also relatively large differences (*i.e.* R >0.500) between the assemblages at the uppermost habitat A and all other habitats, and the channel habitat E *vs* the basin habitats F, G and J (Table 5.1.5.3a). MDS ordination of the hyperbenthic assemblage data recorded in winter showed that the group of samples from habitat A, although relatively dispersed, exhibited a pronounced tendency to separate from those representing all other habitats (Fig. 5.1.5.2a). The groups of samples from habitats C and E were also well separated from those representing the remaining habitats. However, samples from the basin habitats and the channel habitat M were not well differentiated from each other on the ordination plot (Fig. 5.1.5.2a).

One-way SIMPER analyses showed that, during winter, the hyperbenthic faunal compositions at habitat types A, C and E were each typified exclusively by several species (Table 5.1.5.4a). Thus, the assemblages at A were the only ones to be characterised by Mullid sp., *Musculista senhousia*, Sabellid sp. and Capitellid sp. in this season, while the same was true of Daphnia sp. and calanoid sp.12 at habitat C and *Palaemonetes australis*, ctenophore sp., nematode spp. and Ischyrocerid sp.1 at habitat E. These suites of species also commonly distinguished the assemblages of their respective habitats from those at the remaining habitats (Table 5.1.5.4a). However, several species were characteristic of the assemblages of most habitats in winter, such as calanoid sp.4, which typified all habitats except A, calanoid sp.2, which typified all middle and lower estuary habitats except E and harpacticoid spp. 1 and 7, which typified four and five habitats, respectively, throughout the estuary. The first of these

Table 5.1.5.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the hyperbenthic faunal composition among habitat types in the Swan Estuary during (a) winter 2005 and (b) summer 2006. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2005; p=0.1%, Global R=0.331

	A	**C**	**E**	**F**	**G**	**I**	**J**
C	0.597						
E	0.597	0.745					
F	0.503	0.647	0.636				
G	0.610	0.490	0.584	0.023			
I	0.532	0.444	0.212	0.192	0.095		
J	0.627	0.411	0.538	-0.022	0.094	-0.012	
M	0.540	0.353	0.363	-0.056	0.001	-0.024	-0.041

(b) Summer 2006; p=0.1%, Global R=0.386

	A	**C**	**E**	**F**	**G**	**I**	**J**
C	0.235						
E	0.996	0.528					
F	0.844	0.591	0.208				
G	0.462	0.369	0.270	0.001			
I	0.728	0.329	0.556	0.132	0.023		
J	0.691	0.312	0.329	0.447	0.430	0.283	
M	0.601	0.347	0.347	0.137	0.097	-0.152	0.361

Table 5.1.5.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the hyperbenthic faunal assemblages at each habitat in the Swan Estuary during (a) winter 2005 and (b) summer 2006 as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2005

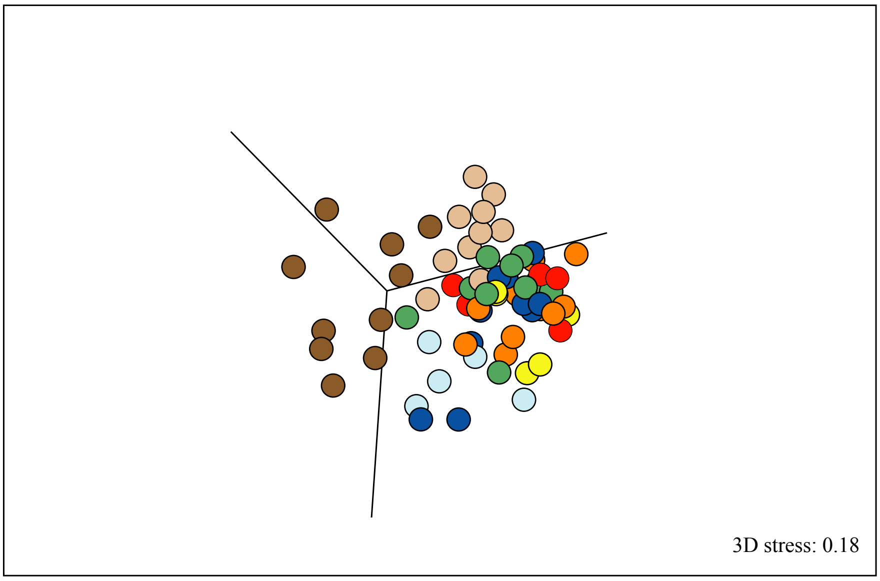
	A	C	E	F	G	I	J	M
A	Mullid sp. *M. senhousia* Sabellid sp. harpacticoid sp.7 harpacticoid sp.1 Capitellid sp.							
C	Daphnia sp.^{C} calanoid sp.4^{C} calanoid sp.12^{C} Mullid sp.^{A}	Daphnia sp. calanoid sp.4 calanoid sp.12 harpacticoid sp.7						
E	*P. australis*^{E} ctenophore sp.^{E}	Daphnia sp.^{C} *P. australis*^{E} ctenophore sp.^{E} calanoid sp.12^{C} Ischyrocerid sp.1^{E}	*P. australis* harpacticoid sp.7 ctenophore sp. nematode spp. calanoid sp.4 harpacticoid sp.1 Ischyrocerid sp.1					
F	Mullid sp.^{A} calanoid sp.4^{F} *M. senhousia*^{A} Sabellid sp.^{A}	Daphnia sp.^{C} calanoid sp.12^{C} calanoid sp.2^{F} calanoid sp.4^{C} Hyalid sp.1^{F} calanoid sp.5^{F}	*P. australis*^{E} ctenophore sp.^{E} Ischyrocerid sp.1^{E}	calanoid sp.4 calanoid sp.2 harpacticoid sp.1 ostracod sp.3 calanoid sp.5 harpacticoid sp.7 Hyalid sp.1				
G	Mullid sp.^{A} calanoid sp.4^{G} *M. senhousia*^{A} Sabellid sp.^{A}	Daphnia sp.^{C} calanoid sp.12^{C} calanoid sp.4^{C} Ischyrocerid sp.1^{C} syllid sp.4^{G}	*P. australis*^{E} ctenophore sp.^{E} Ischyrocerid sp.1^{E}	▨	calanoid sp.4 calanoid sp.2 harpacticoid sp.1 Ischyrocerid sp.1			
I	syllid sp.4^{I} Mullid sp.^{A}	Daphnia sp.^{C} calanoid sp.12^{C} syllid sp.4^{I} Capitellid sp.$^{-}$ Ischyrocerid sp.1^{I} calanoid sp.4^{C}	▨	▨	▨	syllid sp.4 calanoid sp.4 calanoid sp.2		

	A	**C**	**E**	**F**	**G**	**I**	**J**	**M**
J	calanoid sp.4^{J} Mullid sp.^{A} syllid sp.4^{J} Sabellid sp.^{A}	Daphnia sp.^{C} calanoid sp.12^{C} calanoid sp.4^{C} syllid sp.4^{J} Capitellid sp.^{C}	*P. australis*^{E} ctenophore sp.^{E}				calanoid sp.4 syllid sp.4 calanoid sp.2 calanoid sp.5 ostracod sp.1 Capitellid sp.	
M	Mullid sp.^{A} calanoid sp.4^{M} Sabellid sp.^{A} *M. senhousia*^{A}	Daphnia sp.^{C} calanoid sp.12^{C} calanoid sp.4^{C} Capitellid sp.^{C} calanoid sp.5^{M}	*P. australis*^{E} ctenophore sp.^{E} Ischyrocerid sp.1^{E}					calanoid sp.4 calanoid sp.2 harpacticoid sp.7 calanoid sp.5

(b) Summer 2006

	A	C	E	F	G	I	J	M
A	*M. senhousia*							
C	calanoid sp.4^{C} *M. senhousia*^{A} *G. propodentata*^{C} calanoid sp.2^{C} calanoid sp.12^{C} Mysidellinid sp.^{C}	calanoid sp.4 *G. propodentata* calanoid sp.2 calanoid sp.12 Mysidellinid sp.						
E	calanoid sp.4^{E} harpacticoid sp.7^{E} *P. australis*^{E} harpacticoid sp.1^{E} syllid sp.4^{E} cyclopoid sp.1^{E}	harpacticoid sp.7^{E} calanoid sp.4^{E} *P. australis*^{E} harpacticoid sp.1^{E} calanoid sp.2^{C} syllid sp.4^{E} cyclopoid sp.1^{E}	calanoid sp.4 harpacticoid sp.7 *P. australis* harpacticoid sp.1 syllid sp.4 calanoid sp.2 cyclopoid sp.1					
F	harpacticoid sp.7^{F} cyclopoid sp.1^{F} Spirorbid sp.^{F} harpacticoid sp.1^{F} ostracod sp.3^{F} nematode spp.^{F}	harpacticoid sp.7^{F} cyclopoid sp.1^{F} calanoid sp.4^{C} Spirorbid sp.^{F} harpacticoid sp.1^{F} nematode spp.^{F} calanoid sp.2^{C}		cyclopoid sp.1 harpacticoid sp.7 Spirorbid sp. ostracod sp.3 harpacticoid sp.1 *P. australis*				
G	cyclopoid sp.1^{G} harpacticoid sp.7^{G} ostracod sp.3^{G} *M. senhousia*^{A}	cyclopoid sp.1^{G} calanoid sp.4^{C} harpacticoid sp.7^{G} ostracod sp.3^{G} calanoid sp.2^{C}	calanoid sp.4^{E} harpacticoid sp.7^{E} *P. australis*^{E} harpacticoid sp.1^{E}		cyclopoid sp.1 ostracod sp.3 harpacticoid sp.7 calanoid sp.4			
I	cyclopoid sp.1^{I} calanoid sp.4^{I} *M. senhousia*^{A} calanoid sp.2^{I} harpacticoid sp.1^{I} nematode spp.^{I}	cyclopoid sp.1^{I} calanoid sp.4^{C} calanoid sp.2^{C} nematode spp.^{I} harpacticoid sp.1^{I}	calanoid sp.4^{E} harpacticoid sp.7^{E} *P. australis*^{E}			cyclopoid sp.1 calanoid sp.2 calanoid sp.4 harpacticoid sp.1 nematode spp.		
J	calanoid sp.2^{J} *A. semen*^{J} calanoid sp.4^{J} calanoid sp.3^{J} *M. senhousia*^{A} calanoid sp.5^{J} *Oikopleura* sp.^{J} syllid sp.4^{J}	calanoid sp.2^{J} calanoid sp.4^{C} *A. semen*^{J} calanoid sp.3^{J} calanoid sp.5^{J} *Oikopleura* sp.^{J}	calanoid sp.4^{E} harpacticoid sp.7^{E} *P. australis*^{E} harpacticoid sp.1^{E} calanoid sp.2^{J} *A. semen*^{J}	calanoid sp.2^{J} harpacticoid sp.7^{F} *A. semen*^{J} harpacticoid sp.1^{F} Spirorbid sp.^{F}	calanoid sp.2^{J} cyclopoid sp.1^{G} *A. semen*^{J} harpacticoid sp.7^{G}	cyclopoid sp.1^{I} calanoid sp.2^{J} *A. semen*^{J}	calanoid sp.2 calanoid sp.4 *A. semen* calanoid sp.5 syllid sp.4 Ischyrocerid sp.1	
M	cyclopoid sp.1^{M} *M. senhousia*^{A} *P. australis*^{M} calanoid sp.4^{M}	calanoid sp.4^{C} calanoid sp.2^{C} cyclopoid sp.1^{M} *P. australis*^{M}	calanoid sp.4^{E} harpacticoid sp.7^{E} *P. australis*^{E} harpacticoid sp.1^{E} syllid sp.4^{E}				calanoid sp.2^{J} *A. semen*^{J} calanoid sp.5^{J}	cyclopoid sp.1 calanoid sp.4 *P. australis* calanoid sp.2 harpacticoid sp.7

(a) Winter 2005



(b) Summer 2006

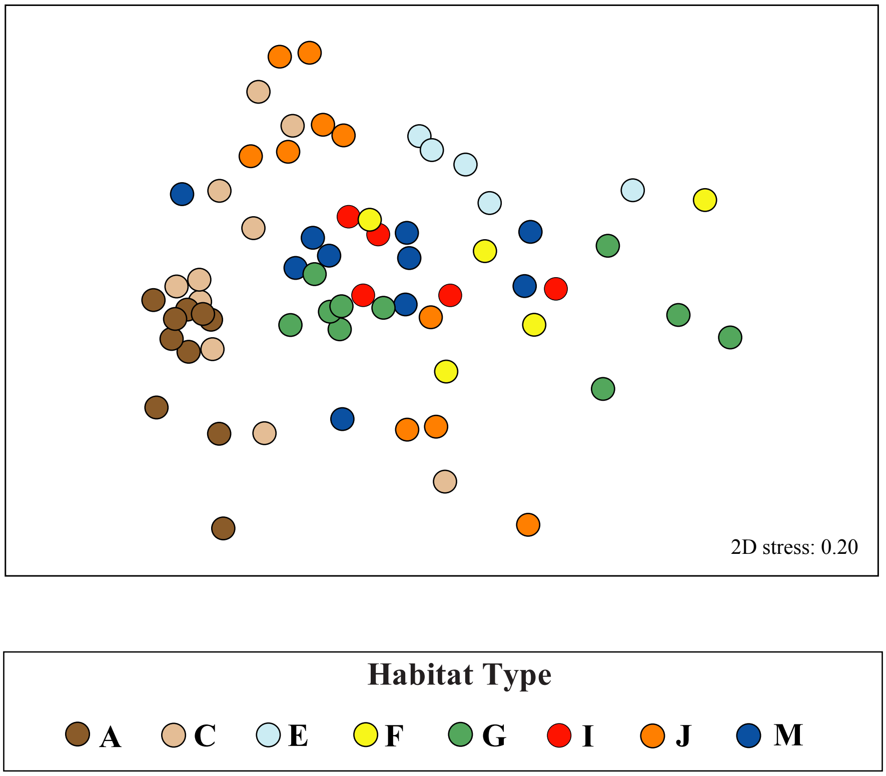


Figure 5.1.5.2: MDS ordination plots constructed from the hyperbenthic faunal assemblage data recorded in each replicate sample at each habitat in the Swan Estuary during (a) winter 2005 and (b) summer 2006.

species generally occurred in the greatest abundances at C, while the remaining three species were rarely important in distinguishing the faunas of significantly different habitats. The remaining species that characterised and/or distinguished the hyperbenthos at each habitat type are given in Table 5.1.5.4a.

The pattern of differences in hyperbenthic faunal composition among habitats during summer 2006 was similar to that described above for winter 2005. Thus, the assemblages at habitat types A, C and E differed significantly from those at all other habitats (p=0.1-3.3%) except for E *vs* F (Table 5.1.5.3b). However, in this season, the assemblages at the basin habitat J also differed significantly from those at all other habitat types (p=0.1-2.5%). The greatest faunal differences were generally detected between the uppermost habitat A and most other habitats. That between A and the lowermost habitat E was particularly pronounced (R=0.996), while the least significant difference was found between the two upper estuary habitat types A and C (R=0.235). Substantial differences in hyperbenthic composition were also detected between C *vs* E and F, and E *vs* I (R=0.528-0.844; Table 5.1.5.3b).

MDS ordination of the hyperbenthic assemblage data recorded in summer showed that samples from habitat type A, which formed a relatively tight group on one side of the plot, were separated to the greatest extent from those representing E, which formed a largely discrete group on the opposite side of the plot (Fig. 5.1.5.2b). The group of samples from A was discrete and well separated from those for all remaining habitat types except C, which were far more dispersed and intermingled with those for A and several other habitats. Samples representing habitat J were dispersed throughout the middle of the ordination and intermingled to the greatest extent with those for habitats C and I (Fig. 5.1.5.2b).

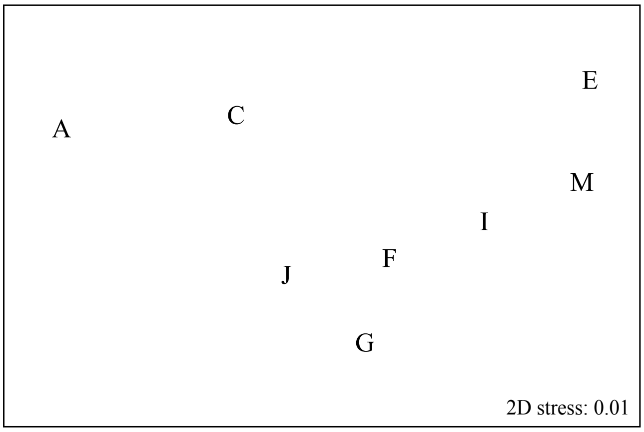
The hyperbenthic assemblage at habitat type A during summer 2006 was shown by SIMPER to be typified only by *M. senhousia*, a species that did not characterise the faunal assemblage of any other habitat in that season (Table 5.1.5.4b). This species was also responsible for distinguishing the fauna at A from that at all other habitats except E and F. The fauna at habitat type C was also typified exclusively by several species, namely the amphipod *G. propodentata*, calanoid sp.12 and Mysidellinid sp, but the only species that commonly distinguished the faunas at C from those at other habitats were calanoid spp. 2 and 4, which also characterised the assemblages of several other habitats. In addition to the latter two species, the assemblages at the remaining habitat types were characterised by several common species, such as cyclopoid sp.1 at all habitats except J, harpacticoid sp.7 at all habitat types except I and J and *P. australis* at the channel habitat types E and M and the basin habitat type F (Table 5.1.5.4b). However, the average abundance of some of the above common species varied markedly among those habitats. For example, calanoid sp.4 and harpacticoid sp.7 were always recorded in greater abundances at habitat E than at other habitats from which it differed significantly. Moreover, the hyperbenthic fauna at habitat types E, F and J were also each typified exclusively by particular species, *i.e.* syllid sp.4 and Spirorbid sp. at habitat types E and F, respectively, and *A. semen* and calanoid sp.5 at habitat J (Table 5.1.5.4b).

5.1.5.4 Matching spatial patterns between the environmental and hyperbenthic assemblage characteristics of habitats

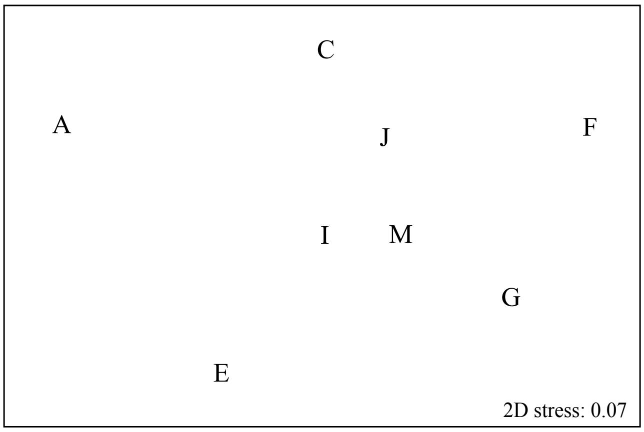
The RELATE procedure showed that the spatial pattern of the relationships among habitat types, as defined by the mean of the enduring environmental measurements used to classify those habitats, was significantly and reasonably well correlated with that displayed by the mean of the hyperbenthic assemblage data in each season, *i.e.* p=1.3%, ρ=0.498 and p=0.7%, ρ=0.602 for winter 2005 and summer 2006, respectively. The extent of the similarity in spatial pattern among habitats in the separate matrices constructed from the enduring environmental and seasonal faunal data are illustrated by the associated MDS plots shown in Fig. 5.1.5.3. RELATE was then used to determine whether the underlying spatial patterns among habitats displayed by the average faunal data in each season were significantly correlated with those exhibited by the suite of water quality measurements (*i.e.* salinity, water temperature and dissolved oxygen concentration) recorded at the same habitats in the same seasons. These tests demonstrated a significant correlation for summer only, and the extent of that correlation was considerable, *i.e.* p=1.5%, ρ=0.759.

The BIOENV procedure was then used to determine if a greater correlation could be achieved between the complementary faunal and water quality matrices by only employing a subset of water quality variables, rather than the full suite. It should be noted that these analyses were carried out using the averages recorded at each site rather than habitat type, in order to maximize the number of samples in the reference (hyperbenthic) matrices and thus reduce the chances of BIOENV finding a subset of water quality variables that provided a good match with those references by chance. For comparability, it should also be noted that, when RELATE was used to match the complementary hyperbenthic and water quality matrices constructed from site averages, the results obtained for summer 2006 were similar to those obtained previously when habitat averages were employed, (*i.e.* p=0.2%, ρ=0.697), whereas those obtained for winter 2005 demonstrated a significant and considerably better match than when habitat averages were used (*i.e.* p=0.2%, ρ=0.336). BIOENV showed that significant and slightly improved

(a) Enduring environmental data



(b) Winter 2005; p=1.3%, ρ=0.498



(c) Summer 2006; p=0.7%, ρ=0.602

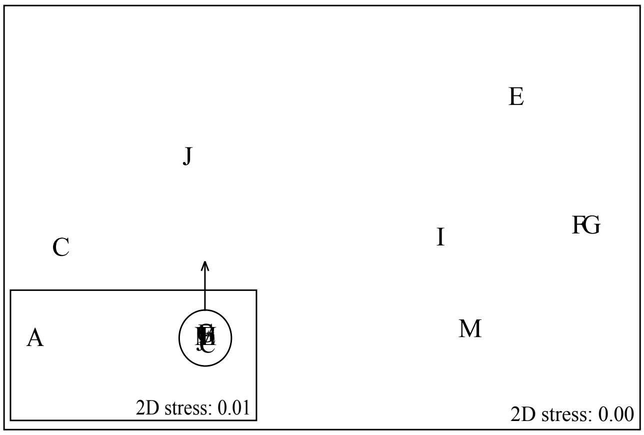


Figure 5.1.5.3: MDS ordination plots constructed from the averages at each habitat type in the Swan Estuary of their (a) enduring environmental measurements and (b-c) hyperbenthic faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the hyperbenthic faunal data are also provided for each season.

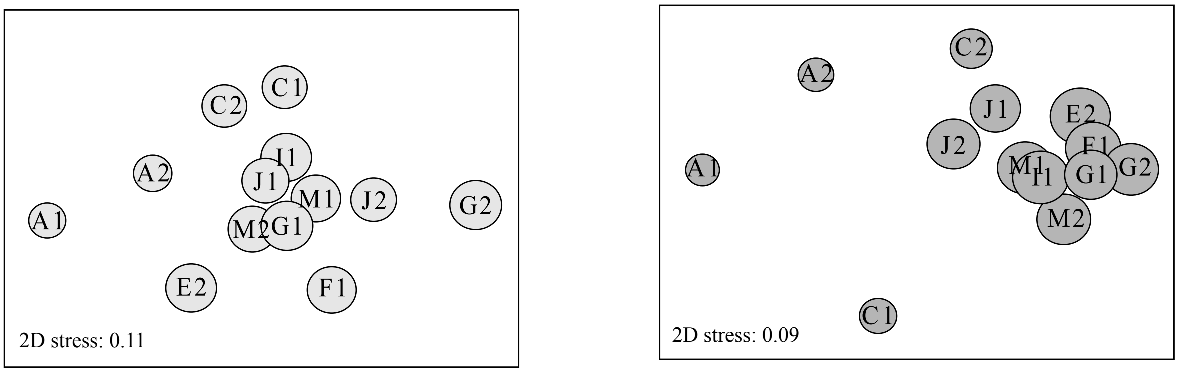
correlations with the faunal matrices were obtained when data for only salinity and dissolved oxygen were employed in summer (p=1%, ρ=0.728), and that for only water temperature was employed in winter (p=1%, ρ=0.484).

The relationships between the spatial patterns exhibited by the hyperbenthic assemblages and the magnitude of each of the above selected water quality variables in each season are illustrated by the MDS and associated bubble plots shown in Fig. 5.1.5.4. Although not particularly marked, the relatively distinct hyperbenthic assemblages at sites representing habitats A and C in winter 2005 were associated with lower water temperatures than those at most remaining sites except J2 in the small basin at the foot of the Swan River (Fig. 5.1.5.4a). During summer 2006, sites representing habitats A and C, which, in most cases, had faunal compositions that were particularly distinct from those at other sites, also had by far the lowest mean salinities recorded throughout the estuary (Fig. 5.1.5.4b). This was also true of the mean dissolved oxygen concentration at habitat A in summer 2006, while that recorded at G, whose faunal composition was among the most dissimilar to that at A, was the largest (Fig. 5.1.5.4c).

5.1.5.5 Composition of hyperbenthic faunal assemblages among seasons

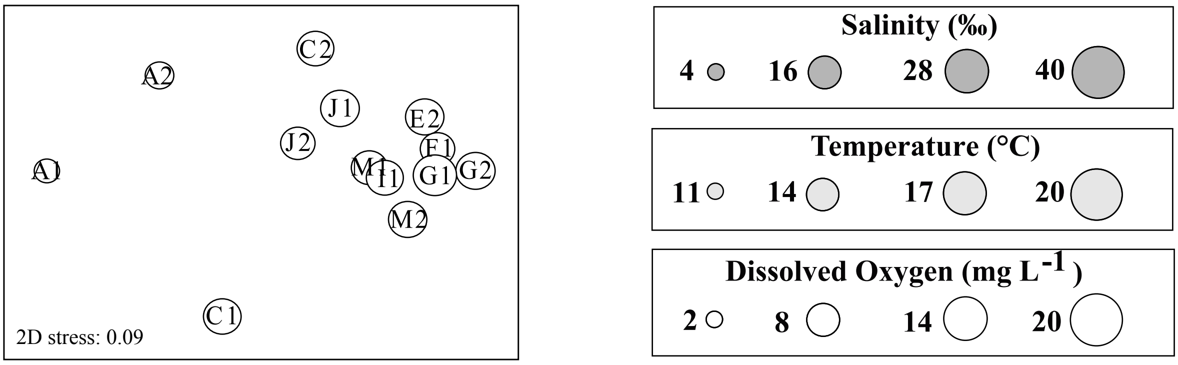
One-way ANOSIM, carried out separately for the data recorded at each habitat type, showed that the hyperbenthic faunal assemblages differed significantly between winter 2005 and summer 2006 in each case (p=0.1-2.7%), except for habitat I. The overall extent of those significant seasonal differences was greatest at habitats F, A and C (Global R=0.402-0.580), and least at habitats J and M (Global R=0.184-0.256). The associated MDS ordination plots of the hyperbenthic assemblage data recorded at each habitat showed that the group of samples from winter 2005 was generally discrete from that for summer 2006, except at habitats G and M, where samples from the two seasons overlapped to some extent (Fig. 5.1.5.5). The samples representing winter were more dispersed than those from summer at habitats A, E and I, while the opposite was true for all remaining habitats except M, at which summer and winter samples were similarly dispersed (Fig. 5.1.5.5).

SIMPER showed that the relatively large seasonal differences in hyperbenthic composition at the main basin habitat F were mainly due to the prevalence of *P. australis*, Spirorbid sp. and cyclopoid sp.1 in summer 2006 but not winter 2005, while the opposite was true for Hyalid sp. At the upper estuary habitat A, however, the notable differences in composition between winter 2005 and summer 2006 were attributable to the fact that, while Sabellid sp., Capitellid sp. and harpacticoid spp. 1 and 7 typified the assemblages in the former season, only *M. senhousia* occurred consistently at this habitat in the latter season. In contrast,



(a) Winter 2005; p=2%, ρ =0.484

(b) Summer 2006; p=1% ρ=0.728



(c) Summer 2006; p=1% ρ=0.728

Figure 5.1.5.4: MDS ordination plots derived from the average hyperbenthic faunal composition recorded at each site in the Swan Estuary in a particular sampling season. The magnitude of those water quality variables selected by the BIOENV routine when one of the matrices constructed from the above faunal data was matched with that constructed from the complementary water quality data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

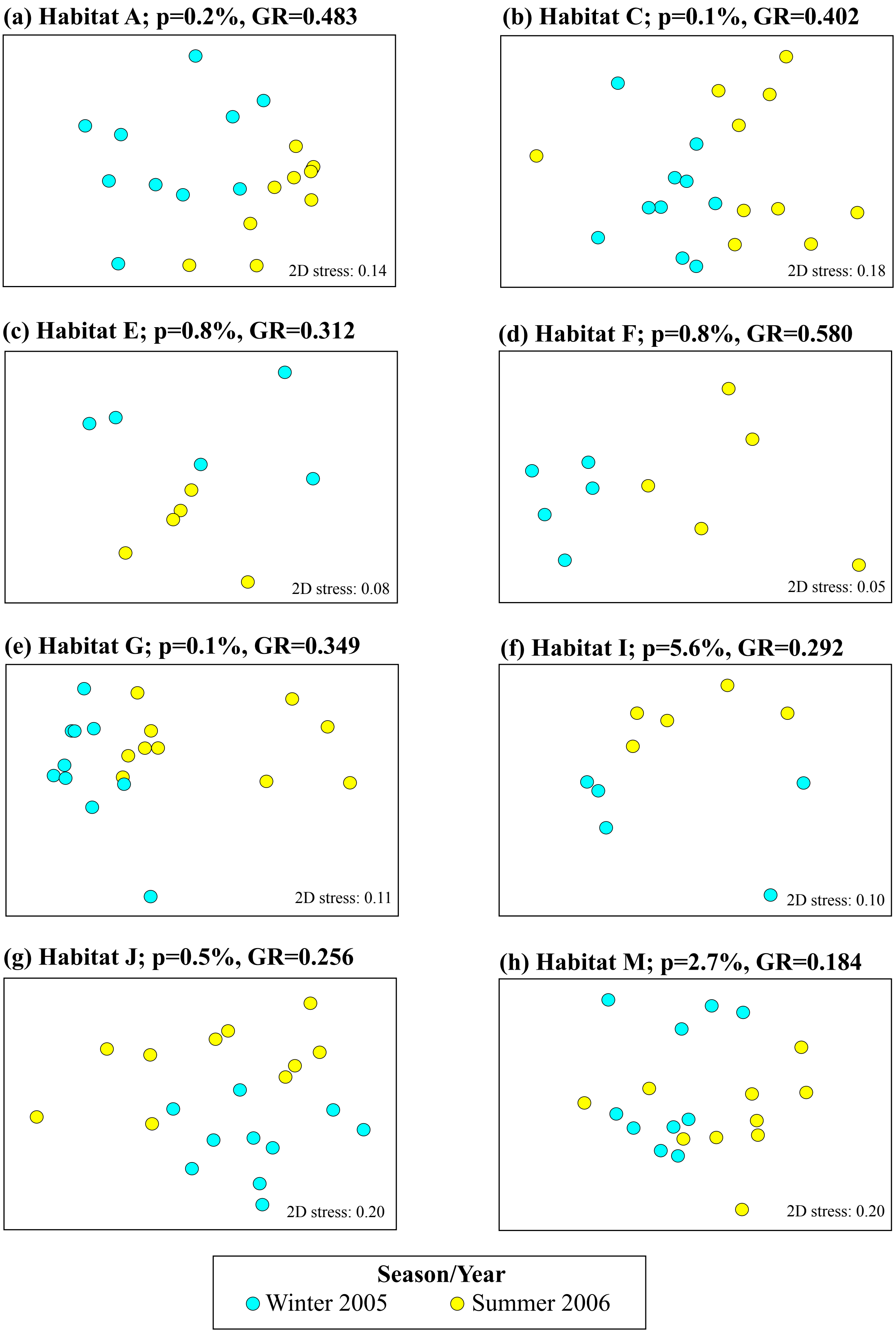


Figure 5.1.5.5: MDS ordination plots constructed from the hyperbenthic faunal assemblage data recorded in each replicate sample in each sampling season at habitat (a) A, (b) C, (c) E, (d) F, (e) G, (f) I, (g) J and (h) M in the Swan Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

the relatively large seasonal differences at the other upper estuary habitat, C, were due to the presence of greater densities of Daphnia sp. and harpacticoid sp.7 in winter, whereas *G. propodentata* and Mysidellinid sp. typified the fauna at this habitat in summer.

The moderate to low seasonal differences detected at the basin habitats G and J were largely attributable to differences in the abundance of species that typified their hyperbenthic assemblages in both seasons. Thus, the winter assemblages at G contained greater densities of calanoid sp.4 than in summer, while the opposite was true for cyclopoid sp.1, harpacticoid sp.7 and ostracod sp.3. At habitat J, the relatively small seasonal differences were due mainly to greater numbers of Capitellid sp. and syllid sp.4 in winter, and greater prevalence of *A. semen* in summer.

The hyperbenthic assemblage at the channel habitat E exhibited greater differences between winter 2005 and summer 2006 than that at the other channel habitat M, which was largely due to the greater prevalence of both syllid sp.4 and cyclopoid sp.1 in summer. The only species to exhibit any notable difference in abundance between seasons at M was cyclopoid sp.1, which was only recorded during summer 2006.

5.2 Discussion

5.2.1 Differences in faunal assemblages among habitats

The species compositions of the nearshore fish, benthic macroinvertebrate, nematode and hyperbenthic assemblages differed significantly among the various habitats throughout the Swan Estuary during each season in which they were sampled between summer 2005 and summer 2007. As discussed in the following subsections, the overall extents and specific pattern of those spatial differences varied among faunal assemblages and seasons. However, it was generally true that the faunal assemblages were most distinct at habitats A and/or C, which were both (i) located in the upper reaches of the system and thus often experienced markedly different water and/or sediment quality characteristics from other habitats, (ii) highly sheltered from wave activity and (iii) characterised by substrate/submerged vegetation types that were not found to any large extent anywhere else in the system, such as snags and littoral reeds. Inspection of the MDS ordination plots constructed from the replicate species composition data in each individual season also showed that, for all faunal assemblages, the samples collected from C were often far more dispersed than those from A, and were frequently the most dispersed of any habitat. This indicates that the faunal compositions occupying that upper estuary habitat were highly variable. The assemblages recorded at habitats in the estuary channel, namely M and, for some faunal types, E and/or N, also often differed markedly from those at habitats elsewhere in the system, but generally not to the same extent and consistency as those habitats in the upper reaches. Moreover, the mean number of species, density and taxonomic distinctness of each faunal assemblage also differed significantly among habitats or their representative sites throughout the estuary. Although there was considerable variability in the above attributes, particularly in the case of the latter two, it was often true that habitats A and/or C contained among the least mean number of species, overall densities and taxonomic diversity.

5.2.1.1 Fish assemblages

The composition of the fish assemblages in the Swan Estuary exhibited large to moderate overall differences among habitats in each of the six seasons during which they were sampled between autumn 2005 and summer 2007. The extents of those spatial differences were most pronounced in spring 2005, followed by summer 2007 and 2006, and were least in winter 2005. Aside from detecting a highly distinct fish assemblage at habitat A and, to a slightly lesser extent, C, in all seasons, and also pronounced ichthyofaunal differences between the channel habitats E, M and/or N *vs* most others in all seasons except both winters, the assemblages of various other habitats were also notably distinct in particular seasons. These included habitat J in the small basin at the foot of the Swan River in spring 2005, winter 2006 and summer 2007, the main basin habitat G in spring 2005 and summer 2007 and habitat Q, also located in the main basin, in summer 2007. As expected, the least differences in fish assemblage composition tended to occur between adjacent pairs of habitats, such as A *vs* C and E *vs* N. This was particularly relevant to habitats located in different areas of the main basin, *i.e.* F, G, I and/or Q, and most notably to F and G, whose fish assemblage compositions did not differ significantly from each other in any season.

The distinctiveness of the fish faunas recorded at habitat A was due largely to the highly consistent occurrence of the atherinid *Leptatherina wallacei* in every season, which was always found in greater abundances at this habitat than any other from which it differed significantly, and also commonly to the marked prevalence of *Pseudogobius olorum* and *Acanthopagrus butcheri*. At least one of these species, which are all able to complete their life cycle within the estuary, also typified and distinguished the faunas recorded in the other upper estuary habitat, C, in every season, as did *A. butcheri* at habitat J in all seasons except winter 2005. This latter species was typically recorded in greater abundances at C than at either A or J, while *P. olorum* was always most abundant at A in those seasons in which it characterised the ichthyofauna at that habitat. The prevalence of *L. wallacei*, *P. olorum* and/or *A. butcheri* in the nearshore waters of the upper Swan Estuary has been detected by several other workers, namely Hoeksema and Potter (2006), who found that the first two of these species represented nearly 77% of the total number of fish recorded in that region over a two year period, Prince *et al.* (1982), Loneragan and Potter (1990), Gill and Potter (1993) and Kanadjembo *et al.* (2001). At least one of these species have also been shown to dominate the nearshore fish assemblages in the upper reaches of other estuaries in south-western Australia, such as the intermittently-open Moore River Estuary (Young *et al.* 1997), permanently-open Nornalup-Walpole Estuary (Potter and Hyndes 1994) and the normally-closed Stokes and Hamersley inlets (Hoeksema *et al.* 2006a).

Leptatherina wallacei is highly euryhaline and is capable of tolerating salinities between *ca* 0 and 55‰, but is generally found in greater abundances in those waters in which salinities are reduced (Prince *et al.* 1982). The inability of this atherinid species to withstand extreme salinities is supported by Young and Potter (2002), who found that it suffered total mortality throughout the Wellstead Estuary when salinities in that normally-closed system continued to rise above *ca* 55‰. Although *L. wallacei* was recorded at all habitats in the Swan Estuary except I and M in the lower reaches of the basin and channel, respectively, it is relevant that the mean salinities at A, at which this species was particularly abundant, were the lowest of any habitat in every season, never exceeding *ca* 20‰ and falling as low as *ca* 3.5‰. Like *L. wallacei, P. olorum* is better adapted to reduced salinities (Gill and Potter 1993) and its successful reproduction in the Swan Estuary is almost entirely limited to the upper reaches of that system (Neira *et al.* 1992). Gill and Potter (1993) also found that the densities of *P. olorum* are highest in areas that are not exposed to wave activity, have relatively high proportions of silt and/or clay comprising the substrate and where fringing and emergent vegetation is the most prevalent. Gee and Gee (1991) have also reported that this small benthic species is particularly good at overcoming low dissolved oxygen conditions by employing "aquatic surface respiration", a process in which fish move to very shallow waters and arch their snouts towards the water surface to ventilate their gills in this oxygen-rich zone. It is thus highly pertinent that the enduring environmental characteristics of habitat A, at which this goby species was most abundant in the Swan Estuary, not only reflected the fact that it experienced the lowest mean salinities in every season (*i.e.* due to its relative proximity to riverine water sources), but also that it is highly sheltered from wave activity (*i.e.* due to its narrow banks and thus extremely limited fetches), contains by far the greatest proportion of emergent reeds in its shallow waters, had the lowest, or very close to the lowest, dissolved oxygen concentration in almost all seasons and that one of its representative sites had among the smallest mean sediment grain size recorded throughout the estuary.

Acanthopagrus butcheri is an extremely hardy species that can withstand a wide range of environmental conditions. Thus, although it exhibits signs of osmotic stress at *ca* 60‰, it can tolerate salinities between *ca* 0 and 80‰ (Partridge and Jenkins 2002, Hoeksema *et al.* 2006b), has been shown to spawn in waters that range in salinity from 3.5 to 45‰ and temperatures from 17.5 to 28.5°C (Sarre and Potter 1999), its larvae are known to hatch at similar rates between the respective salinity and temperatures ranges of 15-35‰ and 16-20°C under normoxic conditions (Hassel *et al.* 2008), its growth, reproductive and age characteristics exhibit substantial differences under different environmental conditions (Sarre and Potter 1999, Cottingham 2008) and it is a highly opportunistic omnivore (Sarre *et al.* 2000). The salinity, temperature and dissolved oxygen conditions at all nearshore habitats throughout the Swan Estuary in each season are well within the tolerance of *A. butcheri* for survival and, during spring to early summer when spawning occurs (Sarre and Potter 1999), for spawning itself and, in almost all locations, for hatching of the larvae. Furthermore, abundant food sources are present throughout the estuary, including both invertebrates (see subsections 5.1.3, 5.1.4 and 5.1.5) and plant material (see Chapter 3.3.1.1). However, the markedly greater numbers of *A. butcheri* recorded at habitats A, C and J, which included both juveniles and adults, presumably reflected a preference for other environmental attributes that were unique to those habitats. Such attributes are likely to include the presence of snags, which were found only at A and, to a lesser extent, C, and which this species is known to shelter among, the presence of deeper waters, which was reflected by the very narrow wave shoaling margins at both A and C and which would facilitate the movements of this larger and highly mobile species, and the tannin-stained waters that were found at all three of these habitats, which would provide protection from predation by piscivorous birds.

The fish assemblages at habitat C were also characterised by several other species in particular seasons, and which were by far the most abundant at this habitat, such as the estuarine species *Papillogobius punctatus* in autumn 2005 and the summers of 2006 and 2007 and *Amniataba caudavittatus* in the first and last of these seasons and spring 2005. Gill and Potter (1993) also found that *P. punctatus* was by far the most abundant in that part of the Swan Estuary that has now been classified as habitat C, and that its distribution was limited to the middle and upper reaches of the system. This goby species can tolerate a relatively wide salinity range of 0-34‰ (Gill 1996), and it is relevant that habitat C experienced the greatest seasonal range in salinity of any habitat in the estuary, *i.e.* 3.8-31‰. *Amniataba caudavittatus* is also euryhaline, and can tolerate fresh to hypersaline conditions (Potter *et al.* 1994). However, in the Swan Estuary, this species predominantly occupies the middle to upper reaches of the system and spawns largely between spring and summer in waters now classified as habitat C and the lower reaches of habitat A. It is relevant that the only known salinity and water temperature ranges in which *A. caudavittatus* is known to spawn in the Swan Estuary (*i.e.* 9-17‰ and 24-27°C, respectively; Potter *et al.* 1994) occur concurrently at the above time of year only at habitats A and C.

The Weeping Toadfish *Torquigener pleurogramma* also characterised the fish assemblages at habitat J in every season except summer 2007. This ubiquitous species ranked either second or third in terms of abundance and contributed between 10 and 23% of the total catch at every habitat throughout the Swan Estuary except A, at which it was never recorded, and C, at which it was not abundant. A very similar spatial distribution of this species in the nearshore waters of the Swan Estuary was also recorded by Potter *et al.* (1988). The considerable numbers of both juvenile and adult *T. pleurogramma* throughout the middle and lower reaches of the Swan Estuary presumably reflects the preference of this marine estuarine-opportunist for the higher salinities recorded in each season at these habitats compared to those in the upper estuary. This species is also known to prefer shallow waters (Potter *et al.* 1988), and thus it is relevant that, unlike habitats in the upper estuary, several of those in the middle estuary had relatively wide wave shoaling margins, *e.g.* habitats J and G. *Atherinosoma mugiloides*, an estuarine atherinid species, also characterised the assemblages at habitat J in autumn 2005 and both summers, and was the most abundant species at this habitat overall. This species, which was recorded at all habitats throughout the estuary, also ranked either first or second in terms of abundance at the main basin habitats G, I and Q, and characterised and/or distinguished at least one of those habitats in all seasons except winter 2005. Such findings are similar to those of Prince *et al.* (1982), who also recorded the greatest numbers of *A. mugiloides* in the middle reaches of the Swan Estuary and found that, possibly through a preference for more saline conditions, its abundance increased in more upstream locations when the salinities of those waters exceeded 20‰. It is thus relevant that the abundance of *A. mugiloides* at J in autumn 2005, when salinities at that habitat reached *ca* 28‰, were the greatest of any habitat throughout the estuary.

The distinctiveness of the fish assemblages at the channel habitats E, M and/or N was, in part, attributable to the estuarine and marine goby *Favonigobius lateralis*, which characterised all of these habitats in every season. Although this species also typified the ichthyofaunas of at least one of the main basin habitats G, I or Q in every season, it was often found in greater abundances at the channel habitats, and in particular E. A similar pattern of spatial distribution was also recorded for this species in the Swan Estuary by Loneragan and Potter (1990) and Gill and Potter (1993), and in other estuaries in south-western Australia by Young *et al.* (1997) and Hoeksema *et al.* (2006a). As this euryhaline but essentially marine species is better adapted to higher salinities (Gill and Potter 1993), it is relevant that the mean salinity at habitats E, M and N varied the least from marine conditions throughout the year, *i.e. ca* 23-37‰. *Favonigobius lateralis* has also been shown to be more common in areas that are not subject to wave activity and have sandy rather than silty substrates, as the latter are known to clog the gills of this benthic species which partially buries itself when resting on the substrate (Gill and Potter 1993). It is thus directly relevant that some of the enduring environmental characteristics of the three channel habitats reflected their substantially greater shelter from wave activity (*i.e.* their short fetches in all directions, combined with the buffering effect of moderate to large areas of submerged vegetation) than habitats in the wide basin of the middle estuary. Furthermore, the mean sediment grain size at sites representing habitat M, which was the only channel habitat at which the properties of the sediment were measured during this study, was larger than that recorded at several sites in the middle and upper estuary.

The fish faunas of the channel habitats were also distinguished from those in other regions of the estuary, and from each other, by several other species in most or particular seasons, such as *Leptatherina presbyteroides, Stigmatophora argus*, *Gymnapistes marmoratus* and *Apogon rueppellii*. Like *F. lateralis*, the first of these species has been found by several workers to be most abundant in the lower region of the Swan Estuary (Prince *et al.* 1982, Loneragan *et al.* 1989) and those of other estuaries in south-western Australia (*e.g.* Valesini *et al.* 1997), which has been attributed to the apparent preference of this euryhaline but essentially marine species for higher salinities (Prince *et al.* 1982). This species has also been shown to be far more abundant in sheltered than exposed nearshore waters (Valesini *et al.* 2004). Such environmental preferences of *L. presbyteroides* were further supported by the current study, in which the greatest numbers of this species were recorded in the channel, and particularly at habitat E. However, relatively high densities of this atherinid species were also recorded at Q, which may be explained by the fact that, due to its location on the southern shore of the wide main basin, this habitat is highly sheltered from the strong south-westerly winds and thus waves that prevail in both summer and winter. *Stigmatophora argus*, *G. marmoratus* and *A. rueppellii* are also largely found in greater salinities, particularly in the case of *S. argus*, which is a marine straggler and thus stenohaline (*e.g.* Chrystal *et al.* 1985). Furthermore, both *S. argus* and *G. marmoratus* are adapted for living in seagrass beds through their specialised body morphology and/or colouration, and *A. rueppellii* are typically associated with seagrass beds (Hyndes *et al.* 2003, Kendrick and Hyndes 2003). The 0+ fish that largely represented the latter species at the channel habitats in both summers, which are known to recruit into the shallows of the Swan Estuary at this time of year, also use seagrass beds as nurseries (Chrystal *et al.* 1985, Hyndes *et al.* 2003). It is thus highly pertinent that each of the channel habitats, and particularly E, which is located closest to the estuary mouth, contain considerable areas of submerged vegetation. In addition to the above species, habitat E and, to a slightly lesser extent, M and N, also contained several other species that are typically associated with seagrass and/or macroalgae and which were not recorded elsewhere in the system, despite the fact that habitats such as G and I in the main basin contained moderately large areas of submerged vegetation, *e.g.* monocanthids such as *Meuschenia freycineti* and *Acanthaluteres spilomelanurus*, syngnathids such as *Pugnaso curtirostris* and *Siphonognathus radiatus* and clinids such as *Cristiceps australis*). Such findings presumably reflect the fact that all of these species are marine stragglers, and can thus only tolerate the essentially marine salinities that occur in the channel in most seasons of the year. They may also reflect the fact that the strap-like leaf morphology and growth patterns of particular seagrass species found only in the channel, *i.e. Zostera* and *Heterozostera* spp., better suits the morphological and behavioural characteristics of the above fish species than those of the paddleweed *Halophila ovalis*, which is predominant in the basin.

In most seasons, the greatest differences in ichthyofaunal composition among habitats in the main basin (*i.e.* F, G, I and Q) occurred between I and/or Q *vs* the remaining habitats. Although the extents of these differences were moderate to low in most cases, the assemblage at I in the lowermost reaches of the basin was markedly distinct from those at F and Q in summer 2007. This was partly attributable to the prevalence at I of *Pelates octolineatus* and *A. rueppellii*, which mainly represented an influx of their 0+ recruits (data not shown), and also *F. lateralis*. The first two of these species are typically associated with seagrass (Travers and Potter 2002, Hyndes *et al.* 2003, Valesini *et al.* 2004) and, like *F. lateralis* and *A. rueppellii*, *P. octolineatus* is essentially a marine species that is typically found in higher salinities. It is thus relevant that, of the main basin habitats, I experienced the greatest salinities during both winters and spring 2005, contained the greatest proportion of submerged vegetation and rock and was far more sheltered from local winds and thus waves. Such an environment would provide an ideal nursery for the juveniles of both *P. octolineatus* and *A. reuppellii*. In contrast to habitat I, the fish assemblages at F in summer 2007 were characterised by various other species, namely *P. punctatus*, *A. caudavittatus* and *A. butcheri*, while those at Q were also typified by the atherinids *A. mugiloides, Atherinosoma elongata* and the goby *P. punctatus*. During other seasons, the ichthyofaunas at I were also commonly distinguished from those at other habitats in the main basin by a greater prevalence of *F. lateralis* and relatively lower abundances of *P. punctatus*, *A. mugiloides* and *L. presbyteroides*, while those at the relatively sheltered habitat Q were most notably distinguished from those at the more exposed habitats F and G by greater densities of *F. lateralis*.

5.2.1.2 Benthic macroinvertebrate assemblages

The composition of the benthic macroinvertebrate assemblages exhibited moderate to large differences among habitats throughout the Swan Estuary in each season in 2005. In contrast to the fish assemblages, the extents of those spatial differences were greatest in winter and least in summer. The smaller differences in benthic macroinvertebrate composition among habitats in summer were paralleled by a far lower mean number of species, low taxonomic distinctness of the assemblage and often lower mean overall densities at most habitats, thus reflecting the fact that those assemblages were relatively depauperate. However, the compositions of both the fish and benthic macroinvertebrate faunas exhibited relatively large differences among habitats in spring 2005.

Aside from the distinctiveness of the benthic macroinvertebrate composition at the upper estuary habitats A and C and the channel habitat M in all or most seasons, those at the main basin habitats G and I and, to a lesser extent, F, were also notable in several cases. The most marked differences in faunal composition between both A and C and the remaining habitats were detected in winter and spring, and that at C was also notably distinct in autumn. The faunal assemblages at the first of these habitats, which contained the lowest overall density of individuals, mean number of species in almost all seasons and taxonomic diversity, were characterised by relatively few species, which comprised the polychaetes *Ceratonereis aequisetis* and *Leitoscoloplos normalis* and the bivalve *Arthritica semen* in all seasons. The first two of these species were particularly ubiquitous and typified the assemblages at most other habitats in each season. Furthermore, *C. aequisetis* ranked within the top three most abundant species at all habitats except I and M in the lower reaches of the basin and channel, respectively. However, both C. *aequisetis* and *L. normalis* were often recorded in greater numbers at habitats other than A in each season, with the exception of the latter species in autumn. In contrast, while *A. semen* was recorded at all habitats, it regularly characterised the assemblages of only A and C and often that of G in the main basin, and occurred most consistently and in the greatest numbers at C. *Ceratonereis aequisetis* and *A. semen* were also found to be highly abundant in the shallow waters of the upper Swan Estuary by Kanadjembo *et al.* (2001) and those of Wilson Inlet on the south-western Australian coast by Platell and Potter (1996). The first of these species is highly fecund and is also omnivorous, feeding directly on plant material (Hutchings 1984) and also other benthic macroinvertebrates (Fauchald and Jumars 1979, Stevens *et al.* 2006), while the latter is physiologically adept at tolerating variable salinities and employs a range of life history strategies for overcoming problems associated with high river flow, such as reproducing very regularly, growing at a rapid rate, having a short life cycle and brooding its eggs and larvae inside the mantle cavity (Wells and Threlfall 1982a, b). *Leitoscoloplos normalis* is also relatively tolerant of variable salinities, and has been recorded in waters ranging from essentially fresh to marine conditions (Hutchings and Murray 1984). Such characteristics thus make these benthic invertebrate species particularly suited to dealing with the physiologically-stressful conditions often found in the upper reaches of estuaries, and it is relevant that habitats A and/or C experienced extreme seasonal changes in salinity (*i.e.* 3.6-19.8‰ and 3.8-31‰, respectively), water temperature (*i.e.* 13.7-26.6°C and 15.2-27.0°C, respectively) and, in summer, the lowest dissolved oxygen concentration (*i.e.* as low as 3.3 mg L^{-1}). Furthermore, the depth of the sediment transition layer (*i.e.* at which sedimentary conditions change from oxic to anoxic) was often among the shallowest at these habitats, and particularly at the uppermost site representing

A (*i.e.* <1.5 cm). Such findings are likely to be associated with the relatively large contributions of sedimentary particulate organic matter recorded at these locations, which can prevent oxygen diffusing through to the interstitial spaces in the sediment. It is also of interest to note that the individuals of species recorded at these upper estuary habitats were typically smaller than those of the same species collected in the middle and lower estuary (pers. obs.), which is also indicative of physiological stress and often seen in highly tolerant species undergoing long-term exposure to anoxic sediments and/or the presence of toxic sulfides (Hagerman 1998, Lee and Lee 2005).

Various other species characterised the benthic macroinvertebrate assemblages at habitat C, such as the polychaete *Capitella capitata* in all seasons except spring, the amphipods *Paracorophium excavatum, Grandidierella propodentata* and *Corophium minor* in autumn and/or winter, and the polychaete *Boccardiella limnicola* in winter. The first of these species was ubiquitous, and also characterised the assemblages at all or most of the main basin habitats F, G and I in every season, and sometimes also those at J in the small upper basin and M in the channel. However, the consistency of occurrence and abundance of *C. capitata* was far greater at the three main basin habitats in each season, where they also ranked first or second in terms of overall abundance. This species has also been shown by Platell and Potter (1996) to be abundant in the shallows of Wilson Inlet, where its distribution was positively associated with the biomass of the seagrass *Ruppia megacarpa*, which grows extensively in the basin of that system. These workers attributed this relationship to the fact that this polychaete is a sediment-ingesting deposit feeder, and would thus benefit from the abundance of decaying plant material present in the substrate surrounding those seagrass beds. It is thus relevant that habitats F, G and I in the main basin of the Swan Estuary each contain considerable areas of seagrass and/or macroalgae. *Paracorophium excavatum* was only recorded at habitats A, C and J and was particularly prevalent at C, where it ranked second in terms of overall abundance. Other species of this genus have also been recorded largely in the upper reaches of other estuaries in Australia and New Zealand (Ford *et al.* 2001, Chapman *et al.* 2002), thus suggesting that it may be more suited to lower salinities. The spatial distribution of this species may also be related to the fact that it is a deposit feeder, and the sediments of habitats A and C contained by far the greatest contributions of particulate organic matter than any other habitat throughout the estuary. In contrast, the other two amphipod species that characterised C in particular seasons made far greater contributions to the overall number of individuals at all or several of the basin and channel habitats. Despite this, *G. propodentata* and *C. minor* were both still recorded in greater densities at C than all other habitats in autumn, and were important in distinguishing the fauna of this habitat from that of others. Kanandjembo *et al.* (2001), who did not record either of these species in the upper reaches of the Swan Estuary, suggest that small crustaceans such as these may not be particularly well adapted for tolerating low and/or marked changes in salinity. Yet, the relatively abundant sedimentary organic matter at those upper estuary habitats would be beneficial for these deposit feeding amphipods. It may thus be relevant that the mean salinity at C in autumn 2005 (*i.e.* 19.6‰) was far higher than that recorded in winter and spring (*i.e.* 3.8-7.6‰), and that the organic matter content throughout the estuary was notably greater in the former season than in summer and winter 2005. Furthermore, although the mean salinity was considerably higher at C in summer 2005 (*i.e.* 28.5‰) than in autumn, the relative lack of both of these amphipod species at this habitat in the former season may be due to concurrent and unfavourable changes in other non-enduring environmental characteristics, such as the lower sedimentary organic matter content and/or dissolved oxygen levels, or attributes of the life-history of these organisms (see subsection 5.2.3.2).

The distinctiveness of the faunal compositions of the main basin habitats F, G and I compared to those in other regions of the estuary, and to each other, was often attributable to the larger numbers and/or more consistent occurrences of relatively common species, such as *C. aequisetis, L. normalis* and/or *C. capitata*, or the presence of other species that exclusively or very consistently typified the assemblages at only one basin habitat in a particular season(s), such as *Velacumantus australis* and *Sanguinolaria biradiata* at I in summer, *Pseudopolydora kempi* at I in autumn and *Prinospio cirrifera* at F in winter. Moreover, G also contained the greatest overall mean density of benthic macroinvertebrates, and the taxonomic distinctness of the assemblages at F and G were among the greatest recorded throughout the estuary, thus indicating that these fauna contained diverse representatives from higher taxonomic groups. The often greater prevalence of the first three of the above species at each of the main basin habitats relative to those in the upper estuary is likely to partly reflect a greater abundance of their collective food sources, namely detrital or non-detrital plant material from the considerable beds of submerged macrophytes, other benthic macroinvertebrates, which occurred in far greater overall numbers at F, G and I than at A, and sedimentary chlorophyll, which was particularly marked at habitat I in spring and summer. Moreover, in addition to the fact that several of the water and/or sediment quality characteristics of the main basin habitats are likely to be less physiologically-stressful than those of the upper estuary habitats (see above), the greater overall numbers of benthic macroinvertebrates at F, G and I compared particularly to A may also reflect the warmer water temperatures of those basin habitats in winter, which would promote faster growth of their juveniles that are known, in other south-western Australian estuaries, to be most abundant at that time of year (Platell and Potter 1996).

Differences in the abundance of the above-mentioned food sources between habitats F, G and I may also partly explain why some species exclusively typified and/or were particularly consistent at just one of those basin habitats in particular seasons. For example, the greater concentrations of sedimentary chlorophyll at habitat I than F and G, which probably reflects both the lower sediment disturbance by wave activity at the more sheltered former habitat and the fact that its smaller mean sediment grain size provides a greater surface area on which microphytobenthos can grow, were paralleled in summer by the prevalence of the gastropod *V. australis*, which uses specialised feeding apparatus to scrape microphytobenthos from sediment grains (Hori 2006), and the deposit/suspension feeding bivalves *S. biradiata* and *P. kempi*, which may use resuspended sedimentary chlorophyll as a food source (Morton *et al.* 1998). The overall abundances of the latter two species were far greater at I than F and G, and aside from exclusively typifying this habitat in particular seasons, they were also more prevalent at I than most other habitats in several of the remaining seasons. Such findings may also reflect a greater affinity of both of these species for higher salinities, a view supported by the fact that the only other habitat at which the mean densities of these species approximated those recorded at I was M located in the channel. Furthermore, it may be relevant that habitats F and G lie within conservation zones due to their importance as bird feeding sites, and the reduced abundances of *S. biradiata* and *P. kempi* at these habitats relative to I may thus also result from predation by wader birds, which are known to feed partly on large thin-shelled infaunal bivalves such as these (Higgins and Davies 1996).

Habitat M was by far the most speciose, and its faunal assemblages were typified exclusively by some species in particular seasons, such as the gastropod *Nassarius* sp. and the polychaete *Heteromastus sp.* in summer, and by other species that were notably prevalent at certain times of year, such as *P. kempi* in spring. Moreover, the benthic macroinvertebrate assemblage at this habitat was sometimes characterised by species that also typified only I, such as the polychaete *Australonereis elhersii* in autumn. Although present in small numbers, this habitat also contained 22 species that were not found at any other estuarine habitat, seven of which were recorded by Wildsmith *et al.* (2005) in the nearshore marine waters along the coast outside the Swan Estuary. Such findings suggest that these species, almost all of which were polychaetes, have an affinity for marine salinities. *Heteromastus* sp. was also recorded in these nearshore marine waters, and thus it is also likely that its restriction to habitat M in the Swan Estuary is linked to its preference for higher salinities (Hutchings and Murray 1984). Moreover, although *Nassarius* sp and *A. elhersii* were recorded at various other habitats throughout the estuary, they were never recorded at A or, in the case of the latter species, C, and attained the greatest or second greatest densities at either I or M. Such distributional patterns suggest these species may also be better suited to greater salinities. In addition to its relatively consistent and/or high salinity (23.8-36.5‰), temperature (16.2-23.8°C) and dissolved oxygen (6.8-9.40 mg L^{-1}) ranges and comparatively deep sediment transition layer, habitat M is also sheltered due to its relatively small fetches and contains diverse substrate and submerged vegetation types, including bare sand interspersed with patches of rock and mixed stands of seagrass (*Halophila ovalis, Zostera* sp. and *Heterozostera* sp.) and macroalgae. Such characteristics provide a hospitable and diverse environment for benthic macroinvertebrate fauna, and have probably contributed to the high species richness found in this environment. However, it is interesting that the taxonomic distinctness of the assemblage at M was not particularly high, and one of its representative sites contained the second least diverse fauna recorded throughout the estuary. Such results indicate that, although the benthic macroinvertebrate fauna at M is speciose, a considerable proportion of those species come from the same lower taxonomic groups, *i.e.* families.

5.2.1.3 Nematode assemblages

The majority of the nematode species collected during this study are undescribed, highlighting the paucity of nematological studies at fine taxonomic levels throughout the world. This study has led to the development of formal taxonomic descriptions of 10 of these species, comprising four species of Axonolaimidae, representing the genera *Ascolaimus, Parascolaimus, Odontophora* and *Parodontophora*, and six species of Desmodoridae, representing single species of *Bolbonema, Eubostrichus, Catanema* and *Leptonemella* and two species of *Onyx* (Hourston and Warwick, in press). Given the lack of rigorous species-level studies of spatial and temporal differences in free-living nematode assemblages in microtidal estuaries throughout the world, relatively little is known about their ecology. This study thus represents an important contribution to that field of research.

The nematode assemblages recorded throughout the Swan Estuary in each season in 2005 exhibited moderate to large differences in species composition among the various nearshore habitats. Unlike the fish and particularly the benthic macroinvertebrate assemblages, the overall extent of the spatial differences in nematode composition was relatively consistent among seasons. However, like the former faunal assemblage, the greatest overall difference in the species composition of nematodes among habitats occurred in spring and the least in winter.

Although large compositional differences occurred between most pairs of habitats in all seasons, the most pronounced occurred between A and most other habitats, except the other upper estuary habitat C, in each case. Moreover, similarly high differences were also detected between both C and J and most other habitats in spring, while this was also true in a few instances in the other seasons.

The distinctiveness of the nematode assemblage at habitat A was due in all seasons to the prevalence of *Theristus* sp.1 and, in at least two seasons, also of *Metalinhomeous* sp., *Parodontophora aurata* and *Metadesmolaimus* sp.2. The first of these species also always characterised habitats C and J located consecutively downstream of A, and the same was true of the last species in some seasons. Although *Theristus* sp.1 and *Metalinhomeous* sp. were found throughout the Swan Estuary, they were only abundant at habitats A, C and/or J, and attained by far their greatest overall densities at the first of these habitats, particularly in the case of *Theristus* sp.1. *Parodontophora aurata* and *Metadesmolaimus* sp.2 were not recorded, however, in the lowermost habitats I and M, and were only abundant at A and C, respectively. In contrast to the abundance and regular occurrence of each of the species that typified A, those that typified C and J in each season often did not occur as consistently and/or in particularly high numbers, and were thus frequently unimportant in distinguishing the nematofaunas of these habitats from those of others. Such findings were also reflected by the fact that C and J both contained far lower overall densities of nematodes than all other habitats throughout the estuary. However, in addition to some of the above-mentioned species, the assemblages at C were also characterised by *Pierrickia* sp. in every season, which also characterised the nematofaunas at A in some cases. Moreover, aside from some of the above species, those that typified J often varied considerably among seasons, some of which were exclusive to that habitat at particular times of year. Such features of the nematofaunas at C and J would have contributed to their differences from those at other habitats, and particularly those in the middle to lower estuary.

It is likely that the distinctiveness of the nematode assemblages at habitats A, C and J compared to those in the more downstream reaches of the Swan Estuary is related to the magnitude of and/or temporal variability in salinity. Thus, these three upper estuary habitats experienced both the lowest salinities in particular seasons (*i.e.* as low as 3.8‰ at A and C and 12‰ at J) and, in the case of C and J, also the largest seasonal ranges in this water quality variable, *i.e.* as high as 28.8 and 36.5‰, respectively. It is thus suggested that the nematode species that characterised the faunas at these habitats, and predominantly those detected in every season, are particularly well adapted to the osmotic stress that would result from such low and/or variable salinities. Warwick (1971) and Austen and Warwick (1989) also found that spatial differences in the structure of nematode assemblages in macrotidal European estuaries was closely correlated with those in salinity. Furthermore, Armenteros *et al.* (2006) found that variation in salinity at a given location, rather than absolute salinity *per se*, was more important in influencing the composition of the nematode fauna in the mangroves of a Cuban gulf. The findings of these latter workers were also supported by those of Attrill (2002) with respect to meiofaunal diversity in the Thames Estuary. The particularly variable salinities recorded at habitats C and J throughout the year may thus have contributed to the relatively low densities, inconsistency of occurrence and/or seasonal differences in their characteristic nematofauna.

As free-living nematodes tend to be selective in the food they ingest, it thus follows that differences in the trophic composition and, to some extent, species composition of nematode assemblages, will be correlated with differences in the type and quantity of available food sources. Thus, in addition to the probable influence of salinity, the importance of *Theristus* sp.1, *Metalinhomeous* sp. and *Metadesmolaimus* sp.2 at habitats A, C and/or J may be related to the fact that these species are non-selective deposit feeders, and the levels of their main food source, namely sedimentary particulate organic matter, were far greater at the two uppermost habitats.

In contrast to the nematofaunal compositions at habitats A, C and J, those in the main basin of the estuary (F, G and I) and channel (M) were often typified partly by *Theristus* sp.2, *Halichoanolaimus duodecimpapillatus* and/or *Spirinia parasitifera* in most seasons. While each of these species were found at all habitats throughout the estuary in almost all cases, *Theristus* sp.2 and *S. parasitifera* were typically only abundant at those in the main basin or channel. This was particularly applicable to the latter species, which ranked either first or second in overall abundance at each of those habitats. Although *H. duodecimpapillatus* was only abundant at habitat I, it occurred consistently, but not in particularly large numbers, at each of the other basin and channel habitats. The large differences that were also detected between the nematofaunal compositions of various pairs of the habitats within the middle to lower estuary, particularly F *vs* I in each season, were often due to differences in the prevalence of species other than those listed above, such as that of *Pontonema* sp.1 and/or *Subsphaerolaimus* sp. at F in all or most seasons and of *B. australis* at I in spring. This latter species was also recorded by Hourston *et al.* (2005) in the nearshore marine waters along the coast outside the Swan Estuary, and species of *Theristus*, *Spirinia* and *Subsphaerolaimus*, which are closely related to those recorded in the estuary, were also found in those coastal waters. As the salinities at habitats in the main basin and particularly the channel approximated those of marine waters in both summer and autumn (*ca* 33-37‰) and exhibited the least variation in salinity throughout the year (*i.e.* falling to *ca* 17-24‰ in winter), it is suggested that the above nematode species may be better suited to higher and/or less variable salinities. Moreover, of the seven species recorded exclusively at the speciose lower estuary habitat M, two were also recorded in these nearby marine waters, thus implying that they may have relatively little ability to cope with salinities lower than those of full strength seawater (Hourston *et al.* 2005).

Aside from differences in the tolerance or affinity of the nematode species that were prevalent in the middle or lower estuary for particular salinities, differences in the nematofaunal compositions of habitats in these regions may also be related to the availability of particular food sources (*e.g.* microphytobenthos and bacteria), the extent and structural complexity of submerged macrophyte beds and/or the degree of wave exposure and hence sediment disturbance. Thus, of the three main basin habitats, I was the most sheltered from wave activity and, in the warmer seasons of summer and spring, contained by far the greatest quantities of sedimentary chlorophyll. This presumably reflects the growth of microphytobenthos, which, along with bacteria, is known to colonise the surface of undisturbed and shallow sediments (Masini and McComb 2001). It thus may be relevant that three of the five species that were abundant at I, namely *N. decoratus, B. australis* and *Theristus* sp.2, were either epistrate/diatom or non-selective deposit feeders, that feed primarily on benthic microalgae/diatoms and bacteria/detritus, respectively. Furthermore, each of these species were recorded in their greatest mean densities at that habitat. However, *Dichromadora* sp., which is also an epistrate/diatom feeder, ranked first in terms of abundance at the relatively exposed basin habitat G and was also abundant at several other habitats, but not I. Despite these findings, it is relevant that the only season in which this species was important in consistently typifying and/or distinguishing the nematofauna at G was spring, which coincided with the greatest concentrations of sedimentary chlorophyll at that habitat and also the time of year when blooms of marine diatoms are known to occur in the Swan Estuary (Thompson 1998). Furthermore, the relatively wide shoaling margin and thus shallow waters at G would encourage the rapid growth of microphytobenthos during warmer seasons. Such environmental conditions may also have contributed to the relatively large number of nematode species recorded at this habitat, particularly during summer. Moreover, the presence of greater structural complexity due to the considerable macrophyte beds, as well as the more regular incorporation of detrital matter into the interstitial spaces of the sediment by wave disturbance, may also have contributed to the relatively high species richness at habitat G. The clear predominance of *Pseudochromadora cazca* at G, particularly during autumn and winter, may also be related to the relatively exposed conditions at this habitat. Thus, this species possesses ambulatory adaptations that allow it to remain closely associated with sand grains, and which would be particularly important during seasons such as winter when wave energy is typically greater.

Despite the fact that each of the main basin habitats contained considerable areas of seagrass/macroalgal beds, which would contribute to the detrital content and/or structural complexity of those habitats, the seagrass beds at the channel habitat M contained mixed stands of *H. ovalis*, *Zostera* sp. and *Heterozostera* sp., and thus comprised a more complex rhizome mat structure than those in the main basin, which contained only *H. ovalis*. Moreover, the sediment at M, unlike those in the main basin, contained considerable portions of shell fragments, which was partly reflected by the greater mean sediment grain size at this habitat. Such increased environmental complexity at M, in addition to its considerable shelter from wave activity and proximity to coastal waters (*i.e.* and thus relative temporal stability of water quality conditions and tendency to be colonised by marine nematode species and diatoms), almost certainly contribute to the considerably higher number of species recorded at this habitat than any other. Furthermore, in addition to some of the previously mentioned species that were abundant in the middle to lower estuary, the other nematode species that dominated and commonly distinguished the assemblages at M, *i.e. Chromadorina* sp., *Comesoma arenae* and *Dichromadora* sp., were all epistrate/diatom feeders or non-selective deposit feeders, which would clearly benefit from the abundant diatom and/or detrital food resources likely to be available at this habitat.

5.2.1.4 Hyperbenthic faunal assemblages

The composition of the hyperbenthic assemblages recorded throughout the Swan Estuary during winter 2005 and the following summer exhibited the least differences among habitats of the four different types of faunal assemblage examined throughout this estuary. Such findings are probably related to the fact that a large proportion of these faunal assemblages comprise ubiquitous planktonic fauna, several of which also have poor swimming abilities and thus little capacity to actively select habitat types within the system. However, during both seasons, the habitat with the most distinct hyperbenthic composition was clearly A located in the uppermost reaches. The hyperbenthic assemblages at the lowermost habitat E were similarly distinct in winter, but less so in summer. However, in both seasons, the faunal composition at the other upper estuary habitat, C, was also notably different from that at E and the main basin habitat F.

Like each of the other faunal assemblages studied in the Swan Estuary, among the greatest total number of hyperbenthic species was recorded at representatives of channel habitats, *i.e.* E and M. Several other workers have also found that the species richness of estuarine hyperbenthic assemblages is greatest in regions where salinities remain closest to those of marine waters (Mees and Hamerlynck 1992, Mees *et al.* 1993, Azeiteiro and Marques 1999). However, the highest number of hyperbenthic species was recorded at habitat G in the main basin, which also supported among the greatest number of nematode species. This habitat also contained among the greatest overall densities of hyperbenthos, as well as benthic macroinvertebrates and nematodes, but among the lowest densities of fish. The lowest densities of hyperbenthos were recorded at habitat A, which paralleled the findings for each of the other faunal assemblages, which were either found in their lowest overall densities at this habitat or the other upper estuary habitat, C. However, unlike the fish and benthic macroinvertebrates, the overall number of hyperbenthic species were lowest at the main basin habitats I and F, rather than A. This also contrasts with the findings of the above workers, who recorded the lowest number of hyperbenthic species in those areas of estuaries with the lowest salinities. Furthermore, it is also interesting to note that the mean taxonomic distinctness and thus diversity of the hyperbenthic assemblage at A was either the highest or close to the highest in both seasons, which opposed the trends exhibited by most of the other faunal assemblages.

The distinctiveness of the hyperbenthic composition at A in both seasons was partly attributable to the fact that, unlike any other habitat, it was characterised by the bivalve *Musculista senhousia.* This species was also the most abundant at A, comprising over half the number of hyperbenthos recorded at that habitat and, while it was found at all other habitats except F and M, it was never abundant. This small mussel species was also found in the benthic macroinvertebrate assemblage at several habitats and, while it was never abundant, it attained its greatest densities at habitats in the upper estuary, and especially C. *Musculista senhousia* is particularly well adapted to coping with low and variable salinities and dissolved oxygen levels (NIMPIS 2005) and, given that habitats in the upper estuary experienced mean salinities as low as 3.8‰ in winter 2005 and as high as 31‰ in summer 2007, and also the lowest mean dissolved oxygen concentrations recorded throughout the estuary (3.3 mg L^{-1}), this species has seemingly found a favourable niche at these locations. Moreover, this highly fecund mussel would have a competitive advantage over less fecund bivalves, such as *Xenostrobus securis*, which was abundant in the nearshore waters of the upper Swan Estuary in the mid 1990s (Kanandjembo *et al.* 2001), but was not recorded in the present study. It is thus possible that *M. senhousia*, an introduced and invasive species, may have contributed to a decline in *X. securis*. The polychaete Sabellid sp. and the juvenile fish Mullid sp. were also among the species that exclusively characterised the hyperbenthos at A in winter 2005, and were often important in distinguishing its faunas from that at other habitats in this season. These species were otherwise recorded only at J and M, respectively. Such distributional patterns of Sabellid sp. may be related to the relatively high turbidity of the waters at habitat A (Thomson *et al.* 2001) and the fact that this species traps larger particles from the water column to build the tough leathery tubes that it inhabits (Bailey-Brock 1976). The low and/or variable salinity and dissolved oxygen conditions at habitat A, combined with the large seasonal fluctuations in water temperature (*i.e.* 13.7-26.6°C between winter 2005 and summer 2006, respectively), would be physiologically-stressful for many hyperbenthic species and may thus explain why the mean number of species and density of hyperbenthos at A in summer 2006 was considerably lower than at all other habitats except C, in most cases. However, the high taxonomic diversity of the hyperbenthic assemblage at habitat A reflects the fact that it comprised species that belonged to various phyla, *i.e.* Arthropoda, Mollusca, Polychaeta and Chordata, whereas those at most habitats in the middle and lower estuary comprised species that mainly represented the phylum Arthropoda, and often the class Crustacea. The phyla recorded at habitat A often contain taxa with a range of adaptations for dealing with stressful environmental conditions, such as seeking refuge within shells or tubes and/or are highly fecund.

The assemblage at the other upper estuarine habitat, C, was exclusively characterised by calanoid sp.12 in both summer and winter and by several other species in each season, such as the cladoceran Daphnia sp. in winter 2005 and the amphipod *Grandidierella propodentata* and the mysid Mysidellinid sp. in summer 2006. Such species were important in distinguishing the faunas at C from those of most other habitats in winter 2005, but were far less important in summer 2006. Several other species characterised the hyperbenthic assemblage at C that were also typical of the faunas at most other habitats, such as calanoid sp.4 in both seasons and calanoid sp.2 in summer, but they were almost always found in greater abundances at C and thus were highly important in distinguishing the hyperbenthos of this habitat. While these two calanoid species were recorded at all habitats throughout the estuary and were abundant at several, their overall densities were greatest at C in the case of sp.2, which was also the top ranking species at this habitat, and second greatest at C in the case of sp.4, which was second most abundant at this habitat. The only other habitat that contained similarly high densities of calanoid sp.2 was J, located just downstream of C, which was also the case for the above-mentioned calanoid sp.12. Such findings indicate that these two calanoid species may be better suited to particular environmental conditions at C and J, such as their lower salinities compared to the main basin and channel habitats, or the accumulations of the unattached red algae *Gracilaria comosa* often detected at these habitats, and which may provide an important direct or indirect food source for these omnivorous invertebrates. While calanoid sp.4 was also found in far higher overall densities at C and J than most other habitats, it reached its greatest densities at the channel habitat E, thus suggesting that factors other than salinity are important in determining its spatial distribution. Such factors could include a greater abundance of preferred food sources that may be associated with the extensive and diverse submerged vegetation beds found at habitat E (Shahidul Islam *et al.* 2005). The lower salinities in the upper estuary relative to that in the middle and lower reaches almost certainly explains the prevalence of the freshwater cladoceran Daphnia sp. at C in winter 2005, when salinities at that habitat fell to 3.8‰. However, similarly low salinities were recorded at A in that season, yet the mean density of Daphnia sp. was considerably lower. The prevalence of Mysidellinid sp. at C may reflect the relatively high proportions of sedimentary organic matter recorded at this habitat, which can provide an important food source for these omnivorous fauna (Fockeday and Mees 1999).

The basin habitats F, G, I and J and the channel habitat M each contained similar hyperbenthic compositions in winter 2005, while the same was also true of summer 2006, with the exception that the assemblage at J differed significantly from that of all other habitats. In both seasons, the hyperbenthos of each of the above habitats was commonly typified by copepod species such as calanoid spp. 2 and 4 and harpacticoid sp.7 and, in summer, also by cyclopoid sp.1, which were often abundant at these habitats. The latter species was particularly abundant at habitats F and G, and was primarily responsible for the large overall densities of hyperbenthos recorded at these habitats. Although each of the main basin habitats F, G and I shared some similarities in terms of their enduring environmental characteristics, such as a moderate amount of submerged vegetation, which comprised predominantly the seagrass *H. ovalis* and, in the case of F and G, also their location within the estuary and relatively high exposure to winds from several directions, the enduring characteristics of habitats M and J differed considerably from each other and those of the main basin habitats in terms of their location in the estuary, extent and composition of substrate and submerged vegetation type and exposure to wind and thus wave activity. The lack of difference in the composition of the hyperbenthic assemblages among these habitats, despite their considerable environmental differences, reflects the wide tolerances of the above copepod species for different physico-chemical conditions. However, despite the above enduring environmental differences, the magnitude of some non-enduring environmental characteristics, such as salinity, were similar among each of the above basin and channel habitats in summer 2006 (*ca* 27.9-32.5‰), and it may be relevant that the only season in which significant differences were detected between the upper basin habitat J *vs* F, G, I and M was winter, when salinities at the former habitat were appreciably lower than those at the remaining habitats, *i.e. ca* 12‰ *vs* 17.2-23.8‰. However, the fact that both of the above calanoid species and harpacticoid sp.7 characterised the assemblages of the upper estuary habitats A and/or C in winter 2005 and/or summer 2006, which both always had markedly lower salinities than all other habitats, further supports the suggestion that these species are highly tolerant of different environmental conditions.

The hyperbenthos of the lowermost habitat E was characterised and distinguished from that of all other significantly different habitats by the decapod *Palaemonetes australis* in both seasons. Although this species was recorded at all habitats and also characterised the assemblages of the other channel habitat M and also F in summer 2006, it was recorded in far lower densities than at E. While this species is highly euryhaline and is known to occur throughout the Swan Estuary and its tributaries (Bray 1976, 1978), its marked preference for the channel habitat E and, to a lesser extent, M, may be related to the greater structural complexity provided by the submerged vegetation beds at those habitats than in other parts of the system. Thus, other species of Palaemonetes are known to be highly associated with vegetation in nearshore coastal areas, as they provide valuable refuge and nursery sites and sources of food, either in the form of epibiota or plant detritus (Robertson and Weis 2007). Other workers in south-western Australian estuaries have also found that this decapod species often occurs in extremely high densities in vegetated areas or those areas containing detrital plant matter (T. Linke, pers. comm.), and that it is a major prey item for several fish species (Platell *et al.* 2006). It is thus relevant that the submerged vegetation beds at habitats E and M are more structurally complex than those found elsewhere in the system due to the fact that they contain mixed stands of up to three seagrass species and a high diversity of macroalgal species (Astill and Lavery 2004), and are thus more likely to provide a greater diversity of food and better shelter than the monospecific stands of *H. ovalis* found at other habitats in the Swan Estuary. Such structural complexity also probably contributes to the relatively high overall number of species found at habitats E and M, and the fact that several ubiquitous copepod species, such as calanoid sp.4, harpacticoid spp. 1 and 7, occurred in greater numbers at E than almost all other habitats in summer 2006. Greater hyperbenthic diversity and density in more structurally complex seagrass environments have also been recorded by several other workers (*e.g.* Edgar 1990, Cunha *et al.* 1999). Moreover, the proximity of habitat E to marine waters also explains why the hyperbenthos at this habitat was characterised and distinguished by marine taxa such as ctenophore sp. in winter 2005.

5.2.2 Spatial relationships between the environmental and faunal characteristics of habitats

The relative spatial differences among habitats in the Swan Estuary, as defined by the suite of enduring environmental variables used to classify those habitats, significantly matched that exhibited by the composition of each of the faunal assemblages in each season in which they were sampled. The extent of those correlations were extremely high in the case of the fish assemblages, moderate to high for the benthic macroinvertebrate assemblages, high in almost all seasons for the nematofauna and moderate for the hyperbenthos. Such results indicate that the spatial pattern in the enduring environmental measurements among habitats provides a good to excellent surrogate for identifying spatial differences in the composition of each of the above faunal assemblages in each season, and thus a sound basis for predicting the faunal species likely to typify any nearshore site in the Swan Estuary at any time of year, simply by assigning it to its most appropriate habitat type using its enduring environmental measurements and the quantitative habitat prediction tool developed in Chapter 3.3.2. Moreover, in almost all cases, the suite of enduring environmental criteria better explained the spatial distribution of the faunal assemblages in each season than the complementary suite of water quality variables or, in the case of the two benthic faunal assemblages, the suite of sediment parameters. This was particularly evident during both summers and winter 2006 for the fish assemblages and in almost all cases for the benthic macroinvertebrate assemblages. While the correlations between complementary faunal and water/sediment quality data were often improved when BIOENV was used to restrict these suites of non-enduring environmental variables to those that best mirrored the spatial distribution of the fauna, the resulting correlations were still lower than or similar to those obtained between the enduring environmental and faunal data in several cases. Such results imply, firstly, that the other elements of the estuarine environment that are captured by the suite of enduring criteria but not by the water or sediment parameters measured in the field, *i.e.* exposure to wave activity, extent of cover by submerged vegetation and other aspects of water and/or sediment quality that are inferred by enduring surrogates such as distance from estuary mouth (*e.g.* turbidity, force of tidal or river flow etc.), are also important in discriminating among the spatial patterns exhibited by fish and invertebrate fauna in the Swan Estuary. They also imply that the enduring variables chosen as surrogates to reflect particular environmental attributes (*e.g.* distance from estuary mouth as a surrogate for spatial differences in a wide range of water and sediment parameters) are likely to be capturing the influence of those attributes on fish and invertebrate distribution in this system.

These findings have important consequences for future studies of faunal assemblage/habitat relationships in the Swan Estuary, as they highlight the value of considering a varied range of environmental variables in combination, rather than just one or a few that reflect only a limited component of the environment, when attempting to explain differences in the spatial distribution of its faunal assemblages. Furthermore, they also demonstrate the value of using measurements of enduring variables as surrogates for capturing spatial differences in particular non-enduring environmental characteristics, which may minimise the need to collect the latter type of data in the field in future studies. The highly variable nature of replicate field measurements for particular non-enduring environmental characteristics, such as those for dissolved oxygen concentration and sediment grain size, also contribute to the difficulties in using such data to establish reliable relationships between spatial differences in their magnitude and the composition of faunal assemblages.

The extent to which the habitat prediction tool and suite of characteristic species that had been established for each habitat in each season could be used to reliably predict the fish, benthic macroinvertebrate and/or hyperbenthic species most likely to occur at any nearshore location in the Swan Estuary at a particular time of year, was examined for various test sites throughout the system. Thus, the fish assemblages were sampled in each season at five additional sites, four of which were classified as habitat C and one which was classified as habitat E, on the basis of measurements for their enduring environmental characteristics. ANOSIM detected significant differences between the fish composition at one or more of the habitat C test sites *vs* those that were primarily chosen to represent this habitat in all sampling seasons except winter 2005. Of the remaining seasons, the extent of those significant differences was relatively low (*i.e.* R <0.500) in almost cases in autumn 2005 and summer 2007. Thus, in the above three seasons, the fish species that characterised the primary representatives of this habitat were, in nearly every case, also among those that characterised the assemblages at each of the test sites. During the remaining three sampling seasons, *i.e.* spring 2005, summer 2006 and winter 2006, significant and relatively large differences in fish composition (*i.e.* R >0.500) were detected between one of the test sites and primary representatives of habitat C in several cases, but at least one of the species that characterised the ichthyofauna at those primary sites also characterised that at every test site in nearly all cases. Furthermore, each of the species that characterised the assemblages at each test site of C in each season were almost always recorded at the primary representatives of that habitat in the same season. With respect to the test site classified as habitat E, the only season in which its ichthyofaunal composition exhibited significant and relatively large differences from those at either of the primary representatives of this habitat, was summer 2006. In each of the remaining five seasons, either no such significant differences were detected (*i.e.* winter and spring 2005 and summer 2007), or the extent of any significant differences was relatively low (*i.e.* autumn 2005 and summer 2007). Furthermore, in almost all seasons, the majority of species that typified the fish faunas at the primary representatives of E also characterised those at the test site.

The hyperbenthic assemblages were also sampled at two additional sites representing the upper estuary habitat C in winter 2005 and summer 2006. As with the fish assemblages at test sites of this habitat, the composition of the hyperbenthos at these two additional sites differed significantly from that at both sites initially chosen to represent C in both seasons, but the extent of those differences was relatively low (*i.e.* ANOSIM R <0.500) in half of the relevant comparisons. Furthermore, at least two of the species that characterised the hyperbenthic fauna at the primary representatives of C in each season also characterised that at each test site in the same seasons. Additional sampling of the benthic macroinvertebrate assemblages was carried out during summer and winter 2005 at two nearshore sites, one of which was classified as habitat I and the other as habitat F on the basis of their enduring environmental characteristics. The composition of the assemblage at the additional site representing I did not differ significantly from that at the site primarily chosen to represent this habitat in either season, and while significant differences were detected between the compositions of the additional and primary sites representing habitat F in both seasons, the extent of those differences was relatively low in winter (*i.e.* ANOSIM R <0.500). Furthermore, the majority of the species that characterised the benthic macroinvertebrate assemblages at each of the above test sites in each season also characterised those at the primary representatives of those habitats in the same seasons.

The above results demonstrate that the current scheme for predicting the fish and/or invertebrate species most likely to typify particular nearshore sites of interest throughout the Swan Estuary at various times of the year is at least reasonably accurate and, in several cases, very accurate. It is noteworthy that the habitat at which both fish and hyperbenthic compositions differed most extensively between test and primary sites was C, which was also the same habitat at which the greatest variability among replicate primary samples was detected for all faunal assemblages in almost all sampling seasons (see subsection 5.2.1). As mentioned previously, such results indicate that the faunal compositions occupying that upper estuary habitat change markedly, and thus it is to be expected that accurate prediction of its characteristic species would be the most difficult. Furthermore, the fact that significant differences in fish composition were detected between many pairs of the six sites representing habitat C in most seasons, indicates that the main cause of the less accurate predictions of its characteristic species was not simply insufficient replication of that habitat during the main sampling regime.

5.2.3 Seasonal differences in faunal assemblage composition among habitats

5.2.3.1 Fish assemblages

The overall extent of the differences in fish assemblage composition among seasons at each habitat was appreciably lower than that among habitats in the various seasons. Among the greatest overall seasonal differences were detected at habitat J, which were largely attributable to the considerable ichthyofaunal differences of summer *vs* winter samples. Such findings presumably reflect, at least in part, the pronounced differences in salinity between examples of these seasons at this habitat (*i.e.*12 *vs* 36.4‰ in winter 2005 and summer 2007, respectively) and perhaps those of other non-enduring environmental variables, such as water temperature (*i.e.* 15.6 *vs* 25°C in winter 2005 and summer 2007, respectively). For example, the greater prevalence of *A. mugiloides* and *P. punctatus* at J in summer than winter most likely reflects the apparent preference of these estuarine species for greater salinities and water temperatures, respectively (Prince *et al.* 1982, Gill and Potter 1993). Moreover, *A. rueppellii,* which also occurs in greater numbers in higher salinities (Chrystal *et al.* 1985), characterised the assemblages at J only during both summers when salinities at this habitat were greatest. The seasonal differences in ichthyofauna at J also reflect the recruitment patterns of the juveniles of particular species. For example, the abundance of *A. rueppelli* at J in both summers was far greater than at any other habitat in any other season. The mean length range of these fish (*i.e.* 37-40 mm) corresponded to that of the 0+ individuals of this species in the Swan Estuary, thus reflecting an influx of the new recruits of this species, which are spawned in spring and are known to move onto the shallow nearshore banks in summer (Chrystal *et al.* 1985). Furthermore, the greater prevalence of *A. butcheri* at J in summer, many of which were less than 60 mm in length, reflects an influx of larger 0+ recruits of this species, which spawns within the vicinity of habitat J in the Swan Estuary between the middle of spring and early summer (Sarre and Potter 1999).

It is interesting to note, however, that the habitat at which the greatest seasonal differences in fish composition were detected, *i.e.* Q in the middle reaches of the main basin, experienced among the narrowest seasonal range in salinity and water temperature, *i.e.* 19.5-36.0‰ and 16.2-25.4°C, respectively. Furthermore, habitat C, at which the greatest range in salinity (3.8-31‰) and second greatest range in water temperature (15.2-27°C) was recorded, experienced relatively small changes in fish composition among seasons. The seasonal differences at Q were primarily due to particularly abundant and consistent catches of both *T. pleurogramma* and *A. mugiloides* in autumn 2005, which were also substantially greater than those recorded at most other habitats in this season. Most individuals of the first of these species were 70-90 mm in length (data not shown), thus indicating that they were mainly 0+ recruits approaching the end of their first year life (Potter *et al.* 1988). Although both *T. pleurogramma* and *A. mugiloides* apparently prefer more saline conditions (Prince *et al.* 1982, Potter *et al.* 1988), the essentially marine salinities recorded at Q in autumn 2005 were also recorded during both summers at this habitat, yet far lower densities of both of these species were recorded in those seasons. Moreover, most of the other basin and channel habitats that also experienced marine salinities in autumn 2005 contained considerably lower densities of *T. pleurogramma* and *A. mugiloides* than Q in this season. Such findings may be partly explained by the fact that mature *T. pleurogramma* leave the Swan Estuary to spawn at sea during summer (Potter *et al.* 1988), thus accounting for the lower densities of this species at Q and most other basin and channel habitats in this season. Moreover, it may be relevant that habitat Q, and also G at which *T. pleurogramma* was similarly abundant in autumn 2005, were among the shallowest of the habitats sampled in the Swan Estuary (*i.e.* as reflected by the relatively shallow slope of the substrate and wide shoaling margin, respectively), and this species is known to exhibit a preference for shallow waters (Potter *et al.* 1988). The relatively small seasonal differences in the ichthyofauna of habitat C reflected the largely similar composition of samples from all seasons, except those from both winters. Thus, the assemblages at this habitat in summer, autumn and spring were characterised by species that are able to tolerate considerable variability in environmental conditions, *i.e. A. butcheri, A. caudavittatus* and *P. punctatus* (Potter *et al.* 1994, Gill 1996, Sarre and Potter 1999, Partridge and Jenkins 2002, Hoeksema *et al.* 2006b), while those in both winters comprised low numbers of those species that prefer lower salinities, *i.e. L. wallacei* and *P. olorum* (Prince *et al.* 1982, Gill and Potter 1993), or the juveniles of marine species known to migrate upstream in the Swan Estuary at this time of year, *e.g. M. cephalus* (Chubb *et al.* 1981). The ichthyofaunal composition of these winter samples varied considerably among replicates, further reflecting their depauperate and inconsistent assemblages.

The small seasonal differences in fish composition at each of the channel habitats E, M and N was largely expected, given that they experienced the least seasonal differences in non-enduring environmental parameters such as salinity and water temperature, and close to the lowest variability in dissolved oxygen. Among the greatest ichthyofaunal differences at each of these habitats, *i.e.* those between spring 2005 and summer 2007, were due partly to a greater prevalence of *T. pleurogramma* in the former season. The densities of this species in spring 2005 were particularly high at habitat E, and were second only to those recorded at the same habitat in winter 2005. The mean length of these fish, and the fact that they were larger in spring than winter 2005 (*i.e.* 77 *vs* 62 mm, respectively), indicated that they were mainly the slightly older 0+ recruits that were initially recorded at E in that latter season, which are known to migrate into the Swan Estuary from nearby marine waters at that time of year (Potter *et al.* 1988). As discussed above, the relatively low densities of *T. pleurogramma* in summer presumably reflects the migration of mature individuals out to nearby marine waters, where they spawn at that time of the year (Potter *et al.* 1988). Several other marine species were notably more prevalent in summer 2007 than in spring 2005 at particular channel habitats, including *A. rueppellii*, *A. ogilbyi* and *H. semifasciata*, which, in the case of the first of these species, reflected an influx of their 0+ recruits and, with the latter two, possibly a preference for the greater salinities that were recorded at those habitats at that time of year.

5.2.3.2 Benthic macroinvertebrate assemblages

The composition of the benthic macroinvertebrate fauna exhibited considerable differences among seasons at each of the main basin habitats F, G and I and, to a lesser extent, the channel habitat M, whereas those at the upper estuary habitats A and C, and also J in the small basin at the foot of the Swan River, underwent relatively small seasonal changes, particularly in the case of A. Various other attributes of these faunal assemblages displayed pronounced seasonality, such as the mean number of species, density and taxonomic distinctness, which were often markedly lower in summer and/or autumn and greatest in winter and/or spring. Moreover, the extent of the differences in benthic macroinvertebrate composition among habitats was substantially greater in winter and spring than in autumn and especially summer.

The generally low species richness, density, diversity and spatial segregation of the benthic macroinvertebrate assemblages in summer and/or autumn presumably reflects, in part, various aspects of the life history of many of these species. Thus, Gaughan and Potter (1995) demonstrated that the densities of polychaete, gastropod and bivalve larvae in Wilson Inlet on the south coast of Western Australia reached their maxima at some time between mid spring and late autumn, and which were subsequently shown by Platell and Potter (1996) to be reflected by marked increases in the juveniles and adults of several benthic macroinvertebrate species during winter in that system. Moreover, the latter workers found that the densities of species such as *C. aequisetis*, *C. capitata* and *A. semen* were far lower in summer, thus implying that these species are subject to mortality around that time of year. Such results for the first of these species are also supported by those of Hutchings and Glasby (1982) and Glasby (1986) in eastern Australian estuaries, who reported that *C. aequisetis,* which has a one year life cycle, becomes sexually mature in late spring before spawning during the warmer months and subsequently undergoing mortality. These findings are also supported by the results of the current study. Thus, at all habitats apart from C, the most distinct seasonal differences in faunal composition occurred between summer or autumn and one or more of the remaining seasons. At habitats A, F, J and M, this was attributable to lower densities of most or all typifying species in one of those former seasons, which often included the ubiquitous species *C. aequisetis* and *C. capitata* and, in the case of A, also *A. semen*.

It is also possible that unfavourable changes in various non-enduring environmental variables, such as the increases in water temperature and salinity and/or the decreases in dissolved and interstitial oxygen concentrations that were recorded at all or most of the above habitats in summer/autumn, had a deleterious effect on the benthic fauna in those seasons. However, those habitats that typically underwent the most extreme changes in various non-enduring environmental parameters throughout the year, *i.e.* A, C and J, exhibited the smallest seasonal changes in benthic macroinvertebrate composition. A similar situation was also recorded for the fish assemblages at habitats A and C (see above). The particularly low impact of the declines in summer of *C. aequisetis, A. semen* and also *L. normalis* on the seasonal differences in benthic macroinvertebrate composition at habitat A, is most likely attributable to the fact that this habitat was typified only by these three species in every season and, unlike other habitats, not colonised by appreciable numbers of different species in other seasons.

The distinctiveness of the faunal assemblages in summer at habitats G and I was also due to the considerably lower densities of various species in that season, which commonly included *G. propodentata, S. biradiata, L. normalis, P. kempi, C. minor* and *A. semen.* Moreover, the assemblages during autumn at both of these basin habitats also differed notably from those recorded in winter and/or spring, which was due largely to lower numbers of almost all of the above species and *C. aequisetis* and *C. capitata* in that former season. Such declines in the density of these faunal species in summer and/or autumn and their prevalence in winter/spring are consistent with the previously-described life history patterns of such taxa and/or the possible deleterious influences of unfavourable changes in particular non-enduring environmental conditions. Furthermore, the relatively high numbers and consistent occurrences of various species from different feeding guilds at I in spring, such as sediment-ingesting deposit feeders (*e.g. L. normalis* and *C. capitata*) and deposit/suspension feeders (*e.g. S. biradiata* and *P. kempi*), which often occurred in greater densities than at G in this season, may also reflect the fact that the sedimentary chlorophyll concentrations at that former habitat in this season were the greatest recorded throughout the study. In contrast to the above trends, other taxa, which commonly included Oligochaete spp., were more prevalent at G and I in summer, which also contributed to the relatively large seasonal differences detected at these habitats. Such findings may reflect the presence of detrital accumulations from the macrophyte beds that occur at these habitats, which are known to be the most productive at this time of year (Hillman *et al.* 1995), and which provides an abundant food source for these benthic invertebrates. High densities of oligochaetes were also recorded in summer by Wildsmith *et al.* (2005) in nearshore coastal habitats along the lower west coast of Australia that contained accumulations of seagrass detritus.

5.2.3.3 Nematode assemblages

The pattern of the extent of seasonal differences in nematofaunal composition among the various habitats was similar, in several respects, to that detected for the benthic macroinvertebrate assemblages. Thus, the greatest, and considerable, seasonal differences in species composition were detected at each of the basin habitats (F, G, I and J) and particularly I, while the least was detected at the upper estuary habitats A and particularly C. However, unlike benthic macroinvertebrates but similar to the fish assemblages, the extent of the seasonal differences in the nematofauna at the channel habitat M was relatively low.

The most pronounced seasonal differences in nematode composition at habitats F, G and I, *i.e.* those between spring and each of the other seasons, were largely attributable to greater and/or more consistent numbers of epistrate/diatom feeders such as *N. decoratus, Dichromadora* sp., *Chromadorina* sp. and non-selective deposit feeders such as *C. arenae* and *Metadesmolaimus* sp.1. The increased abundance of these species in spring was probably also a main cause of the highly conspicuous increase in the mean density of nematodes at each of these main basin habitats in this season. Such findings are likely to be related, at least in part, to the greater abundances of the preferred food sources of these species. Thus, concentrations of sedimentary chlorophyll, and thus presumably microphytobenthos, a main food source of epistrate grazers, increased during spring at most main basin habitats. Furthermore, the abundance of marine diatoms, another main food source of epistrate/diatom feeders, are known to increase in the Swan Estuary during spring (Thompson 1998), and the warmer temperatures associated with this season are also likely to encourage the growth of benthic bacteria that are consumed by non-selective deposit feeders.

The considerable seasonal differences detected in nematofaunal composition at each of the basin habitats, and also those in other regions of the estuary, may also be due to interspecific differences in reproductive success and/or the timing of recruitment of juveniles. For example, Moens and Vincx (2000) found that reproduction and development of two co-occurring nematode species were differentially influenced by both temperature and salinity. While both of these water quality variables differed considerably throughout the year at several habitats in the Swan Estuary, it is interesting to note that the habitat at which they underwent the largest seasonal changes, *i.e.* C, exhibited by far the smallest seasonal differences in nematofaunal composition. In addition to the possible influence of reproductive and recruitment patterns, the differential tolerance of nematode species for seasonal changes in particular non-enduring environmental conditions may also contribute to variation in nematofaunal composition throughout the year. Thus, the most distinct seasonal differences in nematofaunal composition at habitats A, C and J occurred between summer and one or more of the other seasons, and thus at a time of the year when several water and sediment parameters at those habitats, such as salinity, water temperature, dissolved and interstitial oxygen, were at their extremes. Such environmental conditions may have thus contributed to the fact that the lowest overall densities of nematodes were found in this season at both C and J. In contrast, the overall nematode densities at A were greatest in this season, and samples were characterised by a prevalence of *P. aurata* and *Metadesmolaimus* sp.2, both of which are highly resilient species (Wu *et al.* 2000) However, it is interesting to note that the taxonomic diversity of the assemblage at this habitat was markedly lower in summer than all other seasons, particularly at the uppermost site representing A, which indicates that the assemblage was dominated by large numbers of individuals from small numbers of lower taxonomic groups.

5.2.3.4 Hyperbenthic faunal assemblages

The greatest seasonal differences in the composition of the hyperbenthic assemblages were detected at habitats A and C in the upper estuary and F in the upper reaches of the main basin. The overall extents of these differences, which were greater than those detected among habitats in either season, were often due to the prevalence of particular species in one season but not the other. In contrast, the relatively small seasonal differences detected at habitats J and M were largely attributable to differences in the abundance of species that typified the hyperbenthic assemblage in both seasons.

The far greater number of species that typified the hyperbenthic assemblages at habitat A in winter than summer was also reflected by the markedly greater mean number of species and, at the uppermost site representing A, also density of individuals in the former season. Such findings may indicate that environmental conditions at A are more suitable in winter than in summer, such as the far greater dissolved oxygen concentrations and, for the several freshwater species that were only present during winter at this habitat (*e.g.* Daphnia sp., Corixid sp. and

Austrolestes sp.), much lower salinities. They also reflect the fact that a greater number of benthic species, such as the polychaetes Sabellid sp., Capitellid sp., *Caraziella* sp., and syllid spp. 1 and 2, were recorded at A in winter, which is most likely due to the greater sediment disturbance from increased river flow in this season, and which was particularly pronounced at this uppermost habitat. The greater mean number of species in winter at habitat C and, to a lesser extent, density of individuals at site C1, probably also partly reflects the influence of seasonal changes in the above environmental characteristics. For example, the freshwater cladoceran Daphnia sp. typified the winter assemblages at C, but not those recorded in summer. However, several other species were prevalent at C in summer but not winter, such as the mysid Mysidellinid sp and amphipod *G. propodentata*. The notably higher numbers of the first of these species in summer may be related to the fact that maturation success of some mysid species is positively correlated with salinity, and thus such individuals are known to emigrate from estuaries during periods of low salinity (Drake *et al.*, 2002). It is thus relevant that the mean salinity at C in summer 2006 (*ca* 17‰) was far higher than the essentially freshwater conditions recorded at this habitat in winter 2005. Kanandjembo *et al.* (2001) also suggest that small crustaceans such as *G. propodentata* may not be particularly well adapted for tolerating low and/or variable salinity, which may explain their lower abundance at C in winter. This amphipod species was also far less abundant in the benthic macroinvertebrate assemblages at habitat C in winter and spring 2005, when the mean salinity ranged between 3.8 and 7.6‰, than in autumn 2005 when salinities at that habitat reached 19.6‰.

In contrast to the upper estuary habitats, both the mean number of species and density of individuals at the basin habitats F, G, I and J were far higher in summer 2006 than winter 2005. At the main basin habitats F, G and I, these far greater mean densities predominantly reflected the prevalence of cyclopoid sp.1, a swarming copepod that comprised 41-54% of all individuals at those habitats and which did not characterise their hyperbenthic assemblages in winter 2005, but were highly important in characterising and distinguishing these faunas in summer 2006. The assemblages of habitats E and M in the channel were also characterised by this copepod species in summer but not winter. Such findings may be related to the increased salinities, water temperatures and/or food sources (*i.e.* phytoplankton and other crustaceans [Turner *et al.* 1983]) that occur at each of the above habitats in summer, or to the reproductive and recruitment patterns of this species.

The particularly small seasonal differences in hyperbenthic composition at the channel habitat M may be largely expected given the comparatively narrow seasonal range in each of the water quality parameters recorded at this habitat. However, a similarly narrow range in these parameters also occurred at habitat E in the lowermost reaches of the channel, yet notably greater differences were detected in its hyperbenthic composition between summer and winter. In addition to a greater prevalence of cyclopoid sp.1 in summer, that of syllid sp.4 at this time of year was also largely responsible for the seasonal differences in faunal composition detected at this habitat. Such findings may be related to an increase in detritus from the seagrass beds in the lower Swan Estuary, which are known to be most productive at this time of year (Carruthers *et al.* 2007), and provides an important food source for this taxon (Beesley *et al.* 2000). In contrast to these channel habitats, habitat J exhibited pronounced differences in salinity, water temperature and, to a lesser extent, dissolved oxygen between winter 2005 and summer 2006, yet exhibited small seasonal differences in hyperbenthic composition. Such findings parallel those detected for the benthic macroinvertebrate assemblages at this habitat (see above).

6. Relationships between habitat types and faunal assemblages in the Peel-Harvey Estuary

6.1 Results

6.1.1 Water quality parameters

Replicate data for salinity, water temperature and dissolved oxygen, which were recorded at each site representing the 11 habitat types sampled in the Peel-Harvey Estuary during six seasons between winter 2005 and summer 2007, were each subjected to a preliminary three-way PERMANOVA to ascertain whether their spatial differences were most appropriately analysed at the habitat or site level. These tests demonstrated that salinity and water temperature did not differ significantly between sites assigned to the same habitat type, and that was no significant site x season interaction. The concentration of dissolved oxygen did, however, exhibit significant site and site x season effects. However, neither of those effects contributed as much to the overall variation in dissolved oxygen as the habitat type main effect. Given the above results, data for salinity and temperature were then each subjected to a habitat x season PERMANOVA and that for dissolved oxygen was subjected to a site x season PERMANOVA to investigate more thoroughly the extent of their spatio-temporal differences in the Peel-Harvey Estuary (Table 6.1.1.1).

Salinity and water temperature differed significantly among habitats, seasons and the interaction between these main effects ($p=0.001$). For both of these variables, a far greater component of the overall variation was explained by seasonal differences than any other term, with the least variation being attributable to the habitat main effect (Table 6.1.1.1). The lowest mean salinities were almost always recorded during winter 2005, followed by either spring 2005 or winter 2006 (Fig. 6.1.1.1a), while the greatest salinities at each habitat type were always recorded in summer 2007, followed either by summer or autumn 2006. The significant interaction was largely attributable to the fact that there were marked differences in the extent of seasonal variability among the various habitat types. For example, mean salinities ranged between *ca* 6 and 38‰ at the riverine habitat D and between *ca* 12 and 47‰ at habitat J at the bottom of the Harvey Estuary, whereas they only ranged between *ca* 29 and 39‰ at the two channel habitats L and M. Variability in the pattern of seasonal differences among habitats, *i.e.* both in terms of their rank order and relative differences, also contributed to the significant habitat x season interaction (Fig. 6.1.1.1a).

Table 6.1.1.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on data for salinity and water temperature and a site x season PERMANOVA on the dissolved oxygen concentration recorded throughout the Peel-Harvey Estuary during winter and spring 2005, summer, autumn and winter 2006 and summer 2007. df = degrees of freedom. Significant results are highlighted in bold.

	Salinity					**Temperature**				**Dissolved Oxygen**				
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p
Main Effects														
Habitat	10	**619.530**	**43.400**	**4.431**	**0.001**	**34.672**	**9.652**	**1.004**	**0.001**					
Season	5	**4676.900**	**327.630**	**9.373**	**0.001**	**1049.500**	**292.150**	**4.439**	**0.001**	5	**39.367**	**29.908**	**0.822**	**0.001**
Site										19	**19.445**	**14.772**	**1.032**	**0.001**
Two-way Interactions														
Habitat * Season	49	**157.390**	**11.026**	**5.212**	**0.001**	**15.045**	**4.188**	**1.474**	**0.001**					
Season * Site										93	**3.722**	**2.828**	**0.908**	**0.001**
Residual	280	14.275		3.778		3.592		1.895		227	1.316		1.147	

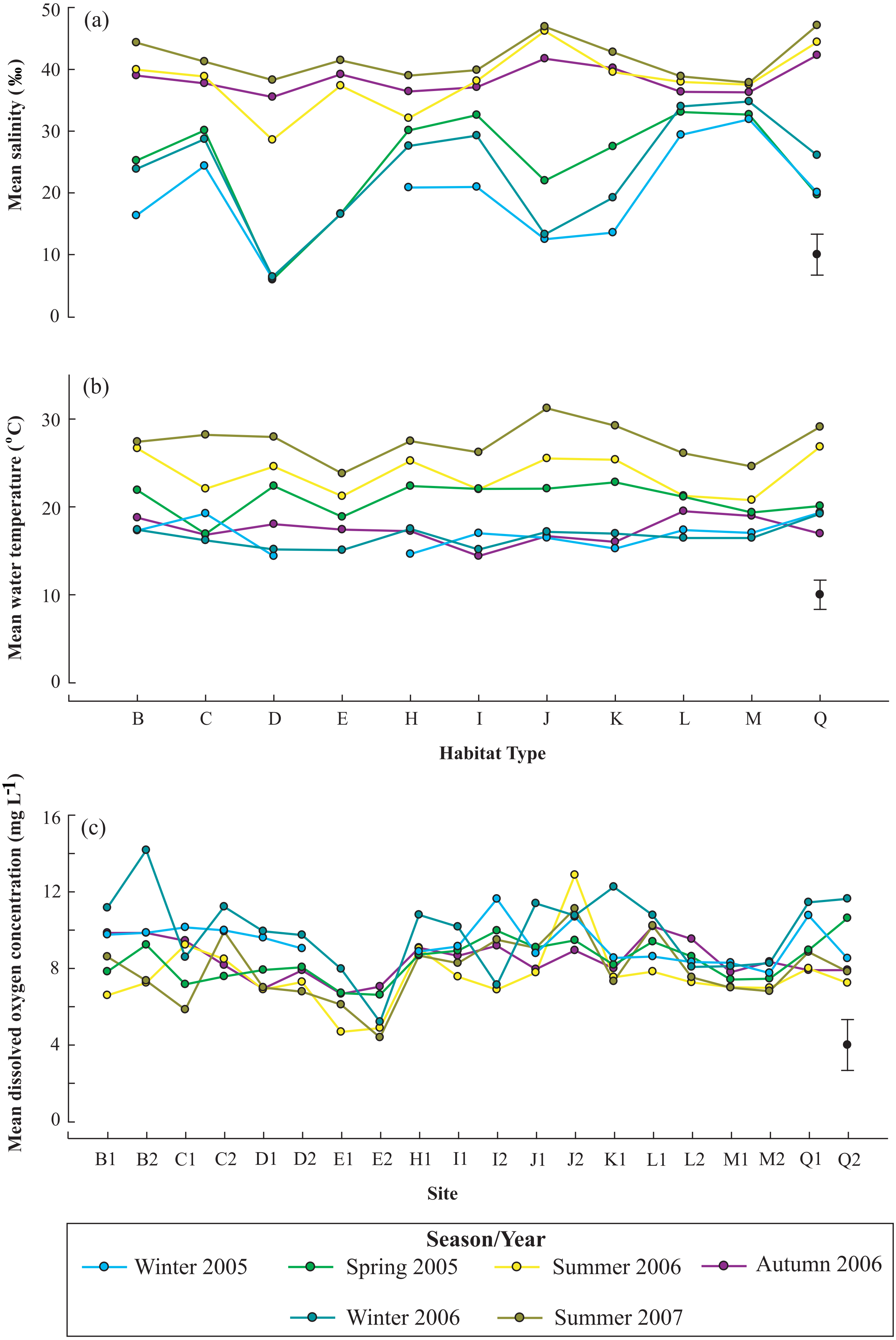


Figure 6.1.1.1: Mean (a) salinity, (b) water temperature and (c) dissolved oxygen concentration at each habitat type/site in the Peel-Harvey Estuary between winter 2005 and summer 2007. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

The lowest mean water temperatures were recorded in winter 2005, winter 2006 or autumn 2006 at each habitat, while, as with mean salinity, the greatest values were always recorded in summer 2007 (Fig. 6.1.1.1b). The second highest mean temperatures were found in summer 2006 at all habitats except I, where mean temperatures in this season were essentially equivalent to those in spring 2005. Again, the significant habitat x season interaction was caused by differences in the seasonal range of mean temperatures among habitats and/or variability in the pattern of seasonal differences among habitats. For example, values ranged between 16.5 and 31.2°C at the shallow habitat J at the bottom of the Harvey Estuary, while they only ranged between 16.5 and 26.1°C at the channel habitats L and M (Fig. 6.1.1.1b).

The mean concentration of dissolved oxygen differed significantly among sites, seasons and the interaction between these two main effects (Table 6.1.1.1). The effect of site differences was slightly greater than that attributable to the interaction, followed closely by the effect of seasonal differences. The lowest dissolved oxygen values were generally recorded at sites representing habitat E in the Serpentine River, which ranged between 4.4 and 8.0 mg L^{-1}, while high mean values were consistently recorded at the very shallow sites representing habitats J and Q at the bottom of the Harvey Estuary, *i.e.* 7.2- 12.9 mg L^{-1} (Fig. 6.1.1.1c). In almost all cases, the lowest dissolved oxygen values were recorded in either summer 2006 or 2007, while the greatest values were recorded in either winter 2005 or winter 2006. However, the relatively important site x season interaction was attributable to the fact that seasonal range, order and relative differences in mean dissolved oxygen varied considerably among the different sites. For example, whereas seasonal mean values ranged between 6.6 and 14.2 mg L^{-1} at sites representing the shallow habitat B in the wide Peel Inlet, they varied only between 7 and 8.3 mg L^{-1} at the channel habitat M. Moreover, whereas values recorded in spring were among the lowest at some habitats, they were second highest at others (Fig. 6.1.1.1c).

6.1.2 Fish assemblages

6.1.2.1 Species mean density and length characteristics at each habitat type

Seventy one fish species and 175 428 fish (*i.e.* after the number of individuals in each sample was adjusted to that in 100 m^2 and summed) were recorded at the 11 habitats sampled throughout the Peel-Harvey Estuary between winter 2005 and summer 2007 (Table 6.1.2.1). Channel habitats L and M were the most speciose (*i.e.* 51 and 46 species, respectively), followed by habitat D in the Murray and Serpentine Rivers (34 species). The least number of species were found at habitat Q (21 species) and J (22 species) at the bottom of the Harvey Estuary (Table 6.1.2.1). The greatest mean density by far was recorded at habitat D, *i.e.* 946 fish 100 m^{-2},

Table 6.1.2.1: Mean density (M), standard deviation (^{SD}), percentage contribution to the overall catch (%), rank by density (R) and length range and median length (L^{Med}) of each fish species recorded at each habitat type in the Peel-Harvey Estuary between winter 2005 and summer 2007. Abundant species (*i.e.* those that contribute >5% to the catch) are highlighted in grey. The life-history category of each species is also provided (^{A}=semi-anadromous, ^{E}=estuarine, ^{EM}=estuarine and marine, ^{F}=freshwater, ^{O}=marine estuarine-opportunist, ^{S}=marine straggler). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of fish in each sample had been adjusted to that in 100 m^2 and summed) are given for each habitat type.

	Habitat type B				Habitat type C				Habitat type D				Habitat type E			
Species name	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**
Atherinosoma elongata ^{E}	$277.08^{586.00}$	48.02	1	$14\text{-}70^{34}$	$123.13^{198.30}$	38.76	1	$12\text{-}114^{39}$	$91.23^{180.19}$	9.64	2	$12\text{-}83^{35}$	$213.36^{493.86}$	53.54	1	$16\text{-}103^{33}$
Hyperlophus vittatus ^{O}	$172.71^{631.64}$	29.93	2	$25\text{-}45^{36}$	$0.13^{0.50}$	0.04	19	$26\text{-}45^{31}$	$761.57^{3028.12}$	80.47	1	$20\text{-}46^{31}$	$75.25^{133.34}$	18.88	2	$18\text{-}47^{32}$
Craterocephalus pauciradiatus ^{E}	$63.64^{161.25}$	11.03	3	$15\text{-}61^{31}$	$36.12^{115.73}$	11.37	4	$20\text{-}64^{35}$	$6.33^{22.91}$	0.67	9	$19\text{-}49^{30}$	$11.84^{38.26}$	2.97	5	$18\text{-}37^{25}$
Favonigobius lateralis ^{EM}	$20.18^{36.84}$	3.50	4	$13\text{-}71^{28}$	$28.23^{35.04}$	8.89	5	$13\text{-}76^{30}$	$0.24^{0.59}$	0.03	17	$38\text{-}74^{60}$	$0.23^{0.43}$	0.06	18	$49\text{-}63^{56}$
Leptatherina presbyteroides ^{EM}	$14.73^{84.41}$	2.55	5	$17\text{-}59^{37}$	$37.90^{113.84}$	11.93	3	$18\text{-}62^{37}$	$13.43^{41.41}$	1.42	4	$18\text{-}58^{29}$	$0.79^{2.09}$	0.20	15	$20\text{-}55^{29}$
Papillogobius punctatus ^{E}	$5.07^{16.12}$	0.88	6	$13\text{-}60^{20}$	$3.45^{8.03}$	1.09	7	$15\text{-}70^{38}$	$1.96^{11.69}$	0.21	12	$12\text{-}64^{20}$	$1.43^{4.87}$	0.36	10	$20\text{-}61^{37}$
Aldrichetta forsteri ^{O}	$5.02^{17.59}$	0.87	7	$25\text{-}142^{50}$	$1.67^{5.22}$	0.53	10	$29\text{-}141^{50}$	$6.93^{24.46}$	0.73	7	$25\text{-}93^{49}$	$0.98^{2.95}$	0.24	13	$40\text{-}235^{71}$
Torquigener pleurogramma ^{O}	$4.47^{11.97}$	0.77	8	$96\text{-}173^{126}$	$2.51^{4.77}$	0.79	9	$43\text{-}179^{113}$	$6.47^{9.02}$	0.68	8	$85\text{-}181^{122}$	$2.09^{4.02}$	0.52	8	$63\text{-}180^{131}$
Leptatherina wallacei ^{E}	$3.80^{12.19}$	0.66	9	$14\text{-}60^{27}$	$58.87^{357.78}$	18.53	2	$20\text{-}43^{30}$	$9.61^{22.70}$	1.02	6	$19\text{-}71^{35}$	$38.20^{70.65}$	9.59	3	$14\text{-}55^{34}$
Pseudogobius olorum ^{E}	$2.29^{4.94}$	0.40	10	$12\text{-}149^{21}$	$0.45^{0.87}$	0.14	12	$17\text{-}59^{38}$	$13.26^{30.66}$	1.40	5	$11\text{-}57^{22}$	$31.15^{58.12}$	7.82	4	$15\text{-}61^{27}$
Atherinosoma mugiloides ^{E}	$1.63^{9.36}$	0.28	11	$29\text{-}51^{36}$	$19.52^{102.54}$	6.14	6	$23\text{-}71^{36}$	$0.81^{5.41}$	0.09	13	$19\text{-}49^{24}$	$0.09^{0.44}$	0.02	20	$29\text{-}40^{34}$
Atherinomorus ogilbyi ^{O}	$1.43^{9.49}$	0.25	12	$44\text{-}88^{70}$	$0.04^{0.25}$	0.01	23	68	$0.35^{0.93}$	0.04	16	$29\text{-}53^{43}$	$0.50^{2.07}$	0.13	16	$29\text{-}66^{47}$
Sillaginodes burrus ^{O}	$0.98^{6.37}$	0.17	13	$36\text{-}107^{50}$	$0.09^{0.44}$	0.03	21	$26\text{-}51^{28}$	$0.02^{0.13}$	<0.01	32	38				
Gerres subfasciatus ^{O}	$0.82^{2.78}$	0.14	14	$17\text{-}171^{21}$	$0.05^{0.37}$	0.02	22	$15\text{-}26^{16}$	$2.44^{6.89}$	0.26	11	$33\text{-}155^{102}$	$1.16^{2.90}$	0.29	11	$31\text{-}158^{101}$
Acanthopagrus butcheri ^{E}	$0.80^{2.62}$	0.14	15	$19\text{-}38^{29}$	$0.02^{0.12}$	0.01	27	28	$0.18^{0.67}$	0.02	19	$59\text{-}341^{87}$	$0.98^{2.75}$	0.24	14	$36\text{-}115^{86}$
Sillago schomburgkii ^{O}	$0.67^{3.77}$	0.12	16	$19\text{-}145^{93}$	$0.11^{0.75}$	0.03	20	$29\text{-}45^{35}$	$0.02^{0.13}$	<0.01	32	147	$0.02^{0.14}$	0.01	24	88
Spratelloides robustus ^{O}	$0.61^{4.03}$	0.11	17	$27\text{-}79^{48}$	$0.02^{0.12}$	0.01	28	26	$25.07^{171.89}$	2.65	3	$27\text{-}38^{32}$				
Mugil cephalus ^{O}	$0.57^{2.39}$	0.10	18	$25\text{-}110^{27}$	$0.23^{1.29}$	0.07	16	$26\text{-}40^{28}$	$0.39^{1.16}$	0.04	15	$23\text{-}256^{149}$	$1.50^{5.76}$	0.38	9	$44\text{-}160^{65}$
Ammotretis elongata ^{O}	$0.16^{0.92}$	0.03	19	$33\text{-}77^{59}$	$0.23^{0.73}$	0.07	17	$26\text{-}90^{56}$					$0.05^{0.28}$	0.01	22	$73\text{-}92^{83}$
Rhabdosargus sarba ^{O}	$0.10^{0.65}$	0.02	20	$130\text{-}173^{140}$					$0.07^{0.40}$	0.01	23	$72\text{-}94^{88}$	$0.02^{0.14}$	0.01	25	85
Sillaginodes punctata ^{O}	$0.08^{0.52}$	0.01	21	$40\text{-}48^{45}$	$0.36^{1.26}$	0.11	15	$25\text{-}53^{37}$								

Species name	Habitat type B				Habitat type C				Habitat type D				Habitat type E			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Pseudorhombus jenynsii ^{O}	$0.06^{0.22}$	0.01	22	$74\text{-}151^{78}$	$0.22^{0.45}$	0.07	18	$52\text{-}177^{91}$	$0.06^{0.21}$	0.01	25	$99\text{-}165^{102}$	$0.05^{0.20}$	0.01	22	$77\text{-}103^{90}$
Afurcagobius suppositus ^{E}	$0.04^{0.26}$	0.01	23	$24\text{-}26^{25}$	$0.45^{2.63}$	0.14	13	$19\text{-}31^{25}$	$0.68^{1.63}$	0.07	14	$16\text{-}78^{34}$	$8.69^{17.72}$	2.18	6	$17\text{-}78^{31}$
Galaxias occidentalis ^{F}	$0.04^{0.18}$	0.01	24	$32\text{-}33^{33}$					$0.13^{0.76}$	0.01	20	$30\text{-}38^{35}$				
Platycephalus speculator ^{EM}	$0.02^{0.13}$	<0.01	25	173												
Amoya bifrenatus ^{EM}	$0.02^{0.13}$	<0.01	25	46					$0.11^{0.53}$	0.01	21	$17\text{-}100^{22}$	$0.07^{0.42}$	0.02	21	$16\text{-}84^{70}$
Amniataba caudavittatus ^{E}	$0.02^{0.13}$	<0.01	27	15					$0.06^{0.28}$	0.01	25	$140\text{-}157^{152}$	$0.16^{0.63}$	0.04	19	$31\text{-}177^{132}$
Contusus brevicaudus ^{O}	$0.02^{0.13}$	<0.01	27	76	$0.04^{0.17}$	0.01	25	$35\text{-}43^{39}$								
Apogon rueppellii ^{EM}					$2.82^{9.65}$	0.89	8	$12\text{-}71^{28}$	$4.44^{18.66}$	0.47	10	$15\text{-}60^{34}$	$8.39^{49.20}$	2.11	7	$27\text{-}59^{41}$
Pelates octolineatus ^{O}					$0.61^{2.51}$	0.19	11	$17\text{-}36^{26}$	$0.22^{0.66}$	0.02	18	$31\text{-}206^{140}$	$0.48^{1.57}$	0.12	17	$41\text{-}138^{101}$
Gymnapistes marmoratus ^{O}					$0.38^{1.44}$	0.12	14	$33\text{-}82^{41}$	$0.11^{0.34}$	0.01	21	$17\text{-}83^{33}$				
Urocampus carinirostris ^{EM}					$0.04^{0.25}$	0.01	23	$57\text{-}68^{63}$	$0.02^{0.13}$	<0.01	30	50	$0.02^{0.14}$	0.01	25	60
Enoplosus armatus ^{S}					$0.04^{0.25}$	0.01	25	$24\text{-}32^{28}$								
Galaxias maculatus ^{F}									$0.07^{0.40}$	0.01	24	$30\text{-}42^{38}$				
Sillago vittata ^{O}									$0.04^{0.25}$	<0.01	27	$20\text{-}22^{21}$				
Nematalosa vlaminghi ^{A}									$0.02^{0.13}$	<0.01	28	194				
Cnidoglanis macrocephalus ^{EM}									$0.02^{0.13}$	<0.01	28	17				
Pomatomus saltatrix ^{O}									$0.02^{0.13}$	<0.01	30	130				
Engraulis australis ^{EM}									$0.02^{0.13}$	<0.01	32	65				
Gambusia affinis ^{F}													$1.02^{5.07}$	0.26	12	$20\text{-}43^{25}$
Number of species		**28**				**28**				**34**				**26**		
Total mean density		**577**				**318**				**946**				**399**		
Number of samples		**44**				**48**				**47**				**38**		
Total number of fish		**25 390**				**15 250**				**44 480**				**15 143**		

	Habitat type H				Habitat type I				Habitat type J				Habitat type K			
Species name	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**
Atherinosoma elongata ^{E}	$51.76^{114.39}$	32.40	1	18-78^{41}	$154.67^{247.70}$	63.01	1	12-72^{40}	$137.28^{306.57}$	65.86	1	14-71^{34}	$18.71^{19.98}$	19.52	1	20-69^{37}
Hyperlophus vittatus ^{O}	$11.88^{43.16}$	7.44	5	28-52^{32}	$0.02^{0.13}$	0.01	24	39	$0.31^{1.41}$	0.15	10	18-40^{29}	$16.70^{47.06}$	17.42	2	26-43^{33}
Craterocephalus pauciradiatus ^{E}	$3.75^{11.25}$	2.35	9	24-47^{34}	$2.52^{8.14}$	1.03	7	22-53^{30}	$12.66^{26.14}$	6.07	3	15-63^{33}	$4.02^{5.83}$	4.20	6	20-56^{32}
Favonigobius lateralis ^{EM}	$16.98^{18.40}$	10.63	3	14-70^{29}	$20.14^{20.96}$	8.21	3	14-118^{28}	$0.05^{0.28}$	0.03	16	14-24^{21}	$3.30^{6.29}$	3.45	7	15-58^{28}
Leptatherina presbyteroides ^{EM}	$22.86^{78.67}$	14.31	2	25-64^{44}	$9.06^{18.47}$	3.69	5	19-62^{32}	$26.87^{60.90}$	12.89	2	18-59^{32}	$11.17^{18.58}$	11.65	5	16-66^{46}
Papillogobius punctatus ^{E}	$3.07^{4.46}$	1.92	10	19-69^{53}	$9.63^{30.35}$	3.92	4	12-104^{24}	$0.04^{0.17}$	0.02	19	19-23^{21}	$0.14^{0.55}$	0.15	17	50-53^{52}
Aldrichetta forsteri ^{O}	$3.94^{9.77}$	2.46	8	27-193^{108}	$0.21^{0.74}$	0.09	15	32-132^{99}	$0.32^{1.46}$	0.16	9	25-62^{48}	$1.90^{3.16}$	1.99	10	26-183^{68}
Torquigener pleurogramma ^{O}	$14.58^{18.58}$	9.13	4	43-161^{113}	$1.83^{4.20}$	0.75	8	83-176^{120}	$5.57^{9.49}$	2.67	6	28-167^{136}	$15.59^{26.68}$	16.26	4	86-166^{121}
Leptatherina wallacei ^{E}	$0.82^{3.77}$	0.52	15	24-52^{31}	$40.14^{160.50}$	16.35	2	17-54^{30}	$6.18^{18.70}$	2.96	5	17-47^{25}	$2.08^{8.64}$	2.17	9	23-51^{28}
Pseudogobius olorum ^{E}	$1.24^{2.22}$	0.77	14	17-49^{33}	$0.17^{0.48}$	0.07	16	28-54^{41}	$0.11^{0.34}$	0.05	12	18-53^{35}	$0.04^{0.18}$	0.04	23	19
Atherinosoma mugiloides ^{E}	$9.00^{13.04}$	5.63	7	19-67^{35}	$0.23^{1.14}$	0.09	14	21-40^{28}	$12.66^{18.04}$	6.07	3	18-67^{32}	$15.84^{25.07}$	16.52	3	16-107^{39}
Atherinomorus ogilbyi ^{O}	$0.41^{1.64}$	0.26	18	29-58^{47}	$0.13^{0.81}$	0.05	17	46-52^{48}	$0.88^{3.13}$	0.42	8	33-75^{56}	$1.62^{5.86}$	1.69	11	33-54^{46}
Sillaginodes burrus ^{O}	$0.11^{0.39}$	0.07	22	27-31^{29}	$0.32^{1.89}$	0.13	13	32-59^{47}	$0.04^{0.17}$	0.02	18	22-76^{49}	$0.07^{0.35}$	0.07	19	33-48^{41}
Gerres subfasciatus ^{O}	$0.04^{0.18}$	0.02	25	16					$0.07^{0.39}$	0.03	15	40-54^{48}				
Acanthopagrus butcheri ^{E}	$0.07^{0.25}$	0.05	23	26-32^{29}	$0.67^{4.17}$	0.27	10	18-37^{32}	$0.02^{0.12}$	0.01	20	26	$0.04^{0.18}$	0.04	21	52
Sillago schomburgkii ^{O}													$0.29^{1.41}$	0.30	15	54-108^{95}
Spratelloides robustus ^{O}									$0.09^{0.62}$	0.04	14	28-30^{29}				
Mugil cephalus ^{O}	$0.04^{0.18}$	0.02	25	26	$0.08^{0.42}$	0.03	20	29-53^{50}	$0.05^{0.28}$	0.03	17	47-177^{54}	$0.61^{1.51}$	0.64	12	26-227^{47}
Ammotretis elongata ^{O}	$0.75^{1.73}$	0.47	16	15-67^{32}	$0.44^{1.19}$	0.18	12	11-78^{42}	$0.02^{0.12}$	0.01	22	23	$0.43^{0.92}$	0.45	13	22-68^{33}
Rhabdosargus sarba ^{O}					$0.06^{0.40}$	0.03	22	14-35^{30}								
Sillaginodes punctata ^{O}	$0.49^{1.30}$	0.31	17	28-124^{47}	$0.48^{2.70}$	0.20	11	30-49^{39}	$0.20^{0.95}$	0.09	11	30-48^{36}	$0.07^{0.24}$	0.07	19	33-55^{44}
Pseudorhombus jenynsii ^{O}	$0.22^{0.75}$	0.14	19	46-325^{86}	$0.11^{0.34}$	0.04	18	50-99^{83}	$0.09^{0.37}$	0.04	13	95-150^{112}	$0.25^{0.54}$	0.26	16	62-189^{101}
Afurcagobius suppositus ^{E}	$2.29^{10.07}$	1.43	12	20-87^{28}	$0.02^{0.13}$	0.01	25	23								
Galaxias occidentalis ^{F}																
Platycephalus speculator ^{EM}																
Amoya bifrenatus ^{EM}																
Amniataba caudavittatus ^{E}					$0.02^{0.13}$	0.01	23	49								
Contusus brevicaudus ^{O}																
Apogon rueppellii ^{EM}	$10.23^{23.07}$	6.41	6	10-57^{24}	$3.01^{8.85}$	1.22	6	13-79^{28}	$0.02^{0.12}$	0.01	20	58	$0.04^{0.18}$	0.04	23	57

Species name	Habitat type H				Habitat type I				Habitat type J				Habitat type K			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Pelates octolineatus ^{O}	$2.44^{5.41}$	1.53	11	$13\text{-}133^{20}$	$1.32^{5.35}$	0.54	9	$12\text{-}56^{30}$					$2.44^{11.25}$	2.55	8	$16\text{-}35^{28}$
Gymnapistes marmoratus ^{O}	$2.21^{8.40}$	1.38	13	$15\text{-}61^{36}$	$0.06^{0.30}$	0.03	21	$42\text{-}57^{54}$					$0.14^{0.70}$	0.15	18	$48\text{-}61^{56}$
Urocampus carinirostris ^{EM}					$0.11^{0.67}$	0.04	18	$49\text{-}59^{56}$								
Enoplosus armatus ^{S}																
Galaxias maculatus ^{F}																
Sillago vittata ^{O}																
Nematalosa vlaminghi ^{A}																
Cnidoglanis macrocephalus ^{EM}																
Pomatomus saltatrix ^{O}																
Engraulis australis ^{EM}													$0.04^{0.18}$	0.04	21	70
Gambusia affinis ^{F}																
Hyporhamphus regularis ^{E}	$0.22^{0.79}$	0.14	19	$67\text{-}103^{83}$									$0.32^{1.07}$	0.34	14	$55\text{-}118^{93}$
Haletta semifasciata ^{S}	$0.15^{0.72}$	0.09	21	$63\text{-}83^{74}$	$0.02^{0.13}$	0.01	25	67								
Stigmatophora argus ^{S}	$0.07^{0.25}$	0.05	23	$24\text{-}109^{67}$												
Dotalabrus alleni ^{S}	$0.04^{0.18}$	0.02	25	64												
Parapercis haackei ^{S}	$0.04^{0.18}$	0.02	25	35												
Lesueurina platycephala ^{S}	$0.04^{0.18}$	0.02	25	20												
Atherinid sp. (juvenile) $^{-}$									$4.94^{33.46}$	2.37	7	$18\text{-}31^{26}$				
Number of species		**29**				**26**				**22**				**24**		
Total mean density		**160**				**245**				**208**				**96**		
Number of samples		**23**				**41**				**48**				**24**		
Total number of fish		**3 674**				**10 065**				**10 006**				**2 301**		

Species name	Habitat type L				Habitat type M				Habitat type Q			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$54.04^{121.02}$	10.69	2	$22\text{-}63^{39}$	$0.07^{0.40}$	0.02	25	$38\text{-}39^{39}$	$64.34^{148.96}$	38.48	1	$18\text{-}68^{34}$
Hyperlophus vittatus ^{O}	$322.36^{863.58}$	63.76	1	$20\text{-}59^{34}$	$273.59^{678.87}$	73.50	1	$20\text{-}67^{35}$	$0.49^{1.92}$	0.29	10	$25\text{-}43^{35}$
Craterocephalus pauciradiatus ^{E}	$15.27^{45.21}$	3.02	6	$23\text{-}51^{37}$	$0.51^{2.39}$	0.14	14	$38\text{-}50^{44}$	$7.68^{25.43}$	4.59	5	$22\text{-}61^{31}$
Favonigobius lateralis ^{EM}	$23.81^{27.68}$	4.71	3	$15\text{-}82^{31}$	$6.22^{10.58}$	1.67	7	$16\text{-}69^{36}$	$2.88^{10.71}$	1.72	7	$18\text{-}55^{34}$
Leptatherina presbyteroides ^{EM}	$17.67^{32.57}$	3.50	5	$16\text{-}61^{35}$	$34.96^{114.99}$	9.39	2	$17\text{-}61^{40}$	$50.71^{88.76}$	30.32	2	$19\text{-}63^{33}$
Papillogobius punctatus ^{E}	$1.98^{5.90}$	0.39	13	$13\text{-}62^{39}$	$0.13^{0.47}$	0.03	23	$24\text{-}68^{59}$	$0.04^{0.18}$	0.02	14	$14\text{-}19^{17}$
Aldrichetta forsteri ^{O}	$3.72^{9.52}$	0.74	11	$24\text{-}204^{90}$	$9.24^{25.29}$	2.48	4	$23\text{-}102^{57}$	$0.39^{1.09}$	0.23	11	$31\text{-}78^{44}$
Torquigener pleurogramma ^{O}	$23.55^{46.20}$	4.66	4	$45\text{-}177^{113}$	$8.58^{24.96}$	2.31	5	$81\text{-}177^{127}$	$3.57^{7.52}$	2.13	6	$108\text{-}165^{136}$
Leptatherina wallacei ^{E}	$2.50^{12.02}$	0.49	12	$17\text{-}50^{35}$					$23.86^{67.22}$	14.27	3	$18\text{-}60^{30}$
Pseudogobius olorum ^{E}	$15.23^{51.04}$	3.01	7	$15\text{-}56^{30}$	$0.29^{1.55}$	0.08	19	$15\text{-}58^{29}$	$0.02^{0.13}$	0.01	19	20
Atherinosoma mugiloides ^{E}	$0.02^{0.12}$	<0.01	42	32					$11.32^{39.93}$	6.77	4	$18\text{-}64^{33}$
Atherinomorus ogilbyi ^{O}	$4.35^{17.21}$	0.86	10	$17\text{-}106^{50}$	$16.47^{89.15}$	4.42	3	$33\text{-}139^{60}$	$0.61^{2.90}$	0.36	9	$30\text{-}53^{44}$
Sillaginodes burrus ^{O}	$0.14^{0.54}$	0.03	25	$120\text{-}172^{144}$	$1.16^{4.40}$	0.31	11	$36\text{-}173^{66}$				
Gerres subfasciatus ^{O}	$0.02^{0.12}$	<0.01	42	143	$0.18^{0.57}$	0.05	21	$55\text{-}156^{136}$	$0.04^{0.18}$	0.02	13	$16\text{-}21^{19}$
Acanthopagrus butcheri ^{E}	$0.29^{1.51}$	0.06	21	$19\text{-}277^{25}$								
Sillago schomburgkii ^{O}	$0.20^{0.62}$	0.04	24	$184\text{-}328^{233}$	$0.48^{1.40}$	0.13	15	$179\text{-}285^{200}$	$1.02^{4.60}$	0.61	8	$22\text{-}135^{105}$
Spratelloides robustus ^{O}	$0.02^{0.12}$	<0.01	46	35	$7.23^{45.55}$	1.94	6	$34\text{-}78^{55}$				
Mugil cephalus ^{O}	$0.48^{2.28}$	0.10	18	$19\text{-}182^{28}$	$0.44^{2.77}$	0.12	16	$25\text{-}69^{45}$	$0.02^{0.13}$	0.01	19	28
Ammotretis elongata ^{O}	$0.38^{0.96}$	0.07	19	$22\text{-}78^{60}$	$1.30^{1.58}$	0.35	10	$19\text{-}123^{65}$	$0.02^{0.13}$	0.01	16	61
Rhabdosargus sarba ^{O}	$0.07^{0.30}$	0.01	36	$17\text{-}91^{70}$					$0.04^{0.26}$	0.02	15	$22\text{-}23^{23}$
Sillaginodes punctata ^{O}	$0.02^{0.12}$	<0.01	46	30	$0.06^{0.38}$	0.01	26	$45\text{-}54^{46}$	$0.12^{0.66}$	0.07	12	$22\text{-}35^{26}$
Pseudorhombus jenynsii ^{O}	$0.14^{0.32}$	0.03	26	$52\text{-}302^{136}$	$0.18^{0.36}$	0.05	22	$59\text{-}238^{105}$	$0.02^{0.13}$	0.01	19	119
Afurcagobius suppositus ^{E}	$0.25^{1.62}$	0.05	23	$19\text{-}35^{24}$								
Galaxias occidentalis ^{F}												
Platycephalus speculator ^{EM}	$0.04^{0.17}$	0.01	40	$133\text{-}136^{135}$	$0.04^{0.18}$	0.01	32	$172\text{-}201^{187}$				
Amoya bifrenatus ^{EM}	$0.81^{1.45}$	0.16	17	$23\text{-}98^{58}$	$0.09^{0.37}$	0.02	24	$43\text{-}77^{52}$				
Amniataba caudavittatus ^{E}	$0.11^{0.63}$	0.02	30	$19\text{-}25^{20}$								
Contusus brevicaudus ^{O}	$0.13^{0.53}$	0.02	27	$38\text{-}72^{50}$	$0.06^{0.21}$	0.01	28	$33\text{-}81^{57}$				
Apogon rueppellii ^{EM}	$7.69^{16.33}$	1.52	8	$14\text{-}80^{46}$	$3.91^{13.14}$	1.05	8	$16\text{-}54^{38}$				

Species name	Habitat type L				Habitat type M				Habitat type Q			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Pelates octolineatus ^{O}	$4.71^{26.20}$	0.93	9	$16\text{-}185^{34}$	$0.44^{2.32}$	0.12	16	$52\text{-}191^{157}$	$0.02^{0.13}$	0.01	17	12
Gymnapistes marmoratus ^{O}	$0.97^{2.10}$	0.19	16	$21\text{-}87^{40}$	$0.64^{1.98}$	0.17	13	$32\text{-}90^{43}$				
Urocampus carinirostris ^{EM}	$0.34^{1.05}$	0.07	20	$19\text{-}65^{52}$	$0.02^{0.13}$	<0.01	36	61				
Enoplosus armatus ^{S}	$0.29^{1.00}$	0.06	22	$16\text{-}39^{23}$	$0.06^{0.28}$	0.01	28	$47\text{-}73^{53}$				
Galaxias maculatus ^{F}												
Sillago vittata ^{O}					$0.06^{0.28}$	0.01	27	$72\text{-}145^{139}$	$0.02^{0.13}$	0.01	17	20
Nematalosa vlaminghi ^{A}												
Cnidoglanis macrocephalus ^{EM}	$0.02^{0.12}$	<0.01	42	49								
Pomatomus saltatrix ^{O}												
Engraulis australis ^{EM}												
Gambusia affinis ^{F}												
Hyporhamphus regularis ^{E}	$0.11^{0.63}$	0.02	30	$94\text{-}124^{119}$								
Haletta semifasciata ^{S}	$1.45^{6.61}$	0.29	15	$33\text{-}127^{77}$	$0.44^{1.92}$	0.12	16	$50\text{-}128^{107}$				
Stigmatophora argus ^{S}	$1.54^{2.86}$	0.31	14	$76\text{-}197^{120}$	$3.71^{13.32}$	1.00	9	$64\text{-}230^{122}$				
Dotalabrus alleni ^{S}												
Parapercis haackei ^{S}												
Lesueurina platycephala ^{S}					$0.06^{0.21}$	0.01	31	$38\text{-}43^{42}$				
Atherinid sp. (juvenile) $^{-}$												
Microcanthus strigatus ^{S}	$0.13^{0.50}$	0.02	27	$7\text{-}37^{24}$								
Acanthaluteres spilomelanurus ^{S}	$0.11^{0.42}$	0.02	29	$21\text{-}46^{32}$	$0.02^{0.13}$	<0.01	36	25				
Scobinichthys granulatus ^{S}	$0.11^{0.29}$	0.02	30	$17\text{-}51^{26}$	$0.02^{0.13}$	<0.01	44	39				
Meuschenia freycineti ^{S}	$0.11^{0.55}$	0.02	30	$24\text{-}35^{33}$								
Syngnathid sp (juvenile) $^{-}$	$0.07^{0.35}$	0.01	34	$52\text{-}59^{58}$								
Monocanthid sp. (juvenile) $^{-}$	$0.07^{0.24}$	0.01	34	$11\text{-}24^{15}$								
Pseudocaranx wrightii ^{S}	$0.07^{0.50}$	0.01	36	$132\text{-}140^{134}$								
Labrid sp. (juvenile) $^{-}$	$0.05^{0.28}$	0.01	38	$17\text{-}29^{24}$								
Arripis truttacea ^{O}	$0.04^{0.17}$	0.01	39	$49\text{-}62^{56}$	$0.04^{0.25}$	0.01	32	$185\text{-}194^{190}$				
Petroscirtes breviceps ^{S}	$0.04^{0.17}$	0.01	40	44								
Omobranchus germaini ^{S}	$0.02^{0.12}$	<0.01	42	28	$0.02^{0.13}$	<0.01	38	27				

Species name	Habitat type L				Habitat type M				Habitat type Q			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Siphamia cephalotes ^{S}	$0.02^{0.12}$	<0.01	46	23	$0.04^{0.25}$	0.01	32	$26\text{-}30^{28}$				
Pseudocaranx dentex ^{S}	$0.02^{0.12}$	<0.01	46	45	$0.22^{1.11}$	0.06	20	$37\text{-}50^{43}$				
Neoodax balteatus ^{S}	$0.02^{0.12}$	<0.01	46	77								
Cristiceps australis ^{S}	$0.02^{0.12}$	<0.01	46	23	$0.06^{0.38}$	0.01	28	$77\text{-}107^{86}$				
Arripis georgiana ^{O}					$1.06^{4.94}$	0.29	12	$42\text{-}150^{128}$				
Brachaluteres jacksonianus ^{S}					$0.04^{0.18}$	0.01	35	$30\text{-}32^{31}$				
Filicampus tigris ^{S}					$0.02^{0.13}$	<0.01	38	176				
Upeneus tragula ^{S}					$0.02^{0.13}$	<0.01	38	71				
Monacanthus chinensis ^{S}					$0.02^{0.13}$	<0.01	38	74				
Acanthaluteres vittiger ^{S}					$0.02^{0.13}$	<0.01	38	45				
Scorpis georgianus ^{S}					$0.02^{0.13}$	<0.01	38	28				
Gonorynchus greyi ^{O}					$0.02^{0.13}$	<0.01	44	112				
Halichoeres brownfieldi ^{S}					$0.02^{0.13}$	<0.01	44	40				
Number of species		**51**				**46**				**21**		
Total mean density		**506**				**372**				**167**		
Number of samples		**48**				**47**				**44**		
Total number of fish		**24 267**				**17 495**				**7 358**		

followed by that at habitat B on the northern shores of Peel Inlet and habitat L, *i.e.* 577 and 506 fish 100 m^{-2}, respectively. The lowest mean density of fish was recorded at habitat K in the middle reaches of the Harvey Estuary, followed by that at habitats H and Q in its northern and southern reaches, respectively, *i.e.* 96-167 fish 100 m^{-2} (Table 6.1.2.1).

At least 70% of the catch at the riverine habitats D and E comprised the estuarine species *Atherinosoma elongata* and the juveniles of the marine estuarine-opportunist *Hyperlophus vittatus*. This was particularly prevalent at habitat D, where more than 80% of the catch consisted of the latter species. However, the abundance of this schooling clupeid at this habitat was highly variable, as reflected by the large standard deviation associated with its mean density. For example, more than 23 000 of the 41 521 *H. vittatus* recorded at habitat D were collected in a single sample. Habitat D also contained several species that were not recorded at any other habitat type, namely the freshwater species *Galaxias maculatus* and semi-anadromous *Nematalosa vlaminghi* and the marine estuarine-opportunist *Pomatomus saltatrix*. The mean density of *A. elongata* at habitat E was more than twice that recorded at D, and the estuarine species *Leptatherina wallacei* and *Pseudogobius olorum* were also among the most abundant species found at this habitat, contributing between 7 and 10% of the total catch. Habitat E was also the only one at which the freshwater species *Gambusia affinis* was recorded (Table 6.1.2.1).

Atherinosoma elongata was the most abundant species recorded at each of the habitats sampled in the two large basins of the Peel-Harvey Estuary, *i.e.* habitats B, C, H, I, J, K and Q, where it contributed between 19.52% (habitat K) and 65.86% (habitat J) of the total catch. Habitat B, located largely between the entrance channel and mouths of the Serpentine and Murray rivers in the Peel Inlet, was also dominated by juvenile *H. vittatus* and the estuarine atherinid *Craterocephalus pauciradiatus*. In contrast, habitat C, located on the north-eastern shore of the Harvey Estuary and containing extensive seagrass beds, was also dominated by the schooling atherinids *L. wallacei, Leptatherina presbyteroides, C. pauciradiatus* and *Atherinosoma mugiloides* and the estuarine and marine goby *Favonigobius lateralis* (Table 6.1.2.1). The most abundant species at habitats H and K, which were situated on the western shore of the middle to northern reaches of the Harvey Estuary and also contained substantial areas of submerged vegetation, were similar to those found at C, but also included *Torguigener pleurogramma*, *H. vittatus* and, in the case of H, also *Apogon rueppellii*, and did not include *L. wallacei* or *C. paucidradiatus*. Habitat type I, which was located on the north-western shore of the Peel Inlet between the two entrance channels and contained moderate quantities of submerged vegetation, was also dominated by *L. wallacei* and *F. lateralis* (Table 6.1.2.1). The fish faunas recorded at the vegetated basin habitats C, H, I and K also contained several other species that are typically associated with seagrass and/or macroalgae and that were not recorded at the less vegetated or bare substrate basin habitats B, J and Q, *i.e. Gymnapistes marmoratus, Urocampus carinirostris, Enoplosus armatus, Hyporhamphus regularis, Haletta semifasciata, Stigamatophora argus, Dotolabrus alleni* and/or *Parapercis haackei* (Table 6.1.2.1). Habitats J and Q, located at the southern end of the Harvey Estuary and was closest to the small Harvey River, were both characterised by relatively high densities of *L. presbyteroides* and *A. mugiloides*. *Craterocephalus pauciradiatus* was also relatively abundant at J, while the same was true of *L. wallacei* at Q (Table 6.1.2.1).

The two channel habitats L and M, which each contained some submerged vegetation and relatively large quantities of rock, were both dominated by *H. vittatus*, which contributed 64-74% of the total catch at these habitats. Again, the high standard deviations associated with the mean density of this species in both habitats reflect the considerable variation in its frequency of occurrence and catch size. The only other species that was relatively abundant at habitats L and M were *A. elongata* and *L. presbyteroides*, respectively. Despite the fish faunas at these habitats each being numerically dominated by only two species, a much greater suite of 24 species, that were largely the juveniles of marine stragglers and/or weed-associated species, were recorded only at these two habitats (Table 6.1.2.1).

6.1.2.2 Spatial and temporal differences in mean species richness, density and taxonomic distinctness

Three-way PERMANOVA tests were initially used to ascertain whether habitats or their representative sites were the most appropriate for investigating spatial differences in the number of species, density and taxonomic distinctness of fish assemblages recorded seasonally throughout the Peel-Harvey Estuary between winter 2005 and summer 2007. As these tests demonstrated that each of these dependent variables were best analysed at the finest level of spatial resolution, they were subsequently subjected to a site x season PERMANOVA to better elucidate their spatial and temporal differences. These analyses detected significant differences among sites, seasons and the interaction between these main effects in all cases ($p=0.001$; Table 6.1.2.2).

With respect to mean number of species, the greatest proportion of the overall variation was explained by the interaction term, followed closely by differences among sites and then seasons. The plot shown in Fig. 6.1.2.1a clearly demonstrates that the main causes of this interaction term are the differences in the seasonal pattern, *i.e.* range, order and relative differences, in mean number of species among sites. Thus, a low and relatively narrow range in

Table 6.1.2.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for site x season PERMANOVAs on the number of species, density and quantitative taxonomic distinctness of fish assemblages recorded throughout the Peel-Harvey Estuary during winter and spring 2005, summer, autumn and winter 2006 and summer 2007. df = degrees of freedom. Significant results are highlighted in bold.

		Number of Species				**Density**				**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Site	19	**2.511**	**12.334**	**0.322**	**0.001**	**5.018**	**3.537**	**0.402**	**0.001**	**1620.100**	**11.715**	**8.147**	**0.001**
Season	5	**5.946**	**29.208**	**0.279**	**0.001**	**37.571**	**26.481**	**0.701**	**0.001**	**1018.000**	**7.361**	**3.456**	**0.001**
Two-way Interaction													
Site * Season	91	**0.617**	**3.031**	**0.326**	**0.001**	**4.070**	**2.868**	**0.826**	**0.001**	**261.380**	**1.890**	**5.626**	**0.001**
Residual	336	0.204		0.451		1.419		1.191		138.290		11.760	

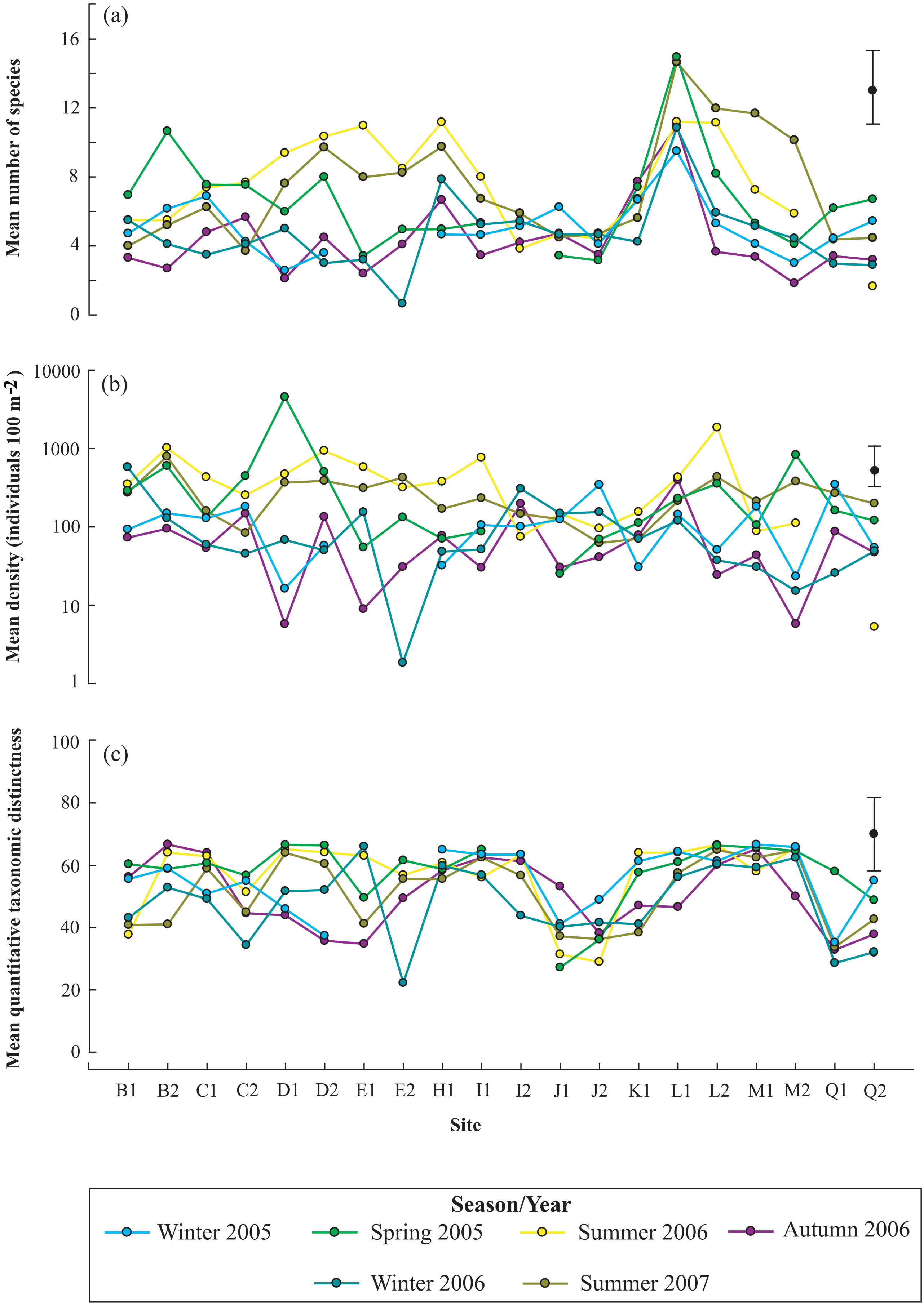


Figure 6.1.2.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the fish assemblages recorded at each site in the Peel-Harvey Estuary between winter 2005 and summer 2007. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

mean number of species was generally recorded at sites representing habitats J and Q (1.7 – 6.7 species) and, to a lesser extent, habitats C, I and K, *i.e.* 3.5 - 8 species. In contrast, the mean number species recorded at the channel site L2 was consistently high, ranging between 9.5 and 14.9. Sites representing habitats D, E and M and also site L2 exhibited among the greatest seasonal range in mean number of species, *e.g.* between 3.4 (autumn 2006) and 11.7 (summer 2007) at site M1. With the exception of a few sites, the lowest mean number of species was typically recorded in either autumn or winter 2006, while the greatest was recorded in either summer 2006 or 2007 and, in cases such as habitats B, Q and largely C, spring 2005 (Fig. 6.1.2.1a).

The site x season interaction, followed closely by season, explained the greatest proportion of the overall variation in mean density of fish (Table 6.1.2.2). Again, the importance of the interaction term was attributable to considerable differences in the seasonal pattern and variability of mean density among sites. For instance, whereas this dependent variable ranged between *ca* 6 (autumn 2006) and 4565 (spring 2005) fish 100 m^{-2} at D1, it ranged only between *ca* 74 (summer 2006) and 307 (winter 2006) fish 100 m^{-2} at I2 (Fig. 6.1.2.1b). Like the mean number of species, the lowest mean density of fish was typically recorded during autumn or winter 2006 at each site, while the greatest was often found in the summer of 2006 or 2007. While the mean densities of fish were not obviously consistently higher or lower at any particular site(s), those recorded at representatives of habitats D and E and also sites L2 and M2 exhibited the greatest range among seasons, while those at I2, J1, J2, K1 and L1 were relatively similar throughout the sampling period (Fig. 6.1.2.1b).

A substantially greater proportion of the overall variation in mean taxonomic distinctness was explained by differences among sites than either season or the interaction term (Table 6.1.2.2). Conspicuously lower values of this diversity index were typically recorded at sites from habitats J and Q, while relatively high values were consistently recorded at sites H1, I1, L2 and M1 and, to slightly lesser extents, at the other sites representing those latter three habitats (Fig. 6.1.2.1c). The considerable differences among sites in both the seasonal range and rank order in the magnitude of this dependent variable were the main cause of the significant interaction term. Consequently, general seasonal trends among sites were less clear, but higher mean values of taxonomic distinctness were often recorded in spring 2005 (Fig. 6.1.2.1c).

6.1.2.3 Composition of fish assemblages among habitats

A preliminary three-way PERMANOVA test demonstrated that the composition of the fish assemblages recorded throughout the Peel-Harvey Estuary between winter 2005 and summer

2007 differed significantly among habitats, sites within habitats and seasons, and that all appropriate interaction terms between those factors were significant (p=0.001). However, the components of variation associated with each of these terms demonstrated that the relative importance of differences among habitats was 1.4-1.8 times that attributable to either the nested site factor or the site x season interaction. Moreover, one-way ANOSIM tests for site, carried out separately for data collected in each season in view of the above significant season main effect and interactions, detected few significant differences in fish faunal composition between sites assigned to the same habitat in all seasons except winter 2006 and, to a lesser extent, autumn 2006. During these seasons, significant differences were detected between the fish faunal compositions at sites assigned to the same habitat in six and four cases, respectively, out of nine, and, in all of those cases, the associated R-statistic exceeded 0.400. However, given the relatively minor intra-habitat differences in ichthyofaunal composition overall, particularly when compared to the extent of inter-habitat differences, the following analyses to more thoroughly examine spatial differences in the fish assemblages throughout the Peel-Harvey Estuary were carried out at the habitat rather than site level. They were also performed separately for the data collected in each season, given the significant seasonal main effects and interactions detected by the above PERMANOVA test.

One-way ANOSIM tests for habitat type, carried out individually for the data recorded in each season, demonstrated that ichthyofaunal composition differed significantly among habitats in each case (p=0.1%), and that the most pronounced overall differences occurred during summer 2006 and summer 2007 (Global R=0.715 and 0.636, respectively), while the least occurred in winter 2005 and autumn 2006 (Global R=0.341 and 0.386, respectively; Table 6.1.2.3).

During both summers, significant differences in fish assemblage composition were detected between of all pairs of habitats, except for C *vs* H and I, and also H *vs* K in summer 2006 and K *vs* Q in summer 2007. In both of these seasons, but particularly summer 2006, the extent of the ichthyofaunal differences between most habitats was considerable, as reflected by the fact that the pairwise R-statistic often exceeded 0.700 (Table 6.1.2.3c and f). The fish faunas at the channel habitats L and M were among the most distinct from those at other habitats, as were those at the riverine habitats D and E, which was particularly applicable to the latter habitat in summer 2006 (*i.e.* pairwise R often >0.900) and, to a lesser extent, D in summer 2007 (Table 6.1.2.3c and f). The MDS ordination plots of the fish faunal data recorded in each summer showed that samples from the channel and riverine habitats each formed relatively distinct groups, with that representing L tending to lie alongside that from M, while, particularly

Table 6.1.2.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal composition among habitat types in the Peel-Harvey Estuary during (a) winter 2005, (b) spring 2005, (c) summer 2006, (d) autumn 2006, (e) winter 2006 and (f) summer 2007. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2005; p=0.1%, Global R=0.341

	B	**C**	**D**	**H**	**I**	**J**	**K**	**L**	**M**
C	0.139								
D	0.422	0.607							
H	0.320	-0.033	0.632						
I	0.237	-0.098	0.673	-0.125					
J	0.463	0.308	0.468	0.588	0.475				
K	0.386	0.162	0.437	0.333	0.086	0.182			
L	0.430	0.387	0.590	0.518	0.387	0.725	0.686		
M	0.410	0.184	0.430	-0.214	0.119	0.537	-0.048	0.341	
Q	0.454	0.198	0.501	0.632	0.330	-0.017	0.296	0.744	0.435

(b) Spring 2005; p=0.1%, Global R=0.451

	B	**C**	**D**	**E**	**H**	**I**	**J**	**K**	**L**	**M**
C	0.213									
D	0.843	0.868								
E	0.672	0.693	0.129							
H	0.315	0.242	0.876	0.522						
I	0.110	0.019	0.965	0.597	-0.222					
J	0.528	0.387	0.528	0.277	0.290	0.301				
K	0.498	0.265	0.800	0.430	0.426	0.315	0.090			
L	0.277	0.252	0.771	0.601	0.406	0.237	0.617	0.278		
M	0.716	0.563	0.556	0.547	0.449	0.277	0.552	0.191	0.346	
Q	0.416	0.150	0.880	0.677	0.371	0.159	0.198	-0.162	0.502	0.550

(c) Summer 2006; p=0.1%, Global R=0.715

	B	**C**	**D**	**E**	**H**	**I**	**J**	**K**	**L**	**M**
C	0.489									
D	0.301	0.575								
E	0.780	0.925	0.362							
H	0.357	0.189	0.485	0.958						
I	0.656	0.173	0.755	0.944	0.639					
J	0.572	0.651	0.882	0.989	0.875	0.917				
K	0.456	0.682	0.656	0.996	0.417	0.913	0.840			
L	0.757	0.739	0.682	0.953	0.579	0.829	0.997	0.800		
M	0.642	0.768	0.729	0.920	0.596	0.742	0.978	0.449	0.651	
Q	0.849	0.903	0.903	0.980	0.917	0.897	0.785	0.719	0.978	0.858

(d) Autumn 2006; p=0.1%, Global R=0.386

	B	C	D	E	H	I	J	K	L	M
C	0.140									
D	0.093	0.586								
E	0.196	0.633	0.176							
H	-0.070	0.105	0.482	0.495						
I	0.065	0.069	0.533	0.496	0.467					
J	0.299	0.708	0.195	0.332	0.612	0.765				
K	0.162	0.542	0.305	0.534	0.448	0.899	0.311			
L	0.110	0.158	0.304	0.416	-0.015	0.157	0.672	0.268		
M	0.179	0.465	0.272	0.297	0.267	0.394	0.515	0.327	0.205	
Q	0.606	0.877	0.389	0.486	0.958	0.897	0.208	0.789	0.782	0.550

(e) Winter 2006; p=0.1%, Global R=0.487

	B	C	D	E	H	I	J	K	L	M
C	0.114									
D	0.454	0.220								
E	0.388	0.312	0.275							
H	0.761	0.263	0.274	0.812						
I	0.410	0.146	0.413	0.771	0.546					
J	0.397	0.328	0.275	0.622	0.667	0.497				
K	0.697	0.145	0.268	0.624	0.208	0.869	0.243			
L	0.419	0.178	0.438	0.700	0.384	0.365	0.787	0.763		
M	0.785	0.476	0.693	0.908	0.353	0.527	0.931	0.833	0.397	
Q	0.681	0.365	0.172	0.526	0.619	0.775	0.411	0.340	0.887	0.900

(f) Summer 2007; p=0.1%, Global R=0.636

	B	C	D	E	H	I	J	K	L	M
C	0.287									
D	0.526	0.829								
E	0.269	0.643	0.449							
H	0.825	0.336	0.699	0.535						
I	0.445	0.258	0.819	0.571	0.524					
J	0.595	0.686	0.841	0.695	0.976	0.936				
K	0.556	0.656	0.689	0.522	0.729	0.877	0.553			
L	0.908	0.747	0.717	0.840	0.360	0.842	0.982	0.875		
M	0.907	0.903	0.759	0.917	0.478	0.844	0.914	0.722	0.238	
Q	0.386	0.625	0.526	0.585	0.596	0.748	0.235	0.149	0.814	0.735

in summer 2006, the group of samples from E tended to lie near that representing D (Fig. 6.1.2.2c and f). However, in both summers, and especially that of 2006, samples from the two channel habitats were not located on the opposite side of the MDS plot from those representing the two riverine habitats. This was also reflected by the fact that, while the pairwise R-statistics between riverine *vs* channel habitats were generally high (*i.e.* 0.682-0.953 and 0.717-0.917 in summer 2006 and 2007, respectively), those for several comparisons between a riverine or channel habitat *vs* a basin habitat were as high or higher (Table 6.1.2.3c and f). SIMPER demonstrated that, in both summers, the fish assemblages at the channel habitats L and M were always or commonly characterised by *T. pleurogramma, F. lateralis* and *L. presbyteroides*, and also by *Ammotretis elongata* in the case of the latter (Table 6.1.2.4c and f). Each of the above species that characterised L were often found in greater abundances at that habitat than any other in both summers, while the same was also true of *Am. elongata* at habitat M. The fish faunas at habitats D and E were commonly characterised by *A. elongata* and *H. vittatus*, and also by *T. pleurogramma* at the former habitat and by *P. olorum* at the latter. These characteristic species were also frequently found in greater numbers at their respective habitat types than many other habitats in those seasons. Some differences in the suite of characteristic species were evident between summer 2006 and 2007 at the above four habitats, which are listed in Table 6.1.2.4c and f.

During summer 2006, the fish assemblages at habitats Q and J at the southern end of the Harvey Estuary were also markedly distinct from those at all other habitats, *i.e.* pairwise R=0.719-0.980 and 0.572-0.997, respectively (Table 6.1.2.3c). Samples from Q formed a relatively dispersed group on the opposite side of the MDS plot from those representing E and L, while samples from J formed a tight and discrete group that lay adjacent to, but markedly distinct from, those from Q (Fig. 6.1.2.2c). SIMPER showed that the fish fauna at habitat Q was relatively depauperate compared to that at all other habitat types, and was characterised only by *A. elongata,* the densities of which were always greater at other habitats. The ichthyofauna at habitat J was also characterised by three other atherinid species, *i.e. A. mugiloides, C. pauciradiatus* and *L. presbyteroides*, all of which frequently occurred more consistently and in greater abundances at J than at most other habitats (Table 6.1.2.4c). Samples from the remaining basin habitats were positioned between those for E/L and J/Q, and differed in the extents to which they formed distinct groups. For example, whereas samples collected from habitat I on the northwestern shore of the Peel Inlet formed a relatively tight group, intermingling only with those from C, samples from habitat B on the north-eastern shore were more dispersed (Fig. 6.1.2.2c). The fish assemblages at I were best distinguished by their greater

Table 6.1.2.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each habitat in the Peel-Harvey Estuary during (a) winter 2005, (b) spring 2005, (c) summer 2006, (d) autumn 2006, (e) winter 2006 and (f) summer 2007, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2005

	B	**C**	**D**	**H**	**I**	**J**	**K**	**L**	**M**	**Q**
B	*F. lateralis* *P. olorum* *A. elongata* *C. pauciradiatus*									
C	▨	*F. lateralis* *L. wallacei*								
D	*F. lateralis*^{B} *P. punctatus*^{B} *P. olorum*^{D} *A. elongata*^{B}	*F. lateralis*^{C} *P. olorum*^{D} *L. wallacei*^{C} *A. elongata*^{C}	*P. olorum* *T. pleurogramma*							
H	*Am. elongata*^{H} *F. lateralis*^{H} *P. punctatus*^{B} *P. olorum*^{B} *T. pleurogramma*^{H} *A. elongata*^{B}	▨	*F. lateralis*^{H} *Am. elongata*^{H} *P. olorum*^{D} *T. pleurogramma*^{D}	*F. lateralis* *Am. elongata* *T. pleurogramma*						
I	*F. lateralis*^{I} *P. punctatus*^{I} *L. wallacei*^{I} *P. olorum*^{B} *Am. elongata*^{I} *T. pleurogramma*^{I} *A. elongata*^{B}	▨	*F. lateralis*^{I} *P. olorum*^{D} *L. wallacei*^{I} *P. punctatus*^{I} *Am. elongata*^{I} *T. pleurogramma*^{D}	▨	*F. lateralis* *Am. elongata* *T. pleurogramma*					
J	*F. lateralis*^{B} *P. punctatus*^{B} *A. elongata*^{J} *A. mugiloides*^{J} *P. olorum*^{B} *T. pleurogramma*^{J} *C. pauciradiatus*^{B}	*F. lateralis*^{C} *L. wallacei*^{C} *A. mugiloides*^{C} *A. elongata*^{J} *T. pleurogramma*^{J}	*A. elongata*^{J} *P. olorum*^{D} *T. pleurogramma*^{J} *A. mugiloides*^{J}	*F. lateralis*^{H} *Am. elongata*^{H} *A. elongata*^{J} *A. mugiloides*^{J} *T. pleurogramma*^{J}	*F. lateralis*^{I} *L. wallacei*^{I} *A. elongata*^{J} *P. punctatus*^{I}	*A. elongata* *A. mugiloides* *T. pleurogramma*				
K	*F. lateralis*^{B} *Am. elongata*^{K} *P. punctatus*^{B} *T. pleurogramma*^{K} *P. olorum*^{B} *A. mugiloides*^{K} *M. cephalus*^{K} *A. elongata*^{B}	▨	*Am. elongata*^{K} *P. olorum*^{D} *F. lateralis*^{K} *T. pleurogramma*^{K} *A. mugiloides*^{K}	*F. lateralis*^{H} *Am. elongata*^{H} *T. pleurogramma*^{K} *A. mugiloides*^{K}	▨	▨	*Am. elongata* *F. lateralis* *T. pleurogramma* *A. mugiloides*			

	B	C	D	H	I	J	K	L	M	Q
L	*T. pleurogramma*^{L} *F. lateralis*^{L} *P. punctatus*^{B} *S. argus*^{L} *P. olorum*^{B} *A. elongata*^{B}	*T. pleurogramma*^{L} *F. lateralis*^{L} *L. wallacei*^{C} *S. argus*^{L} *A. elongata*^{C} *P. olorum*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{L} *P. olorum*^{D} *S. argus*^{L}	*Am. elongata*^{H} *T. pleurogramma*^{L} *F. lateralis*^{L} *S. argus*^{L} *P. olorum*^{L}	*T. pleurogramma*^{L} *F. lateralis*^{L} *P. punctatus*^{I} *L. wallacei*^{I} *S. argus*^{L} *Am. elongata*^{I} *P. olorum*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{L} *A. mugiloides*^{J} *S. argus*^{L} *P. olorum*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{L} *Am. elongata*^{K} *S. argus*^{L} *A. mugiloides*^{L} *P. olorum*^{L} *L. presbyteroides*^{K}	*F. lateralis* *T. pleurogramma*		
M	*F. lateralis*^{B} *P. punctatus*^{B} *P. olorum*^{B} *A. elongata*^{B}	*F. lateralis*^{C} *L. wallacei*^{C} *T. pleurogramma*^{M} *A. elongata*^{C}	*P. olorum*^{D} *T. pleurogramma*^{D} *F. lateralis*^{M} *A. ogilbyi*^{M}		*F. lateralis*^{I} *L. wallacei*^{I} *P. punctatus*^{I} *Am. elongata*^{I} *T. pleurogramma*^{M}	*A. elongata*^{J} *F. lateralis*^{M} *A. mugiloides*^{J} *T. pleurogramma*^{J}		*F. lateralis*^{L} *T. pleurogramma*^{L} *S. argus*^{L} *P. olorum*^{L}	*F. lateralis* *T. pleurogramma* *H. vittatus* *Am. elongata* *P. jenynsii*	
Q	*F. lateralis*^{B} *L. wallacei*^{Q} *P. punctatus*^{B} *P. olorum*^{B} *T. pleurogramma*^{Q} *C. pauciradiatus*^{B} *A. elongata*^{Q}	*F. lateralis*^{C} *L. wallacei*^{C} *A. mugiloides*^{C} *T. pleurogramma*^{Q} *A. elongata*^{Q}	*P. olorum*^{D} *L. wallacei*^{Q} *T. pleurogramma*^{Q} *A. mugiloides*^{Q} *A. elongata*^{Q} *F. lateralis*^{Q}	*F. lateralis*^{H} *Am. elongata*^{H} *L. wallacei*^{Q} *A. elongata*^{Q} *T. pleurogramma*^{Q}	*F. lateralis*^{I} *L. wallacei*^{I} *P. punctatus*^{I} *Am. elongata*^{I} *T. pleurogramma*^{Q} *A. elongata*^{Q}		*Am. elongata*^{K} *L. wallacei*^{Q} *A. mugiloides*^{Q} *T. pleurogramma*^{K} *F. lateralis*^{K} *A. elongata*^{Q} *M. cephalus*^{K} *L. presbyteroides*^{K}	*F. lateralis*^{L} *T. pleurogramma*^{L} *S. argus*^{L} *A. elongata*^{Q} *P. olorum*^{L}	*L. wallacei*^{Q} *F. lateralis*^{M} *A. mugiloides*^{Q} *T. pleurogramma*^{Q} *A. elongata*^{Q}	*L. wallacei* *F. lateralis* *T. pleurogramma* *A. elongata* *A. mugiloides*

(b) Spring 2005

	B	C	D	E	H	I	J	K	L	M	Q
B	*F. lateralis* *A. elongata* *L. presbyteroides*										
C	*L. presbyteroides*^{C} *F. lateralis*^{B} *A. elongata*^{B} *A. forsteri*^{B} *T. pleurogramma*^{C} *S. punctata*^{C} *P. olorum*^{B} *C. pauciradiatus*^{C}	*F. lateralis* *L. presbyteroides* *T. pleurogramma* *A. elongata*									
D	*F. lateralis*^{B} *H. vittatus*^{D} *P. olorum*^{D} *A. forsteri*^{D} *A. elongata*^{B} *T. pleurogramma*^{D}	*F. lateralis*^{C} *H. vittatus*^{D} *L. presbyteroides*^{C} *P. olorum*^{D} *A. forsteri*^{D} *S. punctata*^{C} *T. pleurogramma*^{D} *A. elongata*^{C}	*H. vittatus* *P. olorum* *T. pleurogramma*								
E	*F. lateralis*^{B} *P. olorum*^{E} *T. pleurogramma*^{E}	*F. lateralis*^{C} *L. presbyteroides*^{C} *P. olorum*^{E} *T. pleurogramma*$^{-}$ *S. punctata*^{C} *A. elongata*^{C}	*H. vittatus*^{D} *P. olorum*^{E} *A. forsteri*^{D} *T. pleurogramma*^{D} *A. elongata*^{D}	*P. olorum* *T. pleurogramma*							
H			*H. vittatus*^{D} *F. lateralis*^{H} *P. olorum*^{D} *T. pleurogramma*^{D} *G. subfasciatus*^{D} *L. presbyteroides*^{H} *A. elongata*^{D}	*F. lateralis*^{H} *P. olorum*^{E} *A. suppositus*^{H} *T. pleurogramma*^{E} *L. presbyteroides*^{H} *H. vittatus*^{E}	*F. lateralis* *L. presbyteroides* *T. pleurogramma*						
I			*F. lateralis*^{I} *H. vittatus*^{D} *P. olorum*^{D} *Am. elongata*^{I} *T. pleurogramma*^{D} *L. presbyteroides*^{I} *M. cephalus*^{I}	*F. lateralis*^{I} *P. olorum*^{E} *Am. elongata*^{I} *L. presbyteroides*^{I} *T. pleurogramma*^{E} *H. vittatus*^{E} *A. elongata*^{I}		*F. lateralis*					
J	*F. lateralis*^{B} *A. elongata*^{B} *L. presbyteroides*^{B}	*F. lateralis*^{C} *L. presbyteroides*^{C} *T. pleurogramma*^{C} *A. elongata*^{J} *S. punctata*^{C}	*H. vittatus*^{D} *P. olorum*^{D} *A. forsteri*^{D} *T. pleurogramma*^{D} *A. elongata*^{J}	*P. olorum*^{E} *A. elongata*^{J} *T. pleurogramma*^{E} *H. vittatus*^{E} *A. forsteri*^{E}			*A. elongata* *T. pleurogramma* *L. presbyteroides*				

	B	C	D	E	H	I	J	K	L	M	Q
K	*F. lateralis*^{B} *T. pleurogramma*^{K} *A. elongata*^{B} *A. forsteri*^{B} *L. presbyteroides*^{K} *Am. elongata*^{K} *A. mugiloides*^{K} *L. wallacei*^{K}		*H. vittatus*^{D} *P. olorum*^{D} *F. lateralis*^{K} *A. forsteri*^{D} *L. presbyteroides*^{K} *T. pleurogramma*^{K} *A. mugiloides*^{K} *A. elongata*^{D}	*P. olorum*^{E} *F. lateralis*^{K} *L. presbyteroides*^{K} *T. pleurogramma*^{K} *A. forsteri*^{K} *A. mugiloides*^{K} *H. vittatus*^{E}				*T. pleurogramma* *F. lateralis* *L. presbyteroides*			
L	*T. pleurogramma*^{L} *F. lateralis*^{B} *A. elongata*^{B} *A. forsteri*^{B} *H. vittatus*^{L} *A. butcheri*^{B} *A. bifrenatus*^{L} *P. olorum*^{L}	*L. presbyteroides*^{C} *F. lateralis*^{L} *T. pleurogramma*^{L} *A. forsteri*^{L} *H. vittatus*^{L} *S. punctata*^{C} *P. olorum*^{L} *A. elongata*^{C}	*F. lateralis*^{L} *H. vittatus*^{D} *P. olorum*^{D} *A. forsteri*^{D} *T. pleurogramma*^{L} *G. marmoratus*^{L} *A. elongata*^{D}	*F. lateralis*^{L} *P. olorum*^{E} *T. pleurogramma*^{L} *A. forsteri*^{L} *H. vittatus*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{L} *A. forsteri*^{L} *H. vittatus*^{L} *P. olorum*^{L}		*F. lateralis*^{L} *T. pleurogramma*^{L} *H. vittatus*^{L} *A. forsteri*^{L} *P. olorum*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{L} *L. presbyteroides*^{K} *A. forsteri*^{L} *P. olorum*^{L} *H. vittatus*^{L} *A. mugiloides*^{K}	*F. lateralis* *T. pleurogramma* *P. olorum*		
M	*F. lateralis*^{B} *A. elongata*^{B} *H. vittatus*^{M} *T. pleurogramma*^{M} *A. forsteri*^{B} *Am. elongata*^{M}	*F. lateralis*^{C} *L. presbyteroides*^{C} *H. vittatus*^{M} *Am. elongata*^{M} *T. pleurogramma*^{M} *S. punctata*^{C} *A. elongata*^{C}	*H. vittatus*^{D} *P. olorum*^{D} *A. forsteri*^{D} *Am. elongata*^{M} *F. lateralis*^{M} *T. pleurogramma*^{M} *A. elongata*^{D}	*P. olorum*^{E} *H. vittatus*^{M} *T. pleurogramma*^{M} *Am. elongata*^{M}	*F. lateralis*^{H} *H. vittatus*^{M} *A. suppositus*^{H} *T. pleurogramma*^{M} *Am. elongata*^{M}		*H. vittatus*^{M} *T. pleurogramma*^{M} *Am. elongata*^{M} *F. lateralis*^{M}		*F. lateralis*^{L} *T. pleurogramma*^{L} *A. forsteri*^{M} *H. vittatus*^{M} *Am. elongata*^{M} *P. olorum*^{L}	*T. pleurogramma* *H. vittatus* *Am. elongata* *F. lateralis*	
Q	*F. lateralis*^{B} *L. presbyteroides*^{Q} *A. elongata*^{B} *T. pleurogramma*^{Q}	*F. lateralis*^{C} *L. presbyteroides*^{C} *S. punctata*^{C} *T. pleurogramma*^{Q} *A. forsteri*^{C} *A. elongata*^{Q} *C. pauciradiatus*^{C}	*H. vittatus*^{D} *P. olorum*^{D} *L. presbyteroides*^{Q} *F. lateralis*^{Q} *A. forsteri*^{D} *T. pleurogramma*^{D} *A. elongata*^{Q}	*P. olorum*^{E} *L. presbyteroides*^{Q} *F. lateralis*^{Q} *T. pleurogramma*^{Q} *A. elongata*^{Q} *A. forsteri*^{Q} *H. vittatus*^{E}	*F. lateralis*^{H} *L. presbyteroides*^{Q} *A. suppositus*^{H} *T. pleurogramma*^{Q} *A. elongata*^{Q} *A. forsteri*^{Q}		*L. presbyteroides*^{Q} *F. lateralis*^{Q} *T. pleurogramma*^{Q} *A. elongata*^{J} *A. forsteri*^{Q}		*F. lateralis*^{L} *T. pleurogramma*^{L} *L. presbyteroides*^{Q} *H. vittatus*^{L} *P. olorum*^{L} *A. forsteri*^{L}	*L. presbyteroides*^{Q} *H. vittatus*^{M} *F. lateralis*^{Q} *Am. elongata*^{M} *T. pleurogramma*^{M} *A. forsteri*^{M} *A. elongata*^{Q}	*L. presbyteroides* *F. lateralis* *T. pleurogramma* *A. elongata*

(c) Summer 2006

	B	C	D	E	H	I	J	K	L	M	Q
B	*A. elongata* *H. vittatus*										
C	*F. lateralis*^{C} *H. vittatus*^{B} *T. pleurogramma*^{C} *A. forsteri*^{B} *A. elongata*^{B} *C. pauciradiatus*^{C}	*A. elongata* *F. lateralis* *T. pleurogramma* *C. pauciradiatus*									
D	*T. pleurogramma*^{D} *A. elongata*^{B} *H. vittatus*^{B} *A. suppositus*^{D} *A. forsteri*^{B} *L. wallacei*^{D} *L. presbyteroides*^{D} *P. olorum*^{D} *P. punctatus*^{D}	*F. lateralis*^{C} *T. pleurogramma*^{D} *A. elongata*^{D} *H. vittatus*^{D} *P. punctatus*^{C} *A. suppositus*^{D} *L. presbyteroides*^{C}	*A. elongata* *T. pleurogramma* *H. vittatus* *A. suppositus*								
E	*A. suppositus*^{E} *P. olorum*^{E} *A. elongata*^{B} *G. subfasciatus*^{E} *H. vittatus*^{B} *T. pleurogramma*^{B} *L. wallacei*^{E} *A. forsteri*^{B}	*A. suppositus*^{E} *P. olorum*^{E} *F. lateralis*^{C} *A. elongata*^{C} *L. wallacei*^{E} *H. vittatus*^{E}	*A. suppositus*^{E} *P. olorum*^{E} *A. elongata*^{D} *T. pleurogramma*^{D} *G. subfasciatus*^{E} *L. wallacei*^{E} *H. vittatus*^{D} *L. presbyteroides*^{D} *P. punctatus*^{D}	*A. suppositus* *P. olorum* *A. elongata* *H. vittatus*							
H	*T. pleurogramma*^{H} *G. marmoratus*^{H} *P. punctatus*^{H} *H. vittatus*^{B} *A. mugiloides*^{H} *A. forsteri*^{H} *F. lateralis*^{H} *A. elongata*^{B} *L. presbyteroides*^{H} *C. pauciradiatus*^{B}		*G. marmoratus*^{H} *T. pleurogramma*^{H} *A. forsteri*^{H} *A. rueppellii*^{H} *A. mugiloides*^{H} *A. elongata*^{D} *F. lateralis*^{H} *A. suppositus*^{D} *P. punctatus*^{H} *H. vittatus*^{D} *L. presbyteroides*^{H} *L. wallacei*^{D} *P. olorum*^{H}	*A. suppositus*^{E} *T. pleurogramma*^{H} *P. olorum*^{E} *A. forsteri*^{H} *A. mugiloides*^{H} *A. elongata*^{E} *L. wallacei*^{E} *F. lateralis*^{H} *P. punctatus*^{H} *L. presbyteroides*^{H} *H. vittatus*^{E}	*T. pleurogramma* *A. elongata* *F. lateralis* *P. punctatus* *A. mugiloides* *A. forsteri*						
I	*F. lateralis*^{I} *A. elongata*^{B} *H. vittatus*^{B} *A. forsteri*^{B}		*F. lateralis*^{I} *A. elongata*^{D} *T. pleurogramma*^{D} *H. vittatus*^{D} *P. punctatus*^{I} *A. suppositus*^{D} *L. presbyteroides*^{D} *C. pauciradiatus*^{I}	*A. suppositus*^{E} *F. lateralis*^{I} *P. olorum*^{E} *A. elongata*^{E} *P. punctatus*^{I} *L. wallacei*^{E} *H. vittatus*^{E} *T. pleurogramma*^{E}	*T. pleurogramma*^{H} *G. marmoratus*^{H} *F. lateralis*^{I} *A. elongata*^{I} *A. mugiloides*^{H} *A. forsteri*^{H} *P. punctatus*^{H} *L. presbyteroides*^{H}	*F. lateralis* *A. elongata*					

	B	C	D	E	H	I	J	K	L	M	Q
J	*A. elongata*^{B} *H. vittatus*^{B} *A. mugiloides*^{J} *A. forsteri*^{B} *C. pauciradiatus*^{J} *L. presbyteroides*^{J}	*F. lateralis*^{C} *A. elongata*^{C} *A. mugiloides*^{J} *L. presbyteroides*^{J} *C. pauciradiatus*^{J}	*T. pleurogramma*^{D} *A. elongata*^{D} *H. vittatus*^{D} *A. mugiloides*^{J} *A. suppositus*^{D} *C. pauciradiatus*^{J} *L. presbyteroides*^{J} *P. punctatus*^{D}	*A. suppositus*^{E} *P. olorum*^{E} *A. elongata*^{E} *A. mugiloides*^{J} *L. wallacei*^{E} *L. presbyteroides*^{J} *C. pauciradiatus*^{J} *H. vittatus*^{E} *T. pleurogramma*^{E}	*T. pleurogramma*^{H} *G. marmoratus*^{H} *A. forsteri*^{H} *F. lateralis*^{H} *P. punctatus*^{H} *A. elongata*^{H} *L. presbyteroides*^{J} *A. mugiloides*^{H} *C. pauciradiatus*^{J}	*F. lateralis*^{I} *A. elongata*^{I} *A. mugiloides*^{J} *P. punctatus*^{I} *L. presbyteroides*^{J}	*A. mugiloides* *A. elongata* *C. pauciradiatus* *L. presbyteroides*				
K	*T. pleurogramma*^{K} *A. elongata*^{B} *H. vittatus*^{B} *A. forsteri*^{B} *H. regularis*^{K} *C. pauciradiatus*^{B} *L. presbyteroides*^{K}	*T. pleurogramma*^{K} *A. elongata*^{C} *F. lateralis*^{C} *H. regularis*^{K} *A. forsteri*^{K} *C. pauciradiatus*^{C} *L. presbyteroides*^{K} *A. mugiloides*^{K}	*T. pleurogramma*^{K} *A. elongata*^{D} *A. suppositus*^{D} *H. vittatus*^{D} *H. regularis*^{K} *A. forsteri*^{K} *L. presbyteroides*^{K} *L. wallacei*^{D} *C. pauciradiatus*^{K} *P. punctatus*^{D} *F. lateralis*^{D}	*A. suppositus*^{E} *T. pleurogramma*^{K} *P. olorum*^{E} *A. elongata*^{E} *L. wallacei*^{E} *H. regularis*^{K} *A. forsteri*^{K} *H. vittatus*^{E} *L. presbyteroides*^{K} *C. pauciradiatus*^{K}		*T. pleurogramma*^{K} *F. lateralis*^{I} *A. elongata*^{I} *H. regularis*^{K} *L. presbyteroides*^{K} *P. jenynsii*^{K} *A. forsteri*^{K}	*T. pleurogramma*^{K} *A. elongata*^{J} *H. regularis*^{K} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *L. presbyteroides*^{J} *A. forsteri*^{K}	*T. pleurogramma* *H. regularis* *A. forsteri*			
L	*T. pleurogramma*^{B} *P. olorum*^{L} *F. lateralis*^{L} *H. vittatus*^{L} *A. elongata*^{B} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *A. forsteri*^{B} *P. punctatus*^{L} *A. rueppellii*^{L}	*T. pleurogramma*^{L} *H. vittatus*^{L} *P. olorum*^{L} *A. elongata*^{C} *F. lateralis*^{C} *A. bifrenatus*^{L} *P. punctatus*^{C} *A. rueppellii*^{C} *L. presbyteroides*^{L} *A. forsteri*^{L}	*T. pleurogramma*^{L} *F. lateralis*^{L} *A. elongata*^{D} *H. vittatus*^{L} *A. bifrenatus*^{L} *A. suppositus*^{D} *L. presbyteroides*^{L} *P. punctatus*^{L} *G. subfasciatus*^{D} *L. wallacei*^{D}	*A. suppositus*^{E} *T. pleurogramma*^{L} *F. lateralis*^{L} *P. olorum*^{L} *H. vittatus*^{L} *A. elongata*^{E} *A. bifrenatus*^{L} *L. wallacei*^{E} *G. subfasciatus*^{E} *L. presbyteroides*^{L} *P. punctatus*^{L} *A. rueppellii*^{L}	*G. marmoratus*^{H} *T. pleurogramma*^{L} *H. vittatus*^{L} *A. mugiloides*^{H} *A. bifrenatus*^{L} *A. elongata*^{H} *A. forsteri*^{H} *A. rueppellii*^{H} *F. lateralis*^{L} *P. punctatus*^{H} *L. presbyteroides*^{L}	*T. pleurogramma*^{L} *P. olorum*^{L} *H. vittatus*^{L} *A. elongata*^{I} *A. bifrenatus*^{L} *F. lateralis*^{I} *P. punctatus*^{I} *L. presbyteroides*^{L} *A. rueppellii*^{L} *P. jenynsii*^{L} *A. forsteri*^{L}	*T. pleurogramma*^{L} *F. lateralis*^{L} *P. olorum*^{L} *H. vittatus*^{L} *A. bifrenatus*^{L} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *P. punctatus*^{L} *A. elongata*^{J} *L. presbyteroides*^{L} *A. rueppellii*^{L}	*T. pleurogramma*^{L} *P. olorum*^{L} *F. lateralis*^{L} *H. vittatus*^{L} *A. bifrenatus*^{L} *H. regularis*^{K} *P. punctatus*^{L} *L. presbyteroides*^{L} *A. rueppellii*^{L} *A. forsteri*^{K} *A. elongata*^{L} *A. mugiloides*^{K} *C. pauciradiatus*^{K}	*T. pleurogramma* *F. lateralis* *H. vittatus* *A. bifrenatus* *L. presbyteroides* *A. elongata*		
M	*A. elongata*^{B} *T. pleurogramma*^{M} *A. forsteri*^{M} *Am. elongata*^{M} *H. vittatus*^{B}	*A. elongata*^{C} *A. forsteri*^{M} *Am. elongata*^{M} *F. lateralis*^{C}	*A. elongata*^{D} *T. pleurogramma*^{M} *Am. elongata*^{M} *A. suppositus*^{D} *H. vittatus*^{D} *G. subfasciatus*^{D} *L. presbyteroides*^{D} *P. punctatus*^{D}	*A. suppositus*^{E} *P. olorum*^{E} *A. elongata*^{E} *Am. elongata*^{M} *L. wallacei*^{E} *G. subfasciatus*^{E} *H. vittatus*^{E} *L. presbyteroides*^{M}	*T. pleurogramma*^{H} *A. elongata*^{H} *A. forsteri*^{M} *Am. elongata*^{M} *A. mugiloides*^{H} *P. punctatus*^{H} *F. lateralis*^{H} *H. vittatus*^{M}	*F. lateralis*^{I} *A. elongata*^{I} *Am. elongata*^{M} *A. forsteri*^{M} *T. pleurogramma*^{M}	*Am. elongata*^{M} *T. pleurogramma*^{M} *A. forsteri*^{M} *A. elongata*^{J} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *L. presbyteroides*^{J}	*T. pleurogramma*^{K} *Am. elongata*^{M} *A. forsteri*^{M} *H. regularis*^{K} *H. vittatus*^{M} *L. presbyteroides*^{K}	*T. pleurogramma*^{L} *P. olorum*^{L} *H. vittatus*^{L} *F. lateralis*^{L} *A. forsteri*^{M} *Am. elongata*^{M} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *P. punctatus*^{L} *A. elongata*^{L} *A. rueppellii*^{L}	*Am. elongata* *T. pleurogramma* *A. forsteri* *F. lateralis*	

	B	**C**	**D**	**E**	**H**	**I**	**J**	**K**	**L**	**M**	**Q**
Q	*A. elongata*^{B} *H. vittatus*^{B} *G. subfasciatus*^{B} *A. forsteri*^{B}	*A. elongata*^{C} *F. lateralis*^{C} *T. pleurogramma*^{C} *P. punctatus*^{C} *L. presbyteroides*^{C}	*A. elongata*^{D} *T. pleurogramma*^{D} *H. vittatus*^{D} *A. suppositus*^{D} *L. presbyteroides*^{D} *P. punctatus*^{D}	*A. suppositus*^{E} *P. olorum*^{E} *A. elongata*^{E} *L. wallacei*^{E} *G. subfasciatus*^{E} *H. vittatus*^{E} *T. pleurogramma*^{E}	*T. pleurogramma*^{H} *G. marmoratus*^{H} *A. elongata*^{H} *A. forsteri*^{H} *A. mugiloides*^{H} *F. lateralis*^{H} *P. punctatus*^{H} *L. presbyteroides*^{H}	*F. lateralis*^{I} *A. elongata*^{I} *P. punctatus*^{I}	*A. mugiloides*^{J} *C. pauciradiatus*^{J} *A. elongata*^{J} *L. presbyteroides*^{J}	*T. pleurogramma*^{K} *H. regularis*^{K} *A. forsteri*^{K} *L. presbyteroides*^{K}	*T. pleurogramma*^{L} *F. lateralis*^{L} *P. olorum*^{L} *H. vittatus*^{L} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *P. punctatus*^{L} *A. elongata*^{L} *A. rueppellii*^{L}	*Am. elongata*^{M} *T. pleurogramma*^{M} *A. forsteri*^{M}	*A. elongata*

(d) Autumn 2006

	B	C	D	E	H	I	J	K	L	M	Q
B	*T. pleurogramma* *F. lateralis* *A. elongata*										
C		*F. lateralis* *A. elongata*									
D		*F. lateralis*^{C} *C. pauciradiatus*^{D} *L. presbyteroides*^{D} *A. elongata*^{C} *T. pleurogramma*^{D}	*T. pleurogramma* *C. pauciradiatus* *A. elongata*								
E	*T. pleurogramma*^{B} *F. lateralis*^{B} *A. elongata*^{B} *L. wallacei*^{E}	*F. lateralis*^{C} *A. elongata*^{C} *L. presbyteroides*^{C} *L. wallacei*^{E}	*T. pleurogramma*^{D} *L. presbyteroides*^{D} *C. pauciradiatus*^{D} *A. elongata*^{E}	*L. presbyteroides* *A. elongata* *L. wallacei* *F. lateralis*							
H			*F. lateralis*^{H} *T. pleurogramma*^{H} *A. mugiloides*^{H} *C. pauciradiatus*^{D} *A. forsteri*^{H} *P. octolineatus*^{H}	*F. lateralis*^{H} *T. pleurogramma*^{H} *A. mugiloides*^{H} *A. forsteri*^{H} *P. octolineatus*^{H} *A. elongata*^{E} *L. presbyteroides*^{H}	*F. lateralis* *T. pleurogramma* *A. mugiloides*						
I			*F. lateralis*^{I} *A. elongata*^{I} *T. pleurogramma*^{D} *C. pauciradiatus*^{D} *L. presbyteroides*^{D}	*F. lateralis*^{I} *A. elongata*^{I} *T. pleurogramma*^{I} *L. presbyteroides*^{E} *L. wallacei*^{E}	*T. pleurogramma*^{H} *A. mugiloides*^{H} *A. forsteri*^{H} *A. elongata*^{I} *F. lateralis*^{H} *P. octolineatus*^{H} *L. presbyteroides*^{I}	*F. lateralis* *A. elongata*					
J	*T. pleurogramma*^{B} *F. lateralis*^{B} *A. mugiloides*^{J} *A. elongata*^{B} *L. presbyteroides*^{J}	*F. lateralis*^{C} *T. pleurogramma*^{J} *A. mugiloides*^{C} *A. elongata*^{C} *L. presbyteroides*^{J} *C. pauciradiatus*^{C}	*T. pleurogramma*^{J} *L. presbyteroides*^{D} *C. pauciradiatus*^{D} *A. mugiloides*^{J} *A. elongata*^{J}	*T. pleurogramma*^{J} *A. mugiloides*^{J} *A. elongata*^{J} *L. presbyteroides*^{J} *L. wallacei*^{E}	*F. lateralis*^{H} *T. pleurogramma*^{H} *A. forsteri*^{H} *A. mugiloides*^{H} *P. octolineatus*^{H} *A. elongata*^{J} *L. presbyteroides*^{J}	*F. lateralis*^{I} *T. pleurogramma*^{J} *A. elongata*^{I} *A. mugiloides*^{J} *L. presbyteroides*^{J} *C. pauciradiatus*^{J}	*T. pleurogramma* *A. mugiloides* *L. presbyteroides* *A. elongata*				
K		*F. lateralis*^{C} *A. mugiloides*^{K} *T. pleurogramma*^{K} *C. pauciradiatus*^{K} *A. elongata*^{C} *L. presbyteroides*^{C}		*A. mugiloides*^{K} *P. jenynsii*^{K} *T. pleurogramma*^{K} *C. pauciradiatus*^{K} *A. elongata*^{E} *L. presbyteroides*^{K}		*F. lateralis*^{I} *A. mugiloides*^{K} *P. jenynsii*^{K} *T. pleurogramma*^{K} *A. elongata*^{I} *C. pauciradiatus*^{K}	*A. mugiloides*^{K} *P. jenynsii*^{K} *T. pleurogramma*^{J} *C. pauciradiatus*^{K} *A. elongata*^{J} *L. presbyteroides*^{J}	*A. mugiloides* *T. pleurogramma* *C. pauciradiatus* *A. elongata*			

	B	**C**	**D**	**E**	**H**	**I**	**J**	**K**	**L**	**M**	**Q**
L	▨	▨	*F. lateralis*^{L} *C. pauciradiatus*^{L} *A. elongata*^{L} *P. olorum*^{L}	*F. lateralis*^{L} *C. pauciradiatus*^{L} *A. elongata*^{L} *T. pleurogramma*^{L} *P. olorum*^{L} *L. presbyteroides*^{L}	▨	▨	*F. lateralis*^{L} *T. pleurogramma*^{J} *C. pauciradiatus*^{L} *A. elongata*^{L} *A. mugiloides*^{J} *L. presbyteroides*^{J} *P. olorum*^{L}	▨	*F. lateralis* *C. pauciradiatus* *T. pleurogramma*		
M	*T. pleurogramma*^{B} *F. lateralis*^{B} *Am. elongata*^{M} *A. elongata*^{B}	*F. lateralis*^{C} *A. elongata*^{C}	*L. presbyteroides*^{D} *Am. elongata*^{M} *C. pauciradiatus*^{D} *T. pleurogramma*^{D} *F. lateralis*^{M}	*Am. elongata*^{M} *L. presbyteroides*^{M} *F. lateralis*^{M} *T. pleurogramma*^{M} *L. wallacei*^{E}	▨	*F. lateralis*^{I} *A. elongata*^{I} *Am. elongata*^{M} *T. pleurogramma*^{I}	*T. pleurogramma*^{J} *L. presbyteroides*^{M} *Am. elongata*^{M} *A. mugiloides*^{J}	*A. mugiloides*^{K} *P. jenynsii*^{K} *T. pleurogramma*^{K} *C. pauciradiatus*^{K} *F. lateralis*^{M} *A. elongata*^{K}	*F. lateralis*^{L} *C. pauciradiatus*^{L} *A. elongata*^{L} *P. olorum*^{L}	*Am. elongata* *F. lateralis* *T. pleurogramma*	
Q	*L. presbyteroides*^{Q} *T. pleurogramma*^{B} *F. lateralis*^{B} *A. elongata*^{B} *A. mugiloides*^{Q}	*F. lateralis*^{C} *L. presbyteroides*^{Q} *A. elongata*^{C} *A. mugiloides*^{C} *T. pleurogramma*^{C}	*L. presbyteroides*^{Q} *C. pauciradiatus*^{D} *T. pleurogramma*^{D} *A. mugiloides*^{Q}	*L. presbyteroides*^{Q} *A. elongata*^{E} *T. pleurogramma*^{Q} *A. mugiloides*^{Q} *L. wallacei*^{E}	*F. lateralis*^{H} *T. pleurogramma*^{H} *L. presbyteroides*^{Q} *A. forsteri*^{H} *A. mugiloides*^{H} *P. octolineatus*^{H} *A. elongata*^{Q}	*F. lateralis*^{I} *L. presbyteroides*^{Q} *A. elongata*^{I} *T. pleurogramma*^{I} *A. mugiloides*^{Q}	*L. presbyteroides*^{Q} *T. pleurogramma*^{J} *A. elongata*^{J} *A. mugiloides*^{J}	*L. presbyteroides*^{Q} *A. mugiloides*^{K} *P. jenynsii*^{K} *T. pleurogramma*^{K} *C. pauciradiatus*^{K} *A. elongata*$^{-}$	*F. lateralis*^{L} *L. presbyteroides*^{Q} *C. pauciradiatus*^{L} *A. elongata*^{L} *T. pleurogramma*^{L} *A. mugiloides*^{Q} *P. olorum*^{L}	*L. presbyteroides*^{Q} *Am. elongata*^{M} *F. lateralis*^{M} *A. mugiloides*^{Q} *T. pleurogramma*^{Q}	*L. presbyteroides* *A. mugiloides*

(e) Winter 2006

	B	C	D	E	H	I	J	K	L	M	Q
B	*A. elongata* *F. lateralis*										
C		*F. lateralis* *A. elongata* *C. pauciradiatus*									
D	*A. elongata*^{B} *C. pauciradiatus*^{B} *L. presbyteroides*^{D} *F. lateralis*^{B}	*F. lateralis*^{C} *L. presbyteroides*^{D} *C. pauciradiatus*^{C} *A. elongata*^{C}	*L. presbyteroides* *L. wallacei* *P. olorum*								
E	*A. elongata*^{B} *C. pauciradiatus*^{B} *F. lateralis*^{B}	*F. lateralis*^{C} *C. pauciradiatus*^{C} *A. elongata*^{C} *P. olorum*^{E}	*L. presbyteroides*^{D} *L. wallacei*^{D} *A. elongata*^{E} *P. olorum*^{E}	*A. elongata* *P. olorum*							
H	*A. elongata*^{B} *A. mugiloides*^{H} *T. pleurogramma*^{H} *F. lateralis*^{H} *Am. elongata*^{H}		*A. mugiloides*^{H} *T. pleurogramma*^{H} *L. presbyteroides*^{D} *F. lateralis*^{H} *Am. elongata*^{H} *P. olorum*^{H}	*A. mugiloides*^{H} *T. pleurogramma*^{H} *F. lateralis*^{H} *Am. elongata*^{H}	*A. mugiloides* *T. pleurogramma* *Am. elongata* *F. lateralis*						
I	*F. lateralis*^{I} *A. elongata*^{B} *C. pauciradiatus*^{B} *L. presbyteroides*^{I} *P. punctatus*^{I} *T. pleurogramma*^{I} *P. olorum*^{B}		*F. lateralis*^{I} *A. elongata*^{I} *L. presbyteroides*^{I} *P. punctatus*^{I} *T. pleurogramma*^{I}	*F. lateralis*^{I} *A. elongata*^{I} *L. presbyteroides*^{I} *P. punctatus*^{I} *T. pleurogramma*^{I}	*F. lateralis*^{I} *A. mugiloides*^{H} *A. elongata*^{I} *T. pleurogramma*^{H} *L. presbyteroides*^{I} *P. punctatus*^{I}	*F. lateralis* *A. elongata* *L. presbyteroides* *P. punctatus*					
J	*T. pleurogramma*^{J} *C. pauciradiatus*^{B} *L. presbyteroides*^{J} *A. elongata*^{B} *F. lateralis*^{B}	*T. pleurogramma*^{J} *F. lateralis*^{C} *A. elongata*^{J} *C. pauciradiatus*^{C} *L. presbyteroides*^{J}	*T. pleurogramma*^{J} *L. presbyteroides*^{J} *A. elongata*^{J} *L. wallacei*^{D} *C. pauciradiatus*^{J}	*T. pleurogramma*^{J} *L. presbyteroides*^{J} *A. elongata*^{J} *A. mugiloides*^{J} *C. pauciradiatus*^{J}	*T. pleurogramma*^{H} *A. elongata*^{J} *A. mugiloides*^{H} *L. presbyteroides*^{J} *F. lateralis*^{H} *Am. elongata*^{H} *P. olorum*^{H}	*F. lateralis*^{I} *T. pleurogramma*^{J} *L. presbyteroides*^{J} *A. elongata*^{I} *P. punctatus*^{I} *C. pauciradiatus*^{J}	*A. elongata* *T. pleurogramma* *L. presbyteroides*				
K	*A. mugiloides*^{K} *A. elongata*^{B} *T. pleurogramma*^{K} *C. pauciradiatus*^{B} *M. cephalus*^{K} *F. lateralis*^{B}		*A. mugiloides*^{K} *T. pleurogramma*^{K} *L. presbyteroides*^{D} *M. cephalus*^{K} *L. wallacei*^{D} *A. elongata*^{K}	*A. mugiloides*^{K} *T. pleurogramma*^{K} *M. cephalus*^{K} *A. elongata*^{K}		*F. lateralis*^{I} *A. mugiloides*^{K} *T. pleurogramma*^{K} *A. elongata*^{I} *L. presbyteroides*^{I} *M. cephalus*^{K} *P. punctatus*^{I}		*A. mugiloides* *A. elongata* *M. cephalus* *T. pleurogramma*			

	B	**C**	**D**	**E**	**H**	**I**	**J**	**K**	**L**	**M**	**Q**
L	*F. lateralis*^{L} *A. elongata*^{B} *C. pauciradiatus*^{B} *A. forsteri*^{L} *P. olorum*^{L}		*F. lateralis*^{L} *A. elongata*^{L} *P. olorum*^{L}	*F. lateralis*^{L} *A. elongata*^{E} *P. olorum*^{E}	*F. lateralis*^{L} *T. pleurogramma*^{H} *Am. elongata*^{H} *P. olorum*^{H}	*F. lateralis*^{I} *A. elongata*^{I} *L. presbyteroides*^{I} *P. punctatus*^{I} *T. pleurogramma*^{I} *P. olorum*^{L} *A. forsteri*^{L}	*F. lateralis*^{L} *T. pleurogramma*^{J} *A. elongata*^{J} *C. pauciradiatus*^{L} *P. olorum*^{L} *A. forsteri*^{L}	*F. lateralis*^{L} *A. mugiloides*^{K} *T. pleurogramma*^{K} *M. cephalus*^{K} *C. pauciradiatus*^{L} *P. olorum*^{L} *A. elongata*^{K} *A. forsteri*^{L}	*F. lateralis* *P. olorum*		
M	*A. elongata*^{B} *C. pauciradiatus*^{B} *Am. elongata*^{M} *F. lateralis*^{M}	*F. lateralis*^{C} *Am. elongata*^{M} *C. pauciradiatus*^{C} *A. elongata*^{C}	*Am. elongata*^{M} *F. lateralis*^{M}	*Am. elongata*^{M} *F. lateralis*^{M} *S. burrus*^{M} *A. elongata*^{E}	*A. mugiloides*^{H} *T. pleurogramma*^{H} *F. lateralis*^{H}	*F. lateralis*^{I} *A. elongata*^{I} *L. presbyteroides*^{I} *Am. elongata*^{M} *P. punctatus*^{I} *T. pleurogramma*^{I}	*T. pleurogramma*^{J} *A. elongata*^{J} *Am. elongata*^{M} *L. presbyteroides*^{J} *C. pauciradiatus*^{J}	*A. mugiloides*^{K} *T. pleurogramma*^{K} *Am. elongata*^{M} *M. cephalus*^{K} *A. elongata*^{K} *C. pauciradiatus*^{K}	*F. lateralis*^{L} *Am. elongata*^{M} *S. argus*^{M} *P. olorum*^{L} *A. elongata*^{L}	*Am. elongata* *F. lateralis* *A. forsteri* *S. argus* *S. burrus*	
Q	*A. elongata*^{B} *C. pauciradiatus*^{B} *F. lateralis*^{B}	*F. lateralis*^{C} *C. pauciradiatus*^{C} *L. presbyteroides*^{Q} *A. mugiloides*^{Q} *A. elongata*^{C}		*L. presbyteroides*^{Q} *A. mugiloides*^{Q} *L. wallacei*^{Q} *A. elongata*^{E} *P. olorum*^{E}	*T. pleurogramma*^{H} *A. mugiloides*^{H} *F. lateralis*^{H} *Am. elongata*^{H} *P. olorum*^{H}	*F. lateralis*^{I} *A. elongata*^{I} *L. presbyteroides*^{I} *P. punctatus*^{I} *A. mugiloides*^{Q} *T. pleurogramma*^{I}	*T. pleurogramma*^{J} *L. presbyteroides*^{J} *A. elongata*^{J} *A. mugiloides*^{Q} *L. wallacei*^{J} *C. pauciradiatus*^{J}	*A. mugiloides*^{K} *T. pleurogramma*^{K} *M. cephalus*^{K} *L. presbyteroides*^{Q}	*F. lateralis*^{L} *A. mugiloides*^{L} *P. olorum*^{L} *A. forsteri*^{L} *A. elongata*^{L}	*Am. elongata*^{M} *F. lateralis*^{M} *A. mugiloides*^{Q} *A. elongata*^{Q}	*A. elongata* *L. presbyteroides* *A. mugiloides*

(f) Summer 2007

	B	C	D	E	H	I	J	K	L	M	Q
B	*C. pauciradiatus* *A. elongata*										
C	*C. pauciradiatus*^{B} *F. lateralis*^{C} *A. elongata*^{B}	*F. lateralis* *A. elongata* *C. pauciradiatus*									
D	*C. pauciradiatus*^{B} *G. subfasciatus*^{D} *A. elongata*^{B} *T. pleurogramma*^{D} *L. presbyteroides*^{D} *A. ogilbyi*^{D} *L. wallacei*^{D}	*F. lateralis*^{C} *G. subfasciatus*^{D} *T. pleurogramma*^{D} *C. pauciradiatus*^{C} *A. elongata*^{D} *L. presbyteroides*^{D} *A. ogilbyi*^{D} *L. wallacei*^{D}	*T. pleurogramma* *A. elongata* *G. subfasciatus* *H. vittatus* *A. ogilbyi*								
E	*A. elongata*^{B} *C. pauciradiatus*^{B} *L. wallacei*^{E} *P. olorum*^{E} *T. pleurogramma*^{B}	*F. lateralis*^{C} *A. elongata*^{E} *L. wallacei*^{E} *C. pauciradiatus*^{E} *P. olorum*^{E} *T. pleurogramma*^{C}	*G. subfasciatus*^{D} *A. elongata*^{E} *T. pleurogramma*^{D} *L. wallacei*^{E} *C. pauciradiatus*^{E} *P. olorum*^{E} *L. presbyteroides*^{D} *A. ogilbyi*^{D}	*L. wallacei* *A. elongata* *C. pauciradiatus* *P. olorum*							
H	*C. pauciradiatus*^{B} *A. elongata*^{B} *A. rueppellii*^{H} *F. lateralis*^{H} *P. octolineatus*^{H} *T. pleurogramma*^{H} *P. olorum*^{H}	*A. rueppellii*^{H} *L. presbyteroides*^{H} *P. octolineatus*^{H} *C. pauciradiatus*^{C} *T. pleurogramma*^{H} *F. lateralis*^{C} *A. elongata*^{C} *P. olorum*^{H}	*F. lateralis*^{H} *G. subfasciatus*^{D} *A. rueppellii*^{H} *P. octolineatus*^{H} *A. elongata*^{D} *T. pleurogramma*^{D} *C. pauciradiatus*^{D} *P. olorum*^{H} *A. ogilbyi*^{D}	*F. lateralis*^{H} *A. rueppellii*^{H} *A. elongata*^{E} *L. wallacei*^{E} *C. pauciradiatus*^{E} *T. pleurogramma*^{H} *P. octolineatus*^{H} *P. punctatus*^{H} *P. olorum*^{E}	*F. lateralis* *A. rueppellii* *T. pleurogramma* *P. octolineatus* *A. elongata*						
I	*C. pauciradiatus*^{B} *A. elongata*^{B} *F. lateralis*^{I} *A. rueppellii*^{I} *T. pleurogramma*^{I}	*F. lateralis*^{C} *A. elongata*^{I} *C. pauciradiatus*^{C} *A. rueppellii*^{I} *T. pleurogramma*^{I} *P. olorum*^{C}	*G. subfasciatus*^{D} *F. lateralis*^{I} *A. elongata*^{I} *T. pleurogramma*^{D} *A. rueppellii*^{I} *C. pauciradiatus*^{I} *L. presbyteroides*^{D} *A. ogilbyi*^{D} *L. wallacei*^{D}	*A. elongata*^{E} *L. wallacei*^{E} *F. lateralis*^{I} *A. rueppellii*^{E} *C. pauciradiatus*^{E} *P. olorum*^{E} *P. octolineatus*^{I} *T. pleurogramma*^{I}	*L. presbyteroides*^{H} *A. rueppellii*^{H} *A. elongata*^{I} *P. octolineatus*^{H} *T. pleurogramma*^{H} *F. lateralis*^{H} *C. pauciradiatus*^{I} *P. olorum*^{H}	*A. elongata* *F. lateralis* *A. rueppellii* *C. pauciradiatus*					
J	*A. elongata*^{B} *C. pauciradiatus*^{B} *A. mugiloides*^{J} *T. pleurogramma*^{J}	*F. lateralis*^{C} *A. mugiloides*^{J} *A. elongata*^{C} *C. pauciradiatus*^{J} *T. pleurogramma*^{J}	*G. subfasciatus*^{D} *A. elongata*^{D} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *T. pleurogramma*^{D} *L. presbyteroides*^{D} *A. ogilbyi*^{J} *L. wallacei*^{D}	*A. elongata*^{E} *L. wallacei*^{E} *C. pauciradiatus*^{J} *A. mugiloides*^{J} *P. olorum*^{E} *T. pleurogramma*^{J}	*F. lateralis*^{H} *A. rueppellii*^{H} *L. presbyteroides*^{H} *P. octolineatus*^{H} *C. pauciradiatus*^{J} *A. mugiloides*^{J} *A. elongata*^{J} *T. pleurogramma*^{H} *P. olorum*^{H}	*A. elongata*^{I} *F. lateralis*^{I} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *A. rueppellii*^{I} *P. octolineatus*^{I} *T. pleurogramma*^{J}	*A. mugiloides* *C. pauciradiatus* *T. pleurogramma*				

	B	C	D	E	H	I	J	K	L	M	Q
K	*C. pauciradiatus*^{B} *A. elongata*^{B} *A. mugiloides*^{K} *A. ogilbyi*^{K}	*F. lateralis*^{C} *C. pauciradiatus*^{C} *A. mugiloides*^{K} *A. elongata*^{C} *A. ogilbyi*^{K}	*G. subfasciatus*^{D} *T. pleurogramma*^{D} *A. elongata*^{D} *L. presbyteroides*^{D} *A. mugiloides*^{K} *C. pauciradiatus*^{D} *A. ogilbyi*^{K} *L. wallacei*^{D}	*L. wallacei*^{E} *A. elongata*^{E} *C. pauciradiatus*^{E} *P. olorum*^{E} *A. mugiloides*^{K} *A. ogilbyi*^{K}	*F. lateralis*^{H} *A. rueppellii*^{H} *L. presbyteroides*^{H} *T. pleurogramma*^{H} *P. octolineatus*^{H} *A. elongata*$^{-}$ *A. mugiloides*^{K} *C. pauciradiatus*^{K} *P. olorum*^{H} *A. ogilbyi*^{K}	*F. lateralis*^{I} *A. elongata*^{I} *A. rueppellii*^{I} *A. mugiloides*^{K} *C. pauciradiatus*^{I} *T. pleurogramma*^{I} *A. ogilbyi*^{K}	*C. pauciradiatus*^{J} *A. elongata*^{J} *A. mugiloides*^{J} *T. pleurogramma*^{J} *A. ogilbyi*^{J}	*A. elongata* *A. mugiloides* *P. jenynsii* *A. ogilbyi*			
L	*C. pauciradiatus*^{B} *A. elongata*^{B} *A. bifrenatus*^{L} *T. pleurogramma*^{L} *L. presbyteroides*^{L} *F. lateralis*^{L} *A. rueppellii*^{L} *P. olorum*^{L} *A. ogilbyi*^{L}	*T. pleurogramma*^{L} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *C. pauciradiatus*^{C} *F. lateralis*^{C} *A. elongata*^{C} *A. rueppellii*^{L} *P. olorum*^{L} *A. ogilbyi*^{L}	*G. subfasciatus*^{D} *F. lateralis*^{L} *A. bifrenatus*^{L} *H. vittatus*^{L} *L. presbyteroides*^{L} *A. elongata*^{D} *P. olorum*^{L} *A. rueppellii*^{L} *T. pleurogramma*^{L} *A. ogilbyi*^{L} *L. wallacei*^{D}	*A. elongata*^{E} *F. lateralis*^{L} *T. pleurogramma*^{L} *L. wallacei*^{E} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *C. pauciradiatus*^{E} *P. olorum*^{E} *A. ogilbyi*^{L}	*L. presbyteroides*^{H} *A. bifrenatus*^{L} *A. rueppellii*^{H} *P. octolineatus*^{H} *A. elongata*^{L} *T. pleurogramma*^{L} *P. olorum*^{L} *F. lateralis*^{H} *A. ogilbyi*^{L}	*A. bifrenatus*^{L} *L. presbyteroides*^{L} *A. elongata*^{I} *T. pleurogramma*^{L} *P. olorum*^{L} *A. rueppellii*^{L} *F. lateralis*^{L} *C. pauciradiatus*^{I} *A. ogilbyi*^{L}	*F. lateralis*^{L} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *A. mugiloides*^{J} *C. pauciradiatus*^{J} *A. elongata*^{L} *T. pleurogramma*^{L} *P. olorum*^{L} *A. rueppellii*^{L} *A. ogilbyi*^{L}	*T. pleurogramma*^{L} *F. lateralis*^{L} *A. bifrenatus*^{L} *L. presbyteroides*^{L} *P. olorum*^{L} *A. rueppellii*^{L} *A. elongata*^{L} *A. mugiloides*^{K} *C. pauciradiatus*^{K} *A. ogilbyi*^{L}	*F. lateralis* *T. pleurogramma* *P. olorum* *A. rueppellii*		
M	*C. pauciradiatus*^{B} *A. elongata*^{B} *S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *G. marmoratus*^{M} *A. rueppellii*^{M} *T. pleurogramma*^{M} *S. schomburgkii*^{M} *F. lateralis*^{M}	*S. argus*^{M} *L. presbyteroides*^{M} *F. lateralis*^{C} *Am. elongata*^{M} *G. marmoratus*^{M} *C. pauciradiatus*^{C} *A. rueppellii*^{M} *A. elongata*^{C} *T. pleurogramma*^{M} *S. schomburgkii*^{M}	*S. argus*^{M} *L. presbyteroides*^{M} *G. subfasciatus*^{D} *Am. elongata*^{M} *G. marmoratus*^{M} *A. elongata*^{D} *H. vittatus*^{M} *A. rueppellii*^{M} *T. pleurogramma*^{D} *S. schomburgkii*^{M} *L. wallacei*^{D}	*S. argus*^{M} *L. presbyteroides*^{M} *A. elongata*^{E} *Am. elongata*^{M} *L. wallacei*^{E} *A. rueppellii*^{M} *G. marmoratus*^{M} *C. pauciradiatus*^{E} *P. olorum*^{E} *T. pleurogramma*^{M} *S. schomburgkii*^{M}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *F. lateralis*^{H} *G. marmoratus*^{M} *A. rueppellii*^{H} *P. octolineatus*^{H} *T. pleurogramma*^{H} *A. elongata*^{H} *S. schomburgkii*^{M} *P. olorum*^{H}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *A. elongata*^{I} *G. marmoratus*^{M} *F. lateralis*^{I} *A. rueppellii*^{M} *S. schomburgkii*^{M} *T. pleurogramma*^{M} *C. pauciradiatus*^{I}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *C. pauciradiatus*^{J} *G. marmoratus*^{M} *A. mugiloides*^{J} *A. rueppellii*^{M} *A. elongata*^{J} *H. vittatus*^{M} *S. schomburgkii*^{M} *T. pleurogramma*^{M}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *G. marmoratus*^{M} *A. rueppellii*^{M} *S. schomburgkii*^{M} *T. pleurogramma*^{M} *A. elongata*^{K} *A. mugiloides*^{K} *F. lateralis*^{M}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *A. bifrenatus*^{L} *G. marmoratus*^{M} *F. lateralis*^{L} *H. semifasciata*^{L} *A. rueppellii*^{M} *P. olorum*^{L} *T. pleurogramma*^{L} *A. elongata*^{L} *S. schomburgkii*^{M}	*S. argus* *Am. elongata* *L. presbyteroides* *G. marmoratus* *A. rueppellii* *T. pleurogramma*	
Q	*C. pauciradiatus*^{B} *L. presbyteroides*^{Q} *A. elongata*^{B} *A. mugiloides*^{Q}	*F. lateralis*^{C} *L. presbyteroides*^{Q} *C. pauciradiatus*^{C} *A. elongata*^{Q} *A. mugiloides*^{Q}	*L. presbyteroides*^{Q} *G. subfasciatus*^{D} *T. pleurogramma*^{D} *A. elongata*^{D} *A. mugiloides*^{Q} *A. ogilbyi*^{Q} *L. wallacei*^{D}	*L. presbyteroides*^{Q} *A. elongata*^{E} *L. wallacei*^{E} *C. pauciradiatus*^{E} *P. olorum*^{E} *A. ogilbyi*^{Q}	*F. lateralis*^{H} *L. presbyteroides*^{Q} *A. rueppellii*^{H} *P. octolineatus*^{H} *T. pleurogramma*^{H} *C. pauciradiatus*^{Q} *A. elongata*^{Q} *P. olorum*^{H} *A. ogilbyi*^{Q}	*L. presbyteroides*^{Q} *F. lateralis*^{I} *A. elongata*^{I} *C. pauciradiatus*^{Q} *A. rueppellii*^{I} *T. pleurogramma*^{Q} *A. mugiloides*^{Q}	*L. presbyteroides*^{Q} *A. elongata*^{Q} *C. pauciradiatus*^{J} *T. pleurogramma*^{Q} *A. mugiloides*^{J} *A. ogilbyi*		*L. presbyteroides*^{Q} *F. lateralis*^{L} *T. pleurogramma*^{L} *A. bifrenatus*^{L} *A. elongata*^{Q} *P. olorum*^{L} *A. rueppellii*^{L} *C. pauciradiatus*^{Q} *A. ogilbyi*^{L}	*S. argus*^{M} *L. presbyteroides*^{M} *Am. elongata*^{M} *G. marmoratus*^{M} *A. elongata*^{Q} *A. rueppellii*^{M} *T. pleurogramma*^{M} *S. schomburgkii*^{M}	*L. presbyteroides* *A. elongata* *C. pauciradiatus* *A. mugiloides*

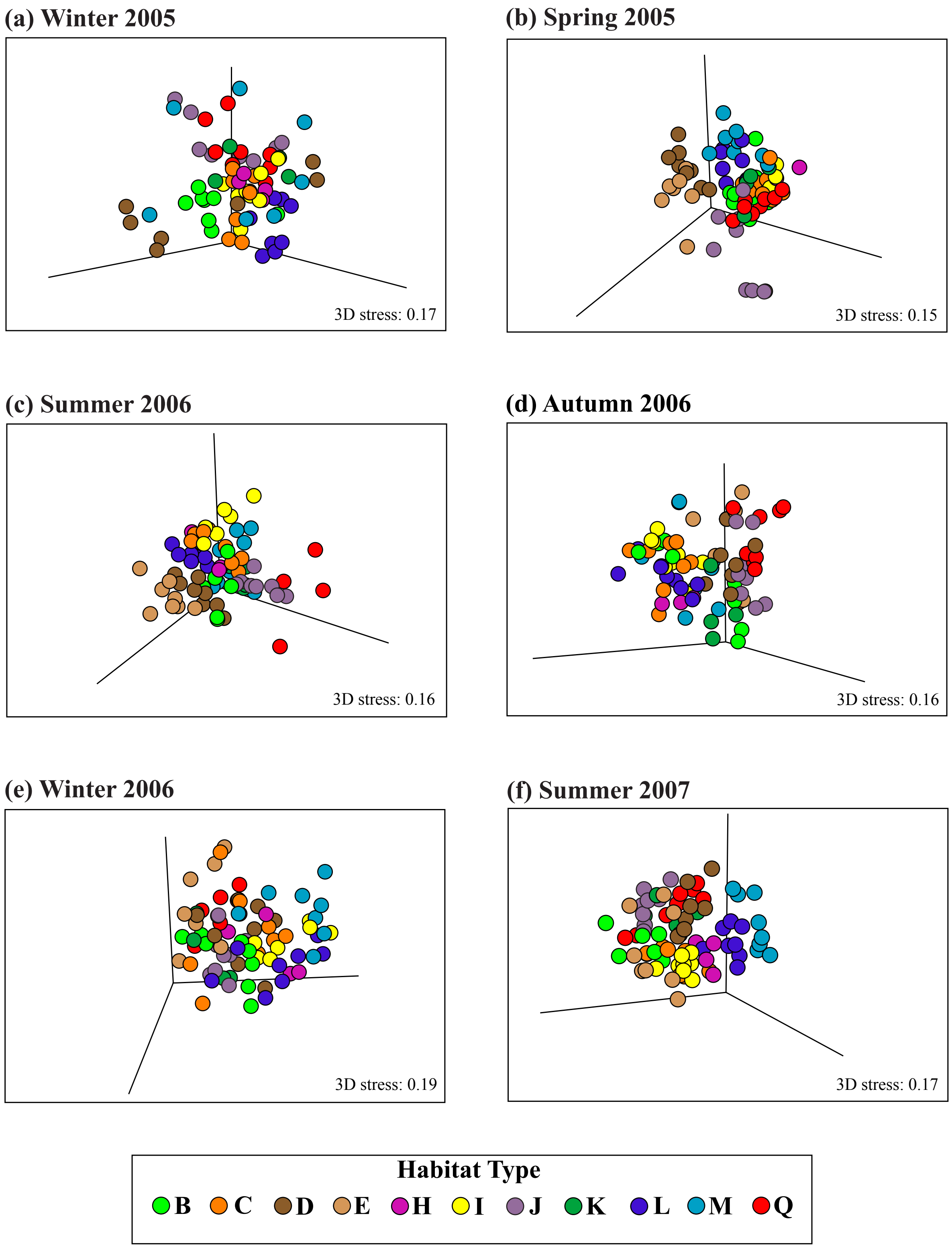


Figure 6.1.2.2: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample at each habitat type in the Peel-Harvey Estuary during (a) winter 2005, (b) spring 2005, (c) summer 2006, (d) autumn 2006, (e) winter 2006 and (f) summer 2007.

prevalence of *F. lateralis* than all other habitats, while those at B almost always contained greater numbers of *H. vittatus* and *A. elongata* than any other habitat (Table 6.1.2.4c).

In summer 2007, the ichthyofaunal compositions of samples from basin habitats H, I, J and Q also differed considerably from those recorded at most other habitats, as reflected by the fact they formed relatively tight and discrete groups on the MDS plot shown in Fig. 6.1.2.2f, and that the R-statistic for each pairwise comparison involving one of these habitats typically exceeded 0.500 (Table 6.1.2.3f). While the fish faunas at most of these habitats were characterised, in part, by *C. pauciradiatus* and *A. elongata*, the former species was most prevalent at J while the latter was most abundant at I (Table 6.1.2.4f). Habitats H and I were also both characterised by *F. lateralis* and *A. rueppellii*, but both of these species were more abundant at H than almost all other habitats in this season. This was also the case for the other two species that characterised habitat H, namely *Pelates octolineatus* and *T. pleurogramma*. Habitats J and Q were further characterised by *A. mugiloides* and, in the case of the latter habitat, also *L. presbyteroides*, the first of which was always most prevalent at J, while the same was nearly always true of the latter species at Q (Table 6.1.2.4f).

Moderate overall differences in fish faunal composition among habitats were detected in spring 2005 and winter 2006, *i.e.* Global R=0.451 and 0.487, respectively (Table 6.1.2.3b and e, respectively). The most distinct habitat in the former season was the riverine habitat D, which was clearly reflected by the fact that the pairwise R-statistics between this and all other habitats except E, J and the channel habitat M were greater than 0.700, followed by the other riverine habitat, E, whose pairwise R-statistics for comparisons with all other habitats except D, J and K exceeded 0.500 (Table 6.1.2.3b). Most of the samples representing habitats D and E formed distinct groups that lay largely on one side of the MDS plot constructed from the spring 2005 fish assemblage data (Fig. 6.1.2.2b), and were both positioned the greatest distance from samples representing the basin habitats C, I and Q. SIMPER demonstrated that the fish faunas at both D and E were characterised by *P. olorum* and *T. pleurogramma* and, in the case of the former habitat, also *H. vittatus* (Table 6.1.2.4b). *Pseudogobius olorum* was always found in greater abundances at habitats D and E, and particularly the latter, than at any other habitat in this season, and the same was true of *H. vittatus* and *T. pleurogramma* at habitat D in all or most cases. While *H. vittatus* was not among the most characteristic of the fish assemblage at E, it was still important in distinguishing the faunas at this habitat from that of several others, and the same applied to *Aldrichetta forsteri* at habitat D. In contrast to the above habitats, the fish assemblages at habitats C, I and Q were each characterised by *F. lateralis* and, with respect to the first and last habitats, also *L. presbyteroides*, *A. elongata* and *T. pleurogramma*. Of these three habitats, *F. lateralis* and *L. presbyteroides* were most prevalent at C, while the same was true of *A. elongata* and *T. pleurogramma* at Q (Table 6.1.2.4b). Samples from the channel habitat M and, to a lesser extent, the other channel habitat L, also formed comparatively distinct groups that lay relatively close to each other on the ordination plot constructed from the spring 2005 data, but their level separation from samples representing other habitats was not as pronounced as in summer 2006 or 2007 (*cf* Fig. 6.1.2.2b and c, f). This was reflected by the fact that the R-statistics for pairwise comparisons involving either of these habitats were often less than 0.600 and, in some cases, were not significant. Furthermore, the ichthyofaunas of these two channel habitats were typified by a largely similar suite of species to those described for the above riverine and/or basin habitats. However, of all of the above habitats, *T. pleurogramma* was most prevalent at L, as was *F. lateralis*, with the exception of habitat B. Furthermore, *H. vittatus* and *A. elongata* were among the most abundant at habitat M, second only to habitats D and B, respectively (Table 6.1.2.4b). Lastly, the composition of the fish assemblages at several basin habitats did not differ significantly from each other in spring 2005, and particularly those involving either H or I (Table 6.1.2.3b).

During winter 2006, the most distinct habitats were E, M and Q, which was reflected by the fact that pairwise R-statistics involving any of these habitats often exceeded 0.600 (Table 6.1.2.3e). On the MDS plot constructed from the fish faunal data recorded in this season, most of the samples from E lay on the opposite side to those from M, while most of those from Q formed a relatively discrete group adjacent to E (Fig. 6.1.2.2e). SIMPER showed that the fish fauna at habitat E was characterised only by *A. elongata* and *P. olorum*, and the abundances of the former species were often greater at most of the basin habitats (Table 6.1.2.4e). Habitat M, on the other hand, was characterised by a considerably larger suite of species, namely *Am. elongata, F. lateralis, A. forsteri, S. argus* and *Sillaginodes burrus*, while the ichthyofauna at Q was typified by the atherinids *A. elongata, L. presybyteroides* and *A. mugiloides*, which were often recorded in higher numbers at channel habitats or other basin habitats (Table 6.1.2.4e). Unlike the above seasons, samples for the other riverine habitat (D) and, to lesser extent, those for the other channel habitat (L), formed relatively dispersed groups that intermingled considerably with samples from other habitat types. This was also reflected by the relatively low pairwise R-statistic values often recorded for comparisons involving either of these habitats (Table 6.1.2.3e). However, as for spring 2005, several pairs of basin habitats did not differ significantly from each other, and particularly those involving C, whose representative samples were highly dispersed on the MDS plot (Fig. 6.1.2.2e). However, of the basin habitats, the fish assemblages at I and J were comparatively distinct, as reflected by the comparatively tight groups of samples representing each of these habitats on the MDS plot shown in Fig. 6.1.2.2e, and the moderate to high R-statistic values for several of their pairwise comparisons (Table 6.1.2.3e). SIMPER demonstrated that the fish fauna at I in winter 2006 was best distinguished by its greater prevalence of *F. lateralis, Papillogobius punctatus*, *A. elongata* and *L. presbyteroides* than all, or almost all, habitats, while that at J was also commonly distinguished by greater numbers of the latter two species and *T. pleurogramma* (Table 6.1.2.4e).

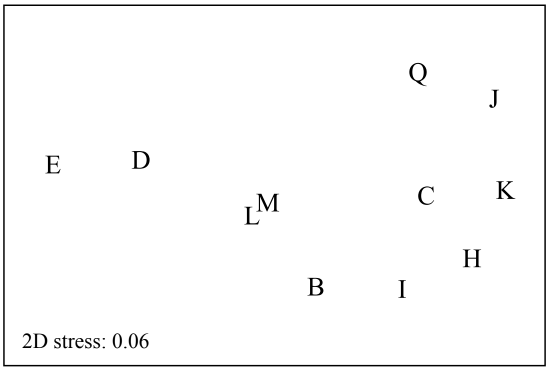
Relatively low overall differences in fish faunal composition among habitats were detected during both winter 2005 and autumn 2006. In both cases, this was partly due to the lack of significant differences between several pairs of basin habitats, and also between some pairs of basin *vs* riverine and/or channel habitats. Secondly, the extents of significant pairwise differences were generally lower than in other seasons (Table 6.1.2.3a and d, respectively). For example, the most distinct habitat types during winter 2005 were, as in other seasons, D, L and, to a lesser extent, Q and J. However, the largest R-statistic detected among pairwise comparisons involving one of these habitats was 0.744, compared to 0.997 in summer 2006, and many were less than 0.600. This was reflected on the MDS plot of the ichthyofaunal data recorded in winter 2005, in which some samples from D lay on the opposite side of the plot from all of those representing L, while the remainder were widely dispersed throughout (Fig. 6.1.2.2a). Furthermore, samples for the other channel habitat M, which formed a relatively tight and discrete group on MDS plots constructed from the data recorded in other seasons, intermingled extensively with those from most other habitats on that constructed from the winter 2005 data. The samples from habitats Q and J, which intermingled extensively with each other, formed a group that tended to lie to one side of the MDS plot, and which was generally equidistant from most of those representing D and L (Fig. 6.1.2.2a). SIMPER showed that the fish fauna at the riverine habitat D was characterised by *P. olorum* and *T. pleurogramma* and, while the first of these species was always more prevalent at D than any other habitat in this season, this was only occasionally the case with the latter species (Table 6.1.2.4a). Habitat L was also characterised by the latter of these species in addition to *F. lateralis*, which were both always more abundant at this habitat. The fish assemblages at habitat Q were typified by the atherinds *L. wallacei, A. elongata* and *A. mugiloides*, and also *F. lateralis* and *T. pleurogramma*. While the first two atherinid species and *T. pleurogramma* were commonly found in greater numbers at Q than other habitats, this was not the case for the remaining two species (Table 6.1.2.4a).

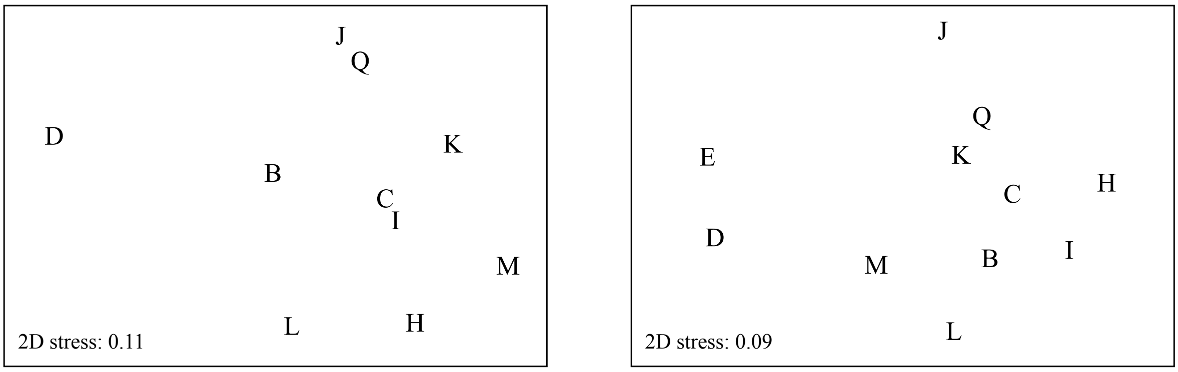
The most distinct habitats in autumn 2006 included the basin habitats Q and J and, to lesser extents, C and K (Table 6.1.2.3d). Thus, in contrast to most other seasons, the ichthyofaunas at habitats in the entrance channel and tidal portions of the rivers were not particularly divergent. Such findings were reflected by the samples from the above basin habitats forming relatively pronounced groups on the MDS ordination plot shown in Fig. 6.1.2.2d, whereas those for several of the riverine and channel habitats were more dispersed. *Leptatherina presbyteroides* and, to a lesser extent, *A. mugiloides*, consistently characterised the fish fauna at Q and distinguished it from other habitats in this season (Table 6.1.2.4d). The fish faunas at C were characterised by *F. lateralis* and *A. elongata*, both of which were always more abundant at this habitat than any other. Habitats K and J were both characterised by *T. pleurogramma*, *A. mugiloides* and *A. elongata*, and also by *C. pauciradiatus* in the case of the former habitat and *L. presbyteroides* in the case of the latter. The first of these species was more prevalent at J than K, while the reverse was true of the second species. Furthermore, *C. pauciradiatus* was always more abundant at habitat K than any other in this season, while this was frequently but not always the case with *L. presbyteroides* and *A. elongata* at habitat J (Table 6.1.2.4d).

6.1.2.4 Matching spatial patterns between the environmental and fish assemblage characteristics of habitats

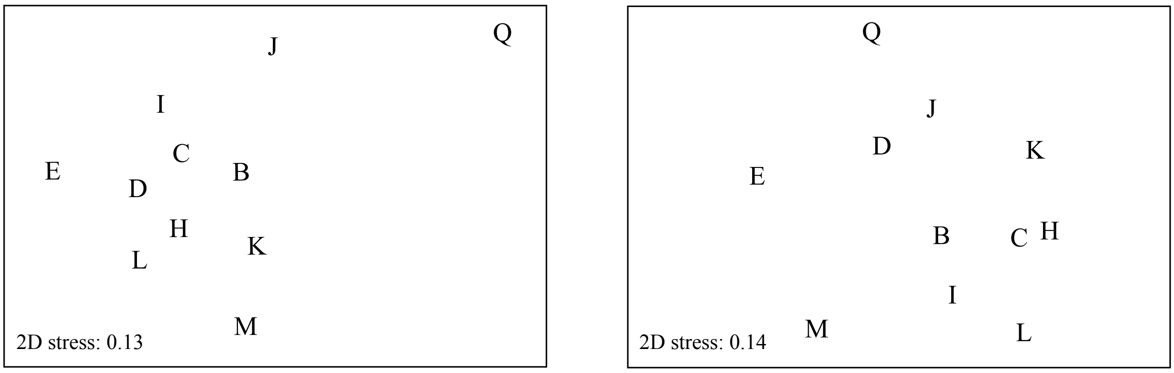
RELATE demonstrated that, in all sampling seasons, the spatial pattern among habitats, as defined by their enduring environmental characteristics, significantly matched that exhibited by the composition of their fish faunas (p=0.1-4.5%). The extent of that correlation was high during winter and spring 2005 (ρ=0.672 and 0.764, respectively), moderate in autumn and winter 2006 (ρ=0.410 and 0.484, respectively) and relatively low in summer 2006 and 2007 (ρ=0.320 and 0.250, respectively). These results are illustrated by the degree of similarity in the spatial distribution of samples among the MDS plots shown in Fig. 6.1.2.3, which were constructed from the averages at each habitat of their (a) enduring environmental characteristics or (b-g) fish faunal composition in a particular sampling season. Thus, whereas the arrangement of points representing the various habitats was similar between the plots constructed from the enduring environmental data and the fish assemblage data recorded in winter and particularly spring 2005 (*cf* Fig. 6.1.2.3a and b, c, respectively), the distribution of the points on those plots constructed from the summer 2006 and 2007 fish faunal data differed considerably from that of the enduring environmental data (*cf* Fig. 6.1.2.3a and d, g, respectively). In the case of summer 2006, this was mainly attributable to the large degree of dissimilarity between habitat Q, and to a lesser extent, J, and the remaining basin habitats, which resulted largely from the first of these habitats containing a particularly depauperate fish fauna. In summer 2007, the relatively poor agreement between the enduring environmental and fish matrices was largely due to the fish assemblages at the riverine habitats, and particularly at E, being relatively similar to those from the basins.

(a) Enduring environmental data

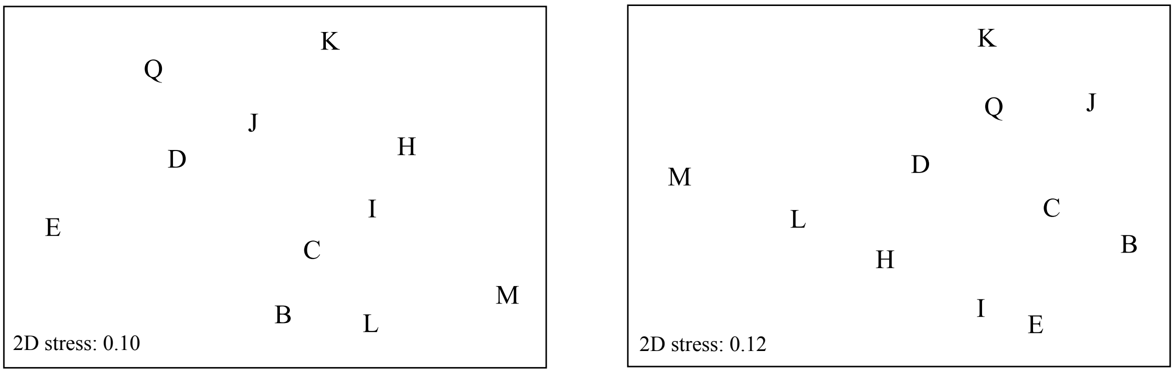



(b) Winter 2005; p=0.2%, ρ=0.672

(c) Spring 2005; p=0.1%, ρ=0.764


(d) Summer 2006; p=2.8%, ρ=0.320

(e) Autumn 2006; p=0.6%, ρ=0.410

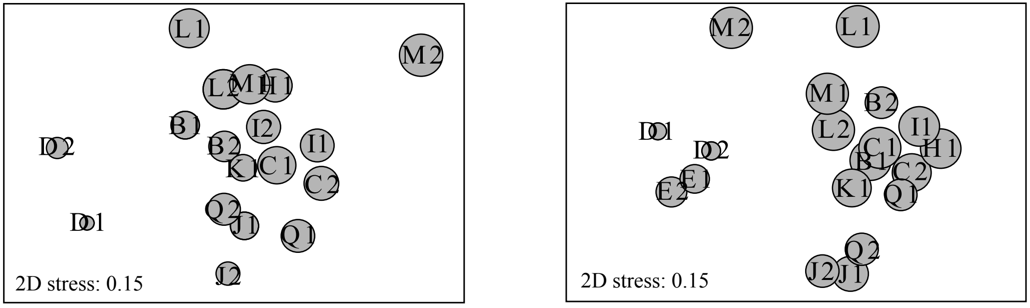

(f) Winter 2006; p=0.5%, ρ=0.484

(g) Summer 2007; p=4.5%, ρ=0.250

Figure 6.1.2.3: MDS ordination plots constructed from the averages at each habitat type in the Peel-Harvey Estuary of their (a) enduring environmental measurements and (b-g) fish faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the fish faunal data are also provided for each season.

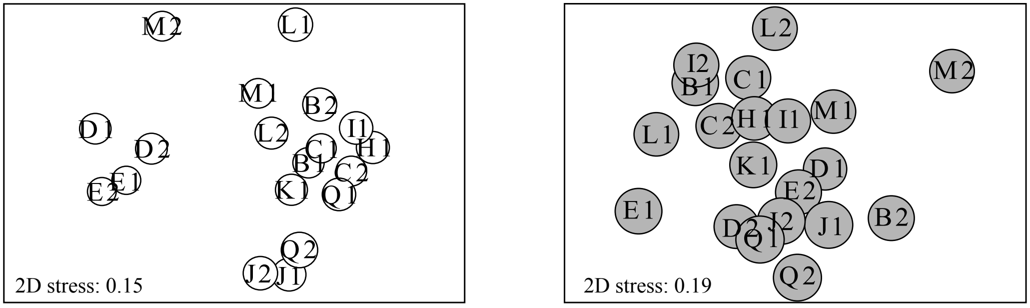
When each of the matrices constructed from the averages of the fish assemblage data recorded at each of the habitats in each individual season were matched with the complementary matrices constructed from the data for a suite of non-enduring water quality parameters (*i.e.* salinity, temperature and dissolved oxygen), significant results were obtained for only four of the six sampling occasions, *i.e.* all except summer 2006 and 2007 (p=0.7-4.5%). Furthermore, in those seasons for which significant results were obtained, the ρ value was low to moderate and always less than that obtained for the corresponding seasons when the enduring environmental and fish matrices were matched, *i.e.* ρ=0.513, 0.404, 0.273 and 0.438 for winter and spring 2005 and autumn and winter 2006, respectively. The BIOENV routine was then employed to determine whether the degree of correlation between the complementary fish and water quality matrices could be improved by employing only data for selected subsets of water quality variables, rather than their full suite. Note that these analyses were carried out using the averages of data collected at each representative site rather than habitat type, in order to maximise the number of samples in the reference (fish) matrices and thus minimise the likelihood of BIOENV finding a subset of water quality variables that provided a good match with those references by chance. For comparability, it should also be noted that the correlations obtained when RELATE was used to match the complementary fish and water quality matrices constructed from site averages were similar to those obtained above when the habitat averages were employed, except for winter 2005, *i.e.* ρ=0.407. BIOENV showed that, while significant results (p=1%) were obtained for all seasons except summer 2006, there were either no or relatively small improvements in the correlation value in all cases, *i.e.* ρ=0.563, 0.450, 0.344, 0.374 and 0.419 for winter and spring 2005 and autumn and winter 2006 and summer 2007, respectively. Data for salinity alone provided an improved match with the fish matrix during winter 2005 and summer 2007, while data for a combination of salinity and dissolved oxygen improved the results for spring 2005 and winter 2006. All water quality variables were selected during autumn 2006, and thus did not improve the correlation with the fish faunal matrix.

The relationships between the spatial patterns exhibited by the fish faunal composition and the magnitude of the water quality parameter(s) selected by BIOENV are illustrated, for each sampling occasion during which significant results were obtained, by the MDS and associated bubble plots shown in Fig. 6.1.2.4. During winter 2005, sites belonging to the riverine habitat D, which clearly had a distinctive fish faunal composition, also had notably lower salinities than those recorded at almost all of the remaining sites (Fig. 6.1.2.4a). One of the sites belonging to the channel habitat M (M2) also had a markedly distinct fish fauna, and had the highest average salinity recorded during that season. However, both the other site belonging to this habitat and



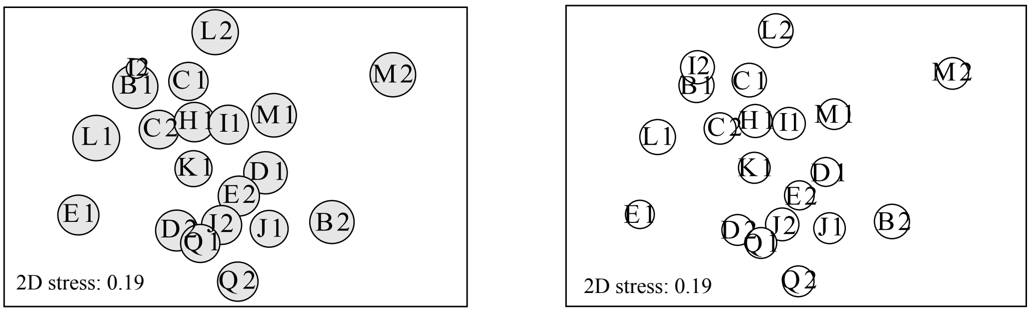
(a) Winter 2005; p=1%, ρ=0.563

(b) Spring 2005; p=1%, ρ=0.450



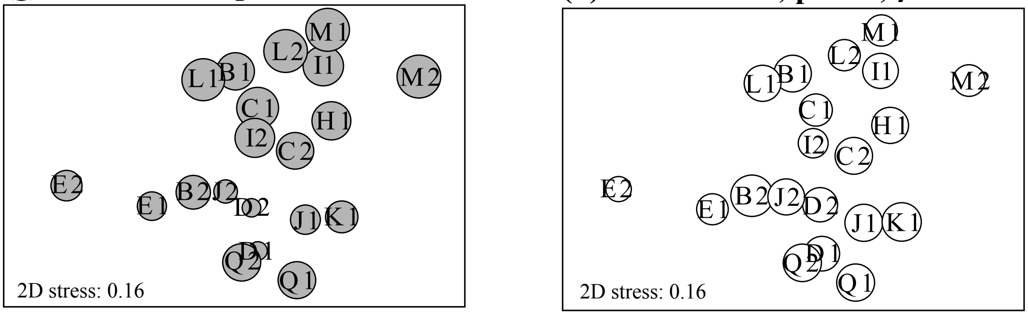
(c) Spring 2005; p=1%, ρ=0.450

(d) Autumn 2006; p=1%, ρ=0.344



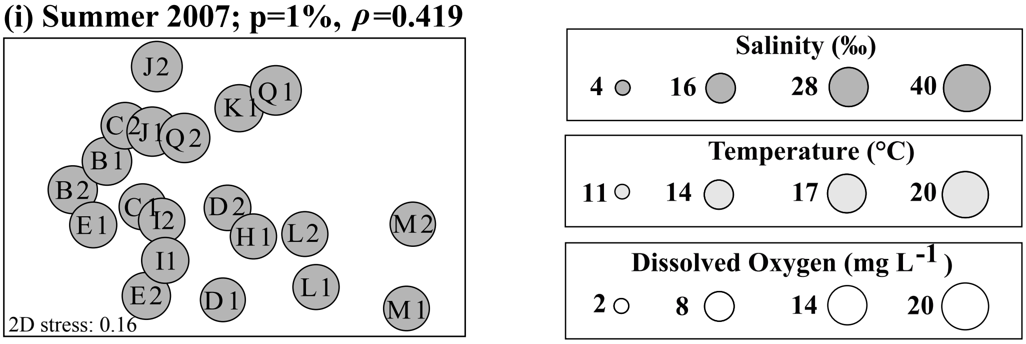
(e) Autumn 2006; p=1%, ρ=0.344

(f) Autumn 2006; p=1%, ρ=0.344



(g) Winter 2006; p=1%, ρ=0.374

(h) Winter 2006; p=1%, ρ=0.374



(i) Summer 2007; p=1%, ρ=0.419

Figure 6.1.2.4: MDS ordination plots derived from the average fish faunal composition recorded at each site in the Peel-Harvey Estuary in a particular sampling season. The magnitude of the water quality variables selected by the BIOENV routine when one of those matrices constructed from the above faunal data was matched with that constructed from the complementary water quality data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

those representing the other channel habitat (L) had comparable salinities to M2, yet their fish faunal compositions shared more similarities with those of particular basin sites, whose average salinity was markedly lower. Further evidence that salinity "explained" only a portion of the spatial variability in fish assemblage composition during winter 2005 was provided by sites representing habitat C, and particularly C1, whose ichthyofaunal compositions were similar to those of several other basin sites, yet their average salinity was noticeably higher (Fig. 6.1.2.4a).

During spring 2005, sites from the riverine habitats D and E had a similarly distinct fish fauna from the remaining sites and the lowest salinities. However, average salinities were far lower at sites from D (*ca* 6‰) than E (*ca* 16‰), and yet the composition of their fish faunas was relatively similar (Fig. 6.1.2.4b). Individual sites representing the channel habitats L and M also had a distinct fish faunal composition and, while they also had among the highest average salinities recorded in that season, those at several other sites were as just as high, yet their fish faunal compositions were clearly different. With respect to dissolved oxygen in this season, concentrations at the ichthyofaunally-distinct habitat E were the lowest, while some of the highest concentrations were recorded at sites representing the shallow habitats J and Q and L1, whose fish assemblages were also relatively distinct. However, high concentrations were also recorded at particular sites representing habitats B and I, and yet their fish faunal composition was not notably different from that at several other basin sites (Fig. 6.1.2.4c).

Differences in the magnitude of salinity clearly did not fully explain spatial differences in ichthyofaunal composition in autumn 2006, winter 2006 or summer 2007 (Fig. 6.1.2.4d, g and i, respectively). Thus, during both the first and last of these seasons, comparatively little difference in salinity was evident throughout the estuary, and yet there were obvious differences in ichthyofaunal composition (Fig. 6.1.2.4d and i, respectively). Moreover, during winter 2006, the ichthyofaunal composition of samples representing the riverine habitat D was similar to that at several other habitats, despite the mean salinities at D being far lower than those of most other habitats (Fig. 6.1.2.4g). Some parallels between dissolved oxygen concentration and fish faunal composition could be detected during both autumn and winter 2006. For example, in the first of these seasons, sites E1 and B2 had relatively distinct fish faunal compositions, which were also among the most dissimilar to each other, and also contained the lowest and close to the highest mean dissolved oxygen concentrations, respectively (Fig. 6.1.2.4f). However, site D1, which also contained a low dissolved oxygen concentration in that season, did not contain a similar fish assemblage composition to that of E1. Moreover, the dissolved oxygen concentration at site B1 was similar to that at B2, and yet their fish faunal compositions were markedly different (Fig. 6.1.2.4f). In winter 2006, the particularly distinct fish faunal composition at site E2 was associated with the lowest mean dissolved oxygen concentration recorded throughout the system. However, relatively low concentrations were also recorded at the other site representing this habitat in this season, yet it was faunistically-similar to site B2, which had the greatest average dissolved oxygen concentration recorded during this season (Fig. 6.1.2.4h). Relatively weak relationships were also found between the spatial patterns of fish faunal distribution and the magnitude of water temperature during autumn 2006. Thus, although the notably distinct fish assemblage composition at site M2 in the channel was associated with one of the largest mean water temperatures recorded throughout the estuary, high temperatures were also recorded at both sites from the other channel habitat L and B1, yet they contained markedly different ichthyofaunal compositions to that at M2 (Fig. 6.1.2.4e).

6.1.2.5 Composition of fish assemblages among seasons

One-way ANOSIM tests, carried out separately on the data recorded at each habitat, demonstrated that the composition of the fish assemblages differed significantly among sampling seasons in each case, *i.e.* p=0.1%. However, the extents of those seasonal differences were generally less than those detected among habitats, *i.e.* Global R=0.217-0.542 *vs* 0.341-0.715.

The greatest seasonal differences were evident at habitat H, followed by those at the riverine habitats D and E and the other basin habitats K and Q (Fig. 6.1.2.5). At the first of these habitats, samples from winter 2005, summer and autumn 2006 and summer 2007 formed tight and discrete groups on the MDS plot shown in Fig. 6.1.2.5e, while those for spring 2005 and winter 2006 were widely dispersed. Consequently, no significant differences in ichthyofaunal composition were detected between autumn and winter 2006, or between spring 2005 and winter 2005 or 2006. The greatest pairwise differences were between winter 2005 and summer 2006 and 2007 (*i.e.* R=0.938-1.000), whose samples essentially lay on opposite sides of the MDS plot (Fig. 6.1.2.5e), then between winter 2005 and autumn 2006 (*i.e.* R=0.750). SIMPER showed that the fauna during winter 2005 was distinguished from that in each of the above three seasons primarily by more consistent and abundant catches of *Am. elongata*. The faunas in winter 2005 were further distinguished from those in summer 2006 by a greater prevalence of *F. lateralis* in the former season and of *T. pleurogramma* and *P. punctatus* in the latter, while greater occurrences of *A. rueppellii* in summer 2007 were also important in distinguishing the ichthyofaunas in this season from those recorded in winter 2005.

The ichthyofaunal composition differed significantly between all pairs of seasons at habitats D and E, with the exception of autumn *vs* winter 2006 at the latter habitat, which was, however, only just not significant (p=5.6%). At both of these habitats, samples representing

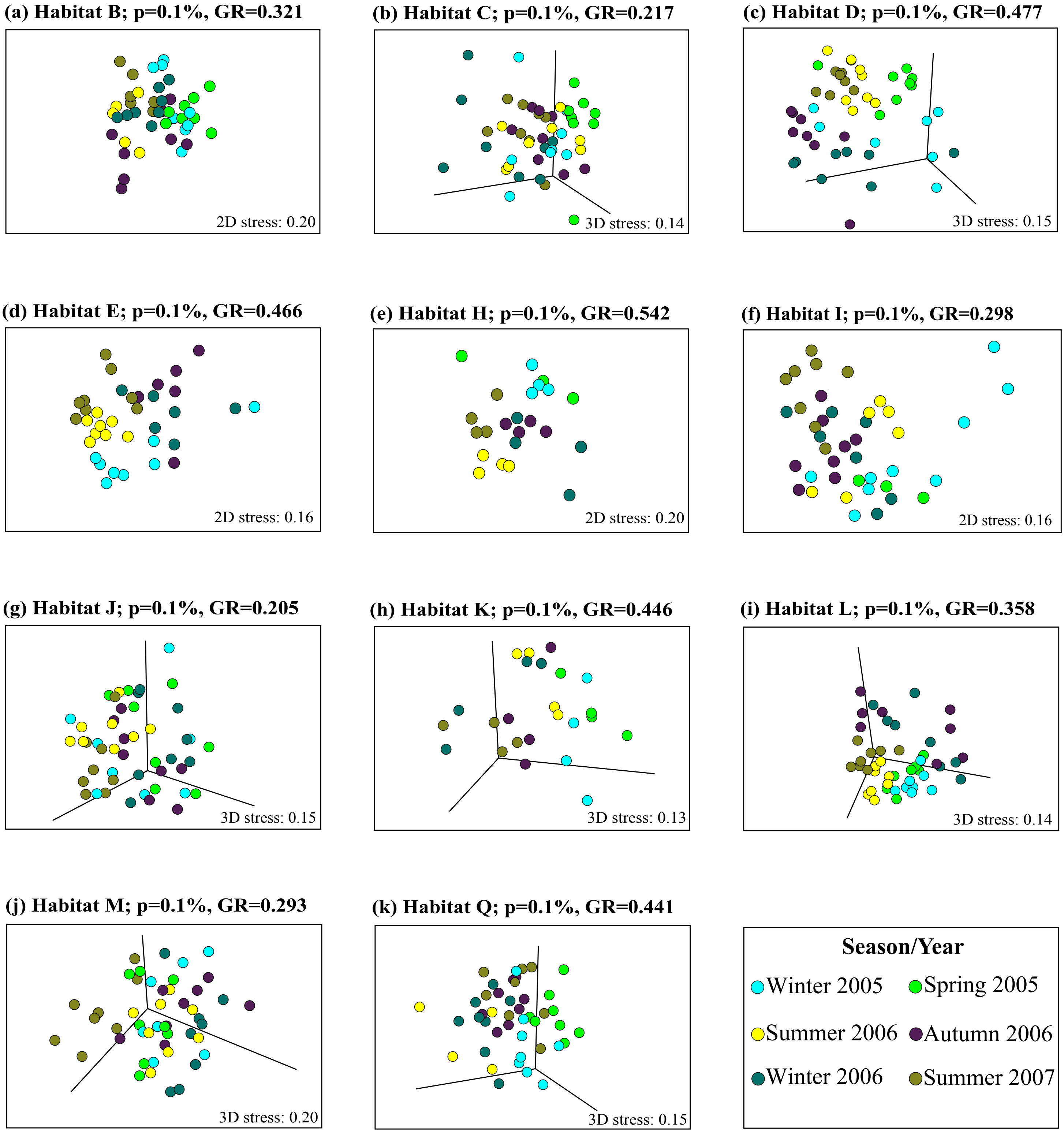


Figure 6.1.2.5: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample in each sampling season at habitat (a) B, (b) C, (c) D, (d) E, (e) H, (f) I, (g) J, (h) K, (i) L, (j) M and (k) Q in the Peel-Harvey Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

summer 2006 and 2007 and, in the case of D, also autumn 2006, formed relatively tight and discrete groups on the MDS plots shown in Fig. 6.1.2.5c and d, whereas those representing both winters were relatively dispersed. The greatest seasonal differences at D (*i.e.* R=0.602-0.715) were detected between autumn 2006 *vs* spring 2005 and summer 2006, which were due to the greater prevalence of *H. vittatus* and *P. olorum* in the second of these seasons and *A. elongata, T. pleurogramma, H. vittatus* and *Afurcagobius suppositus* in the latter, and also for spring 2005 *vs* winter 2006 and summer 2007, which were attributable mainly to more consistent and abundant catches of *H. vittatus, P. olorum* and/or *T. pleurogramma* during the first of these seasons. Seasonal differences at E were most pronounced for summer 2006 *vs* autumn and winter 2006 (R=0.710-0.727), which was mainly due to a far greater prevalence of *A. suppositus, P. olorum* and *A. elongata* during the first of these seasons.

The fish faunal composition at habitat K did not differ between several pairs of seasons, but relatively pronounced differences occurred between spring 2005, whose samples formed a comparatively tight group of samples on the MDS plot shown in Fig. 6.1.2.5h, and winter 2006, summer 2007 and autumn 2006, and also between summer 2007 and winter 2005 (R=0.635-0.729). The faunas in spring 2005 were characterised and distinguished from those in each of the above seasons mainly by more abundant and consistent catches of *F. lateralis, T. pleurogramma* and *L. presbyteroides*, while those in winter 2005 were distinguished from those in summer 2007 by greater catches of *Am. elongata, F. lateralis* and *T. pleurogramma* in the former season and *A. elongata* in the latter. The fish assemblage composition differed significantly between every pair of seasons at habitat Q in the southern Harvey Estuary, but was most pronounced for summer 2006 *vs* spring 2005 and summer 2007 (R=0.710-0.772), followed by those for winter 2005 *vs* summer and autumn 2006 and for winter 2006 *vs* spring 2005 (R=0.653-0.682). Samples from summer 2006, which formed a relatively dispersed group on the opposite side of the MDS plot from those collected in spring 2005 (Fig. 6.1.2.5k), were distinct because of their relatively low fish numbers, while those in spring 2005 were characterised by consistent catches of *L. presbyteroides, F. lateralis*, and *T. pleurogramma*, those in summer 2007 by a greater prevalence of *L. presbyteroides* and *A. elongata* and those in winter 2005 by greater catches of *L. wallacei, T. pleurogramma* and *A. elongata*. Samples collected in winter 2005 were mainly distinguished from those taken in autumn 2006 by more abundant catches of *L. presbyteroides* in the latter season, while those in winter 2006 were set apart from those in spring 2005 by notably greater catches of *F. lateralis, L. presbyteroides* and *T. pleurogramma* in the latter season.

Relatively moderate seasonal differences in ichthyofaunal composition were detected at habitats B and L in the Peel Inlet and entrance channel, respectively (Global R=0.321-0.358).

The most pronounced differences at the former habitat were between spring 2005 and both summers (R=0.664-0.699; Fig. 6.1.2.5a), which were due mainly to greater numbers of *F. lateralis* in the former season, *A. elongata* in both summers and *H. vittatus* and *C. pauciradiatus* in summer 2006 and 2007, respectively. Similarly, the greatest differences in fish composition at L occurred between winter 2005 and both summers, and also between summer 2006 and winter 2006 (R=0.571-0.656; Fig. 6.1.2.5i). Several species were more prevalent in both summers than in winter 2005, namely *P. olorum, Amoya bifrenatus, L. presbyteroides, A. elongata* and *A. rueppellii*, while the opposite was true for *F. lateralis* and *S. argus*. *Hyperlophus vittatus* and *T. pleurogramma* were also recorded in considerably greater numbers in summer 2006. Each of the species listed above as more prevalent in summer 2006 than winter 2005 were also found in greater numbers in that former season than winter 2006, except for *A. rueppellii.* Moreover, *F. lateralis* was more prevalent in summer 2006 than in the winter of that year.

The extents of seasonal differences in fish assemblage composition at the remaining habitats was relatively low, and particularly in the case of the basin habitats J, C and I and the channel habitat M (Global R=0.205-0.298). The greatest seasonal differences occurred between summer 2007 and spring 2005 at habitats C and I, and between the first of these seasons and winter 2006 at habitats J and M. Such results are partly reflected by the fact that, on the MDS plots shown in Fig. 6.1.2.5b, f, g and j, respectively, the samples representing summer 2007 formed a relatively tight group. Greater catches of both *L. presbyteroides* and *F. lateralis* in spring 2005 were mostly responsible for such seasonal differences at habitat C, while a greater prevalence of *F. lateralis* and *Am. elongata* in spring 2005 and *A. elongata* and *A. rueppellii* in summer 2007 mainly distinguished these ichthyofaunas at I. Greater abundances of *A. elongata* and *T. pleurogramma* in winter 2006 and *C. pauciradiatus* and *A. mugiloides* in summer 2007 were primarily responsible for distinguishing the faunas recorded in these seasons at habitat J, while greater and more consistent catches of *S. argus, L. presbyteroides, G. marmoratus, Am. elongata* and *A. rueppellii* were caught during summer 2007 than winter 2006 at habitat M.

6.1.3 Hyperbenthic faunal assemblages

6.1.3.1 Species mean density at each habitat type

Sampling of the hyperbenthic faunal assemblages at six habitat types throughout the Peel-Harvey Estuary in winter 2005 and summer 2006 yielded 1565 individuals, after the number of individuals in each sample had been adjusted to that in 1 m^3 and summed (Table 6.1.3.1). This fauna represented 72 species and eight phyla, namely Annelida,

Table 6.1.3.1: Mean density (M), standard deviation (SD), percentage contribution (%) and rank by density (R) of each hyperbenthic faunal species recorded at each habitat type in the Peel-Harvey Estuary during winter 2005 and summer 2006. Abundant species (*i.e.* those that contribute >5% to the overall mean density) are highlighted in grey. Each taxon has been assigned to its respective phyla (P) and class (C) (*i.e.* A-Arthropoda, An-Annelida, Ch-Chordata, Cn-Cnidaria, M-Mollusca, N-Nematoda, Pl-Platyhelminthes, S-Sipuncula, Ad-Adenophorea, Az- Anthozoa, B-Bivalvia, C-Crustacea, Cl-Chelicerata, G-Gastropoda, O-Osteichthyes, P-Polychaeta, Sp-Sipunculan, T-Turbellaria, U-Uniramia). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of hyperbenthic fauna in each sample had been adjusted to that in 1 m^3 and summed) are given for each habitat type.

		Habitat type B				**Habitat type D**				**Habitat type H**			
Species name	**P/C**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
calanoid sp.4	A/C	25.35	81.29	49.34	1	992.21	3525.18	75.52	1	0.77	1.56	0.73	13
harpacticoid sp.7	A/C	10.48	20.47	20.40	2	29.05	94.39	2.21	6	11.45	15.52	10.86	2
ostracod sp.1	A/C	7.70	18.48	14.99	3	0.32	1.36	0.02	29	2.78	4.3	2.64	7
harpacticoid sp.1	A/C	4.11	6.09	8.00	4	60.00	213.06	4.57	2	5.89	7.53	5.58	5
cyclopoid sp.3	A/C	1.68	3.17	3.27	5	1.99	6.04	0.15	20	0.63	1.98	0.60	16
Hyalid sp.2	A/C	0.37	0.50	0.72	6	15.48	47.06	1.18	8	50.93	142.37	48.28	1
nematode spp.	N/Ad	0.35	0.78	0.68	7	44.36	178.22	3.38	3	0.01	0.03	0.01	33
Gastrosaccus sorrentoensis	A/C	0.24	0.74	0.47	8	35.89	90.21	2.73	5	1.57	2.15	1.49	9
Austrocochlea rudis	M/G	0.16	0.40	0.31	9								
calanoid sp.2	A/C	0.16	0.25	0.31	9	1.22	5.44	0.09	26	0.55	1.02	0.52	17
Favartia planilirata	M/G	0.13	0.51	0.25	11								
syllid sp.5	An/P	0.13	0.51	0.25	11								
Palaemonetes australis	A/C	0.10	0.30	0.19	13	3.70	11.43	0.28	14	4.57	7.56	4.33	6
Tanypodin sp.	A/U	0.09	0.19	0.18	14	3.50	15.20	0.27	15	0.47	1.49	0.45	20
Ischyrocerid sp.2	A/C	0.07	0.28	0.14	15	13.56	39.87	1.03	9	10.05	20.37	9.53	3
Mullid sp.	Ch/O	0.06	0.19	0.12	16								
Polyclad sp.1	Pl/T	0.05	0.19	0.10	17								
calanoid sp.12	A/C	0.04	0.11	0.08	18								
Halacarid sp.2	A/Cl	0.04	0.17	0.08	18	0.01	0.04	0.01	31				
ostracod sp.3	A/C	0.02	0.04	0.04	20	0.62	2.52	0.05	27	0.70	1.38	0.66	15
Actinia tenebrosa	Cn/Az	0.01	0.04	0.02	21					0.23	0.65	0.22	21
calanoid sp.5	A/C	0.01	0.04	0.02	21								
cyclopoid sp.1	A/C	0.01	0.04	0.02	21	0.72	2.97	0.05	27	0.54	1.48	0.51	18
Gobiid sp.3	Ch/O	0.01	0.03	0.02	21	1.51	5.43	0.11	24				
Torquigener pleurogramma	Ch/O	0.01	0.03	0.02	21								

Species name	P/C	Habitat type B M	SD	%	R	Habitat type D M	SD	%	R	Habitat type H M	SD	%	R
Capitellid sp.	An/P					44.21	121.27	3.37	4				
Serpulid sp.	An/P					22.42	55.88	1.71	7				
Blenniid sp.	Ch/O					11.91	53.28	0.91	10				
Ischyrocerid sp.1	A/C					6.00	26.80	0.46	11	1.52	2.95	1.44	10
Corophium minor	A/C					4.44	19.79	0.34	12	0.16	0.47	0.15	23
Musculista senhousia	M/B					3.79	15.16	0.29	13				
syllid sp.1	An/P					2.94	9.17	0.22	16	0.05	0.17	0.05	31
Phyllodoce sp.	An/P					2.43	10.85	0.18	17				
Arthritica semen	M/B					2.24	10.00	0.17	18	0.16	0.50	0.15	23
Australonereis elhersii	An/P					2.22	9.90	0.17	18				
Ceratonereis aquisetis	An/P					2.01	8.93	0.15	20				
Aorid sp.	A/C					1.78	7.60	0.14	22	0.15	0.47	0.14	27
Apogon sp.	Ch/O					1.70	7.61	0.13	23				
Leucothoid sp.1	A/C					1.33	5.97	0.10	25	0.49	1.48	0.46	19
Ampithoid sp.	A/C					0.08	0.34	0.01	30				
flabelliferan sp.2	A/C					0.05	0.24	0.01	31				
Spirorbid sp.	An/P					0.05	0.24	0.01	31	1.04	1.80	0.99	11
Hyalid sp.1	A/C					0.01	0.04	0.01	31	0.09	0.22	0.09	28
Leucothoid sp.2	A/C					0.01	0.05	0.01	31				
caprellid sp.1	A/C					0.01	0.04	0.01	31	2.15	5.89	2.04	8
Oribatid sp.	A/Cl					0.01	0.03	0.01	31				
Tanais dulongii	A/C									6.04	16.83	5.73	4
flabelliferan sp.1	A/C									1.01	2.48	0.96	12
Gynodiastylid sp.	A/C									0.77	2.12	0.73	13
Hyperlophus vittatus	Ch/O									0.21	0.66	0.20	22
Gymnapistes marmoratus	Ch/O									0.16	0.50	0.15	23
Nassarius nigellus	M/G									0.16	0.50	0.15	23
Saldid sp.	A/U									0.07	0.21	0.07	29
Culicid sp.	A/U									0.07	0.21	0.07	29
Favonigobius lateralis	Ch/O									0.04	0.11	0.04	32
Number of species			**25**				**37**				**33**		
Total mean density			**51**				**1 314**				**106**		
Number of samples			**15**				**20**				**10**		
Total number of hyperbenthos			**771**				**26 276**				**1 055**		

Species name	P/C	Habitat type K				Habitat type L				Habitat type Q			
		M	SD	%	R	M	SD	%	R	M	SD	%	R
calanoid sp.4	A/C	1.25	2.05	2.05	7	0.14	0.21	0.60	22	2.36	1.36	23.34	1
harpacticoid sp.7	A/C	3.61	4.26	5.91	5	3.11	6.86	13.36	3	0.34	0.86	3.36	6
ostracod sp.1	A/C	6.87	9.77	11.25	3	2.09	6.64	8.98	4	2.06	5.29	20.38	2
harpacticoid sp.1	A/C	3.64	4.55	5.96	4	3.92	8.38	16.85	2	0.28	0.39	2.77	8
cyclopoid sp.3	A/C					0.39	1.21	1.68	12				
Hyalid sp.2	A/C	12.89	29.63	21.11	2	0.79	2.34	3.39	8	1.51	2.69	14.94	3
nematode spp.	N/Ad	0.03	0.09	0.05	36	1.34	3.72	5.76	5	1.26	2.72	12.46	4
Gastrosaccus sorrentoensis	A/C	0.41	0.58	0.67	14	0.55	1.46	2.36	10	1.07	3.15	10.58	5
Austrocochlea rudis	M/G												
calanoid sp.2	A/C	0.17	0.37	0.28	16	0.23	0.36	0.99	17	0.31	0.65	3.07	7
Favartia planilirata	M/G												
syllid sp.5	An/P												
Palaemonetes australis	A/C	0.88	2.55	1.44	10	5.10	22.25	21.92	1				
Tanypodin sp.	A/U	0.03	0.10	0.05	36	0.01	0.03	0.04	33	0.03	0.11	0.30	15
Ischyrocerid sp.2	A/C	22.48	68.23	36.81	1	0.68	2.59	2.92	9	0.23	0.73	2.27	10
Mullid sp.	Ch/O	0.25	0.52	0.41	15								
Polyclad sp.1	P/T												
calanoid sp.12	A/C					0.05	0.17	0.21	24				
Halacarid sp.2	A/Cl	0.15	0.28	0.25	18					0.02	0.05	0.20	17
ostracod sp.3	A/C	3.00	5.53	4.91	6	0.03	0.08	0.13	28	0.09	0.11	0.89	12
Actinia tenebrosa	Cn/Az	0.04	0.13	0.07	31								
calanoid sp.5	A/C					0.01	0.02	0.04	33				
cyclopoid sp.1	A/C	0.05	0.15	0.08	27	0.07	0.20	0.30	23				
Gobiid sp.3	Ch/O	0.08	0.26	0.13	22								
Torquigener pleurogramma	Ch/O												
Capitellid sp.	An/P	0.04	0.14	0.07	31	0.19	0.64	0.82	19	0.04	0.11	0.40	13
Serpulid sp.	An/P					0.90	2.25	3.87	7	0.01	0.02	0.10	19
Blenniid sp.	Ch/O												
Ischyrocerid sp.1	A/C	0.65	1.29	1.06	13	0.16	0.58	0.69	21	0.03	0.10	0.30	15
Corophium minor	A/C	0.91	2.19	1.49	9	0.01	0.04	0.04	33	0.27	0.85	2.67	9
Musculista senhousia	M/B												

Species name	P/C	Habitat type K				Habitat type L				Habitat type Q			
		M	SD	%	R	M	SD	%	R	M	SD	%	R
syllid sp.1	An/P	0.01	0.04	0.02	40	0.05	0.11	0.21	24				
Phyllodoce sp.	An/P					0.01	0.03	0.04	33				
Arthritica semen	M/B	0.16	0.51	0.26	17	1.02	2.64	4.38	6	0.14	0.42	1.38	11
Australonereis elhersii	An/P	0.07	0.16	0.11	23					0.04	0.11	0.40	13
Ceratonereis aquisetis	An/P	0.04	0.12	0.07	31	0.03	0.15	0.13	28				
Aorid sp.	A/C	0.10	0.31	0.16	21	0.01	0.05	0.04	33				
Apogon sp.	Ch/O					0.01	0.06	0.04	33				
Leucothoid sp.1	A/C	0.66	1.60	1.08	12								
Ampithoid sp.	A/C	0.75	1.95	1.23	11	0.01	0.03	0.04	33	0.02	0.07	0.20	17
flabelliferan sp.2	A/C												
Spirorbid sp.	An/P					0.31	0.94	1.33	15				
Hyalid sp.1	A/C	0.05	0.12	0.08	27								
Leucothoid sp.2	A/C												
caprellid sp.1	A/C	0.03	0.10	0.05	36	0.22	0.64	0.95	18				
Oribatid sp.	A/Cl	0.01	0.04	0.02	40								
Tanais dulongii	A/C	1.13	1.60	1.85	8	0.18	0.61	0.77	20				
flabelliferan sp.1	A/C												
Gynodiastylid sp.	A/C	0.07	0.15	0.11	23	0.38	1.23	1.63	13				
Hyperlophus vittatus	Ch/O												
Gymnapistes marmoratus	Ch/O												
Nassarius nigellus	M/G	0.04	0.13	0.07	31	0.36	1.05	1.55	14				
Saldid sp.	A/U												
Culicid sp.	A/U	0.12	0.39	0.20	19								
Favonigobius lateralis	Ch/O												
Halacarid sp.1	A/Cl	0.11	0.23	0.18	20								
Anthurid sp.	A/C	0.06	0.20	0.10	25								
Sipunculun sp.	S/Sp	0.06	0.20	0.10	25								
calanoid sp.1	A/C	0.05	0.15	0.08	27								
calanoid sp.3	A/C	0.05	0.16	0.08	27	0.03	0.13	0.13	28				
Portunus pelagicus	A/C	0.04	0.13	0.07	31								
Mysidellinid sp.	A/C	0.03	0.10	0.05	36	0.04	0.19	0.17	27				

Species name	P/C	Habitat type K				Habitat type L				Habitat type Q			
		M	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**	**M**	**SD**	**%**	**R**
Nassarius pauperatus	M/G					0.41	1.82	1.76	11				
Dentimitrella lincolnensis	M/G					0.30	1.36	1.29	16				
harpacticoid sp.8	A/C					0.05	0.16	0.21	24				
Gobiid sp.2	Ch/O					0.03	0.13	0.13	28				
Littorinid sp.1	M/G					0.03	0.10	0.13	28				
syllid sp.4	An/P					0.01	0.05	0.04	33				
Urocampus sp.	Ch/O					0.01	0.06	0.04	33				
Number of species			**41**				**41**				**19**		
Total mean density			**61**				**23**				**10**		
Number of samples			**10**				**20**				**10**		
Total number of hyperbenthos			**611**				**466**				**101**		

Arthropoda, Chordata, Cnidaria, Mollusca, Nematoda, Platyhelminthes and Sipuncula. The Crustacea was by far the most speciose class, containing 32 species, followed by the Polychaeta and Osteichthyes, which each contained eight species (Table 6.1.3.1).

The greatest number of hyperbenthic species was recorded at habitats K and L (41), in the middle reaches of the Harvey Estuary and the natural entrance channel, respectively, followed by that at habitat D in the tidal portion of the Murray River (37). The least number of species was found at habitat Q in the southern reaches of the Harvey Estuary (19), followed by that at B on the northern shore of the Peel Inlet (25). By far the greatest overall mean density of hyperbenthic fauna was recorded at habitat D (1314 individuals m^{-3}), which was an order of magnitude higher than the next greatest mean density of 106 individuals m^{-3} at habitat H. The overall mean density of hyperbenthos was lowest at habitat Q, at just 10 individuals m^{-3} (Table 6.1.3.1).

The species that were abundant, *i.e.* those that contributed ≥5% to the total mean density, varied considerably among habitat types. For example, the only species that was abundant at the upper estuary habitat D was the copepod calanoid sp.4, which comprised nearly 76% of all individuals and occurred in far greater densities than at any other habitat. Indeed, the mean density of this species at D was nearly 40 times greater than at habitat B, at which it was the next most abundant (Table 6.1.3.1). Considerable differences were also evident among the species that dominated each of the habitats located throughout the basins of the estuary, *i.e.* B, H, K and Q. Thus, whereas calanoid sp.4 was the top-ranking species and comprised *ca* 49% of the total number of individuals recorded at B, the only other basin habitat at which this species was abundant was Q, at which it also ranked first but represented only *ca* 23% of the total fauna. Harpacticoid spp. 7 and 1 and ostracod sp.1 were also abundant at B, accounting for 8-21% of the overall hyperbenthos, and at least one of these species was abundant at habitats H, K and Q. Secondly, while the assemblages at habitats H and K were both dominated by the amphipods Hyalid sp.2 and Ischyrocerid sp.2, which ranked in the top three in both cases, the former species comprised over 48% of the hyperbenthos at habitat H but less than half that at K, while the opposite was true for the latter species. The tanaid *Tanais dulongii* was also abundant at H, but was only recorded at one other basin habitat (*i.e.* K) and even then, in lower numbers. Thirdly, while Hyalid sp.2, nematode spp. and the mysid *Gastrosaccus sorrentoensis* were abundant at Q, the latter two species were found in only low numbers at each of the other basin habitats (Table 6.1.3.1). Lastly, with the exception of Q, each basin habitat contained three to four species that were not recorded at any other habitat type. The hyperbenthic assemblages at the channel habitat L were dominated by the decapod *Palaemonetes australis* (*ca* 22%), which was either not abundant or not present at the other habitats. Harpacticoid spp. 1 and 7 (13-17%) and ostracod sp.1 and nematode spp. (5-9%) were also abundant at this habitat (Table 6.1.3.1). Seven other hyperbenthic species, which mainly belonged to the phyla Mollusca, *e.g. Nassarius pauperatus, Dentimitrella lincolnensis* and Littorinid sp.1, were recorded exclusively at habitat L (Table 6.1.3.1).

6.1.3.2 Spatial and temporal differences in mean number of species, density and taxonomic diversity

Initial three-way PERMANOVA tests of the replicate hyperbenthic data recorded at each site representing each habitat type in each season were employed to ascertain whether spatial differences in the number of species, overall density and taxonomic diversity were most appropriately analysed at the site or broader habitat type level. As none of these tests detected a significant site or site x season effect, the data for each of these dependent variables were then subjected to a habitat x season PERMANOVA to better elucidate their spatial and temporal differences. These tests showed that the number of species differed significantly among all terms in the model, whilst density differed significantly among habitats and the habitat x season interaction, and taxonomic distinctness did not exhibit any significant differences (Table 6.1.3.2). The components of variation, and thus relative importance, was much greater for the interaction term than for habitat and/or season for both of the first two dependent variables, and approximately equal for both main effects in the case of number of species (Table 6.1.3.2).

The relatively large habitat x season interaction detected for the mean number of species was mainly attributable to the fact that the trends in this dependent variable among habitats during summer were essentially opposite to those in winter (Fig. 6.1.3.1a). Thus, in summer 2006, the least number of species were found at habitats B and D and the greatest by far at habitat H (*ca* 5 *vs* 17 species), whereas in winter 2005, the greatest number of species were recorded at L followed closely by B and D (*ca* 9-11 species), while the lowest were found at habitats Q and H (*ca* 6 species; Fig. 6.1.3.1a).

The trends in the mean density of hyperbenthic fauna among habitats were also largely opposing in summer and winter, combined with large differences in the level of variability among habitats between the two seasons (Fig. 6.1.3.1b). Thus, in summer 2006, the mean densities were lowest at habitat D and those at H were significantly greater than at all other habitats (*ca* 21 and 109 individuals m^{-3}, respectively), while, in winter 2005, the greatest densities by far were found at habitat D (*ca* 1150 individuals m^{-3}), while the least were recorded at habitats L and Q, followed by that at H (*ca* 5-22 individuals m^{-3}; Fig. 6.1.3.1b).

Table 6.1.3.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on the number of species, density and quantitative taxonomic distinctness of the hyperbenthic faunal assemblages recorded throughout the Peel-Harvey Estuary during winter 2005 and summer 2006. df = degrees of freedom. Significant results are highlighted in bold.

		Number of Species				**Density**				**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main effects													
Habitat	5	**1178.60**	**2.12**	**6.83**	**0.035**	**1552.50**	**3.29**	**8.99**	**0.003**	218.28	0.71	-2.56	0.644
Season	1	**2169.40**	**3.91**	**6.96**	**0.025**	541.56	1.15	1.45	0.296	1043.60	3.41	4.70	0.071
Two-way Interaction													
Habitat * Season	4	**1716.90**	**3.09**	**12.74**	**0.005**	**2095.60**	**4.44**	**15.06**	**0.001**	277.02	0.91	-2.01	0.463
Residual	74	554.86		23.56		471.79		21.72		306.03		17.49	

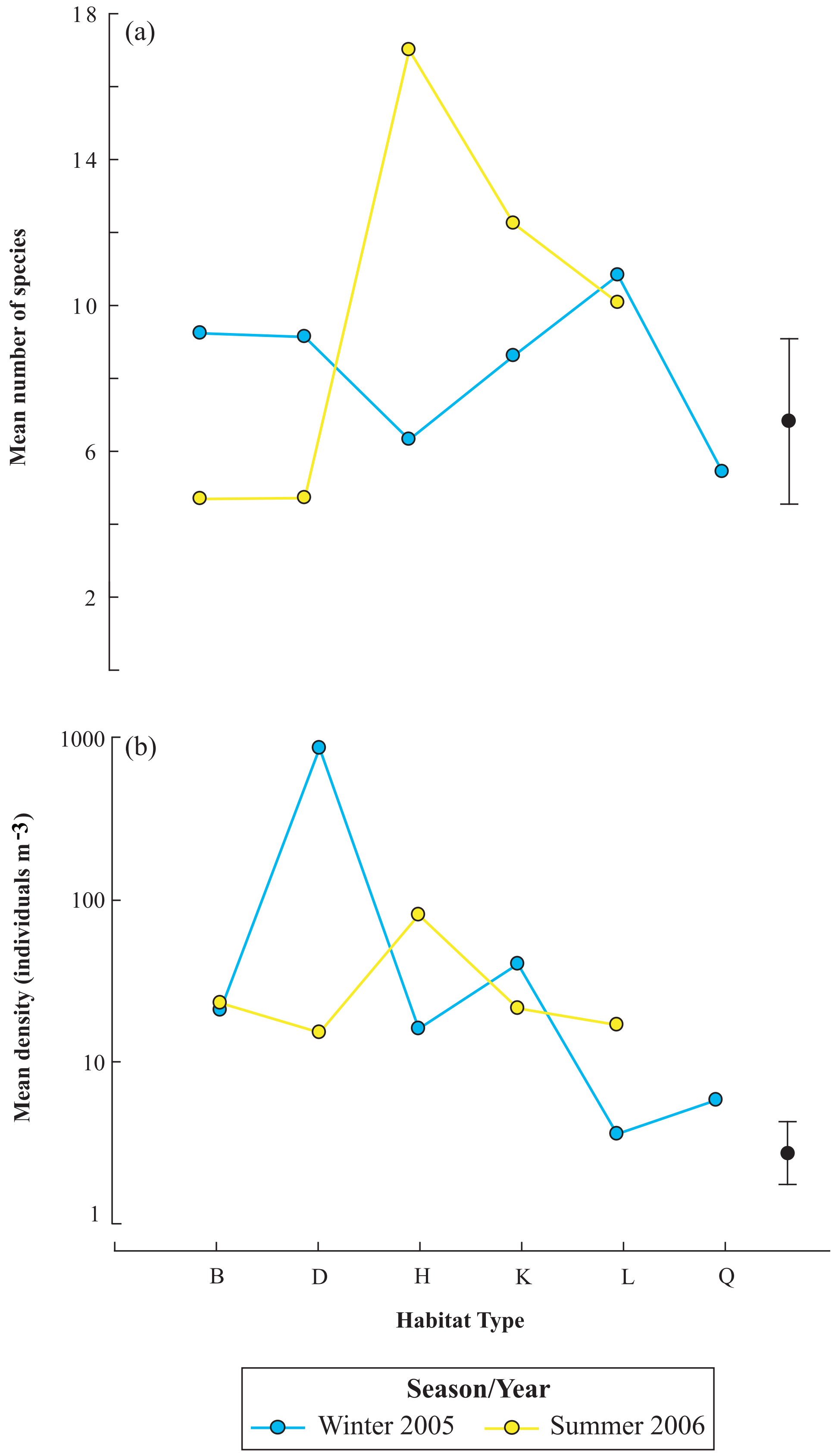


Figure 6.1.3.1: Mean (a) number of species and (b) density of the hyperbenthic faunal assemblages recorded at each habitat type in the Peel-Harvey Estuary during winter 2005 and summer 2006. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

6.1.3.3 Composition of hyperbenthic faunal assemblages among habitat types

A preliminary three-way PERMANOVA test was used to ascertain whether habitat types or their representative sites were most appropriate for examining spatial differences in the hyperbenthic assemblage data recorded during winter 2005 and summer 2006. As no significant results were detected for any term in the model, the replicate species abundance data were then subjected to a habitat x season PERMANOVA to ascertain whether there were any spatio-temporal differences in hyperbenthic composition after the nested site term had been removed. This test detected significant results for both main effects and the interaction term (p=0.001). One-way ANOSIM tests for habitat type, which were subsequently carried out for the hyperbenthic faunal data collected in each individual season to more thoroughly investigate the extent and nature of those spatial differences, showed that, while hyperbenthic composition differed significantly among habitats in both winter 2005 and summer 2006 (p=0.1%), the overall extents of those differences were relatively low, *i.e.* Global R-statistic=0.288 and 0.271, respectively (Table 6.1.3.3). This was also illustrated by the MDS ordination plots constructed from the hyperbenthic assemblage data recorded in each season, which showed that groups of samples representing most habitat types were not well differentiated (Fig. 6.1.3.2). Several pairs of habitats did not differ significantly from each other in each season, namely H *vs* D, K and L in winter 2005 and K *vs* H and L and B *vs* D and L in summer 2006 (Table 6.1.3.3).

During winter, the greatest differences in hyperbenthic composition occurred between habitat B on the northern shore of Peel Inlet and habitat K in the middle reaches of the Harvey Estuary (R=0.538). However, relatively large differences also occurred between the assemblages at habitat Q in the southern Harvey Estuary and K, and between those at the channel habitat L and K and D (R=0.414-0.491; Table 6.1.3.3a). The least significant differences were detected for Q *vs* B and L (R=0.188-0.233). These trends were also reflected by the distribution of samples representing each habitat on the MDS plot constructed from the faunal composition data recorded in this season (Fig. 6.1.3.2a). Thus, most of the samples from K were largely discrete from those groups representing B, L and Q, the latter three of which intermingled extensively. Samples from habitat D were the most dispersed, but the majority tended to lie to one side of the plot, and opposite from most of those for Q and L (Fig. 6.1.3.2a).

Despite the relatively small differences in faunal composition among habitats during winter, one-way SIMPER analyses showed that the assemblages at several habitats were exclusively typified by certain hyperbenthic species (Table 6.1.3.4a). Thus, the assemblage at habitat B was the only one to be typified and regularly distinguished by Tanypodin sp. and ostracod sp.1 and, with the exception of habitat Q, also by Hyalid sp.2. The relatively large

Table 6.1.3.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the hyperbenthic faunal composition among habitat types in the Peel-Harvey Estuary during (a) winter 2005 and (b) summer 2006. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2005; p=0.1%, Global R=0.288

	B	**D**	**H**	**K**	**L**
D	0.345				
H	0.282	0.153			
K	0.538	0.370	0.060		
L	0.221	0.414	0.116	0.415	
Q	0.188	0.376	0.319	0.491	0.233

(b) Summer 2006; p=0.1%, Global R=0.271

	B	**D**	**H**	**K**
D	0.169			
H	0.732	0.614		
K	0.380	0.349	0.116	
L	0.011	0.217	0.303	0.161

Table 6.1.3.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the hyperbenthic faunal assemblages at each habitat in the Peel-Harvey Estuary during (a) winter 2005 and (b) summer 2006, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

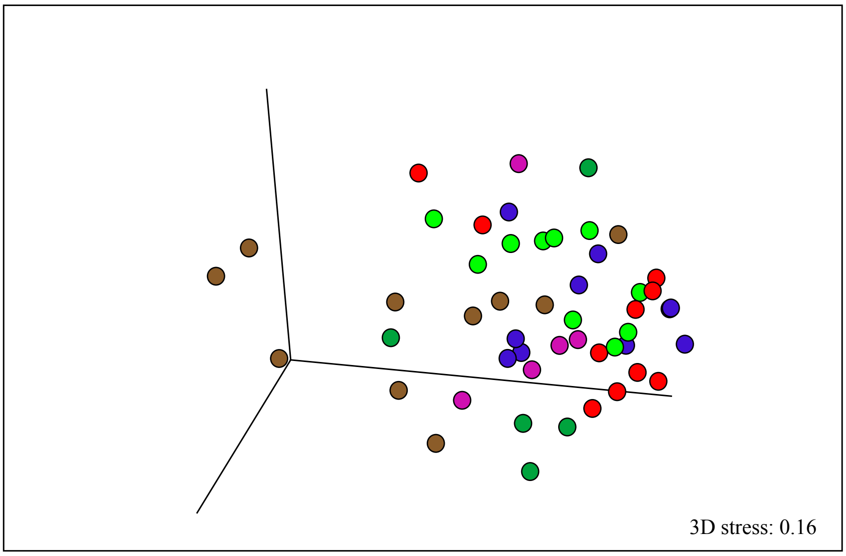
(a) Winter 2005

	B	D	H	K	L	Q
B	harpacticoid sp.1 calanoid sp.2 calanoid sp.4 harpacticoid sp.7 Tanypodin sp. ostracod sp.1 Hyalid sp.2					
D	Capitellid sp.^{D} calanoid sp.4^{D} Gobiid sp.3^{D} harpacticoid sp.1^{D} calanoid sp.2^{B} harpacticoid sp.7^{D} ostracod sp.1^{B} Hyalid sp.2^{B}	Capitellid sp. harpacticoid sp.1 calanoid sp.4 harpacticoid sp.7 nematode spp. *M. senhousia* Serpulid sp. Gobiid sp.3				
H	ostracod sp.3^{H} harpacticoid sp.7^{H} harpacticoid sp.1^{H} calanoid sp.2^{H} ostracod sp.1^{B} Tanypodin sp.^{B} *G. sorrentoensis*^{H} Hyalid sp.2^{B}		harpacticoid sp.1 ostracod sp.3 calanoid sp.2 harpacticoid sp.7			
K	ostracod sp.3^{K} Ampithoid sp.^{K} Mullid sp.^{K} harpacticoid sp.7^{B} harpacticoid sp.1^{K} calanoid sp.2^{B} Tanypodin sp.^{B}	ostracod sp.3^{K} Capitellid sp.^{D} calanoid sp.4^{D} Ampithoid sp.^{K} Gobiid sp.3^{D} harpacticoid sp.7^{D} harpacticoid sp.1^{D} *G. sorrentoensis*^{D}		ostracod sp.3 harpacticoid sp.1 Ampithoid sp.		
L	ostracod sp.1^{B} calanoid sp.12^{L} harpacticoid sp.1^{L} harpacticoid sp.7^{B} calanoid sp.2^{L} calanoid sp.4^{B} Tanypodin sp.^{B} nematode spp.$^{-}$ Hyalid sp.2^{B}	calanoid sp.4^{D} Capitellid sp.^{D} calanoid sp.2^{L} Gobiid sp.3^{D} harpacticoid sp.1^{D} Serpulid sp.^{D} harpacticoid sp.7^{D}		ostracod sp.3^{K} Ampithoid sp.^{K} Mullid sp.^{K} harpacticoid sp.1^{K} calanoid sp.2^{L} harpacticoid sp.7^{K} nematode spp.^{L} calanoid sp.4^{K}	calanoid sp.2 harpacticoid sp.1 Serpulid sp.	
Q	calanoid sp.2^{B} ostracod sp.1^{B} harpacticoid sp.1^{B} harpacticoid sp.7^{B} ostracod sp.3^{Q} Tanypodin sp.^{B} calanoid sp.4^{B} Hyalid sp.2^{Q}	Capitellid sp.^{D} harpacticoid sp.1^{D} calanoid sp.4^{D} Gobiid sp.3^{D} harpacticoid sp.7^{D} ostracod sp.3^{Q} nematode spp.^{D} Serpulid sp.^{D} calanoid sp.2^{Q}	harpacticoid sp.1^{H} ostracod sp.3^{H} calanoid sp.2^{H} harpacticoid sp.7^{H} *G. sorrentoensis*^{H}	ostracod sp.3^{K} Ampithoid sp.^{K} harpacticoid sp.1^{K} Mullid sp.^{K} Culicid sp.^{K} calanoid sp.2^{Q} Hyalid sp.2^{K}	calanoid sp.2^{L} harpacticoid sp.1^{L} ostracod sp.3^{Q} Hyalid sp.2^{Q} calanoid sp.4^{Q}	calanoid sp.4 ostracod sp.3 harpacticoid sp.1 Hyalid sp.2 calanoid sp.2 nematode spp.

(b) Summer 2006

	B	**D**	**H**	**K**	**L**
B	harpacticoid sp.7 cyclopoid sp.3 harpacticoid sp.1 ostracod sp.1				
D		cyclopoid sp.1 cyclopoid sp.3 Hyalid sp.1 Hyalid sp.2 Oribatid sp. harpacticoid sp.1 harpacticoid sp.7			
H	Spirorbid sp.^{H} harpacticoid sp.7^{B} caprellid sp.1^{H} *P. australis*^{H} *T. dulongii*^{H} Hyalid sp.2^{H} cyclopoid sp.3^{B} Gynodiastylid sp.^{H} Ischyrocerid sp.2^{H} *G. sorrentoensis*^{H} Ischyrocerid sp.1^{H} ostracod sp.1^{H} harpacticoid sp.1^{B} flabelliferan sp.1^{H}	Spirorbid sp.^{H} caprellid sp.1^{H} *P. australis*^{H} *T. dulongii*^{H} Hyalid sp.2^{H} Hyalid sp.1^{H} Gynodiastylid sp.^{H} harpacticoid sp.7^{H} ostracod sp.1^{H} Ischyrocerid sp.1^{H} Ischyrocerid sp.2^{H} *G. sorrentoensis*^{H} harpacticoid sp.1^{H} flabelliferan sp.1^{H}	Spirorbid sp. *P. australis* harpacticoid sp.7 ostracod sp.1 *G. sorrentoensis* *T. dulongii* caprellid sp.1 Ischyrocerid sp.2 Hyalid sp.2		
K	harpacticoid sp.7^{B} cyclopoid sp.3^{B} ostracod sp.1^{K} harpacticoid sp.1^{B} *T. dulongii*^{K} Hyalid sp.1^{K} Ischyrocerid sp.1^{K} Hyalid sp.2^{K} Gynodiastylid sp.^{K} Ischyrocerid sp.2^{K}	ostracod sp.1^{K} Hyalid sp.1^{K} harpacticoid sp.7^{K} cyclopoid sp.3^{D} *T. dulongii*^{K} Ischyrocerid sp.1^{K} harpacticoid sp.1^{K} Hyalid sp.2^{K} Gynodiastylid sp.^{K} Ischyrocerid sp.2^{K}		ostracod sp.1 harpacticoid sp.7 *T. dulongii* Hyalid sp.2 harpacticoid sp.1 Gynodiastylid sp. Ischyrocerid sp.2	
L		cyclopoid sp.3^{D} harpacticoid sp.7^{L} cyclopoid sp.1^{D} *A. semen*^{L} harpacticoid sp.1^{L}	Spirorbid sp.^{H} *P. australis*^{H} caprellid sp.1^{H} Gynodiastylid sp.^{H} Hyalid sp.2^{H} *T. dulongii*^{H} Ischyrocerid sp.2^{H} Ischyrocerid sp.1^{H} ostracod sp.1^{H} harpacticoid sp.7^{H} *G. sorrentoensis*^{H} harpacticoid sp.1^{L} flabelliferan sp.1^{H} cyclopoid sp.3^{L}		harpacticoid sp.7 harpacticoid sp.1 *A. semen* *N. nigellus* cyclopoid sp.3 ostracod sp.1 Serpulid sp. calanoid sp.2

(a) Winter 2005



(b) Summer 2006

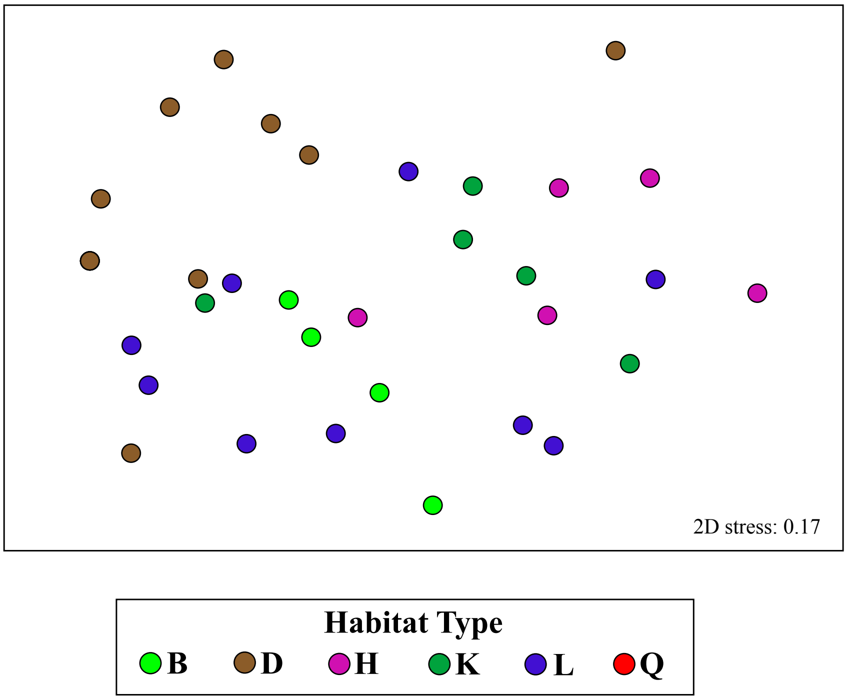


Figure 6.1.3.2: MDS ordination plots constructed from the hyperbenthic faunal assemblage data recorded in each replicate sample at each habitat in the Peel-Harvey Estuary during (a) winter 2005 and (b) summer 2006.

difference between the hyperbenthic faunas at habitats B and K was also attributable to their sharing only one characteristic species in common, *i.e.* harpacticoid sp.1, which typified the assemblages at all habitats in this season (Table 6.1.3.4a). Moreover, the assemblages at habitat K were exclusively typified and regularly distinguished by Ampithoid sp. and, while ostracod sp.3 also typified this and several others habitats, it was always recorded in greater abundances at K. Likewise, habitat L, which had a notably different hyperbenthic fauna from those at D and K, contained greater numbers of the ubiquitous calanoid sp.2 than all other habitats from which it differed significantly. The assemblage that characterised D also comprised several species that did not typify the hyperbenthic fauna of any other habitat in this season, *i.e.* Capitellid sp., Gobiid sp.3 and *M. senhousia*, the first two of which were also particularly important in distinguishing the fauna of this habitat. Various other species typified the assemblages at several habitats but were notably more abundant at just one habitat, such as calanoid sp.4 and harpacticoid spp. 1 and 7 at D (Table 6.1.3.4a).

One-way ANOSIM demonstrated that the extent of the differences in hyperbenthic composition between various pairs of habitats in summer 2006 was quite dissimilar to that for winter 2005. Thus, faunal differences were the greatest for H *vs* B and D, and the extent of those differences were considerably greater than those detected in winter (*i.e.* R=0.614-0.732). Moreover, the least significant difference was detected between the channel habitat L and riverine habitat D (*i.e.* R=0.217; Table 6.1.3.3b). The MDS ordination plot of the hyperbenthic faunal data recorded in this season showed that samples from habitat D, although dispersed, tended to lie to one side of those representing the remaining habitats and on the opposite side from most of those for H (Fig. 6.1.3.2b). Most samples from habitat B, which formed a relatively distinct group between those for D and H, were largely discrete from those for that latter habitat type. Samples from the remaining habitat types however, intermingled extensively on the ordination plot (Fig. 6.1.3.2b).

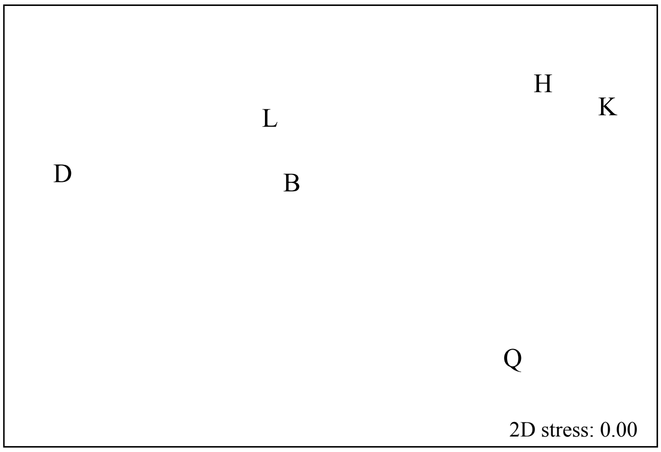
SIMPER demonstrated that the hyperbenthic assemblage at habitat H during summer 2006 was exclusively typified and regularly distinguished by Spirorbid sp., *P. australis*, *G. sorrentoensis* and caprellid sp.1 (Table 6.1.3.4b). In addition to these species, the large faunal differences detected between this habitat and B were also due to their characteristic assemblages sharing only two species, namely the widely distributed harpacticoid sp.7 and ostracod sp.1, the first of which was most prevalent at B while the opposite was true for the latter species. Various other taxa also exclusively typified the assemblages of several other habitats during summer, such as the amphipod Hyalid sp.1 and the mite Oribatid sp. at the riverine habitat D, the cumacean Gynodiastylid sp. at K and the bivalve *Arthritica semen*, gastropod *Nassarius nigellus* and the polychaete Serpulid sp. at L. Furthermore, *T. dulongii* and Ischyrocerid sp.2 were characteristic of just H and K, which were situated relatively close to each other in the Harvey Estuary (Table 6.1.3.4b).

6.1.3.4 Matching spatial patterns between the environmental and hyperbenthic assemblage characteristics of habitats

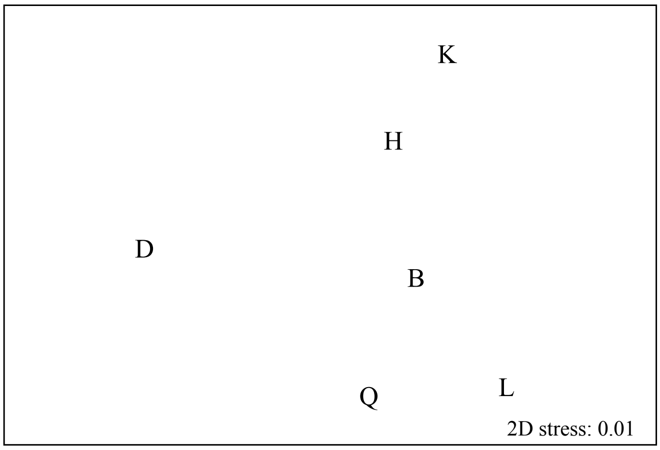
The RELATE procedure showed that the distance matrix derived from the enduring environmental variables that defined the six habitat types in the Peel-Harvey Estuary was significantly correlated with the resemblance matrix derived from the mean hyperbenthic faunal compositions recorded at the same habitat types in winter 2005 (*i.e.* p=4.8%, ρ=0.418), but not that for summer 2006 (*i.e.* p=46.2%, ρ=0.067). The spatial patterns among habitats, as defined by both the enduring environmental and seasonal faunal data, are illustrated by the MDS plots shown in Fig. 6.1.3.3. Thus, the significant and moderate match between the enduring and winter faunal matrices were clearly attributable to the similar distribution of most habitats except L and, to a lesser extent, B (*cf* Fig. 6.1.3.3a and b), while the insignificant match between the enduring and summer matrices resulted from the dissimilar distribution of all habitats except D and L (*cf* Fig. 6.1.3.3a and c).

RELATE was then used to ascertain the correlation between each of the above faunal matrices and the complementary distance matrices derived from the suite of water quality variables (*i.e.* salinity, water temperature and dissolved oxygen concentration) recorded at each habitat type in each season. These tests did not detect a significant match in either case (*i.e.* p=14.6%, ρ=0.339 and p=45.5%, ρ=0.103 for winter and summer, respectively). The BIOENV procedure was subsequently used to determine if the correlation between the complementary faunal and water quality matrices could be improved by only employing a subset of the above water quality variables, rather than the full suite. It should be recognised that these analyses were carried out using the averages recorded at each site rather than habitat type, in order to maximize the number of samples in the reference (hyperbenthic) matrices and thus reduce the chances of BIOENV finding a subset of water quality variables that provided a good match with those references by chance. For comparability, it should also be noted that, when RELATE was used to match the complementary hyperbenthic and water quality matrices constructed from site averages, the results for summer 2006 were similar to those obtained above when habitat averages were employed. However, RELATE detected a significant and improved match when site averages of the winter 2005 data were used, *i.e.* p=0.3%, ρ=0.545. BIOENV

(a) Enduring environmental data



(b) Winter 2005; p=4.8%, ρ=0.418



(c) Summer 2006; p=46.2%, ρ=0.067

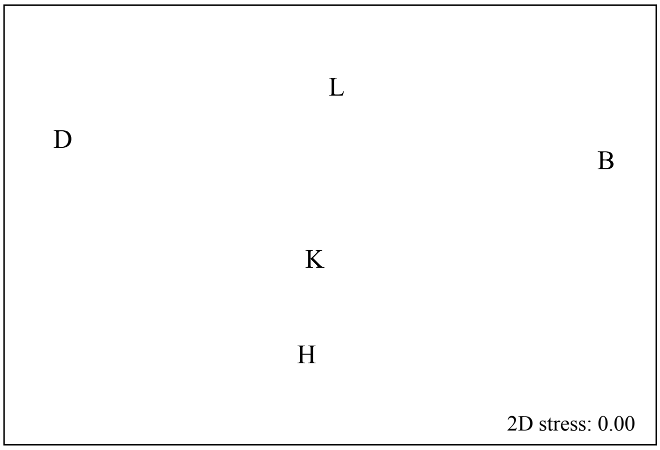


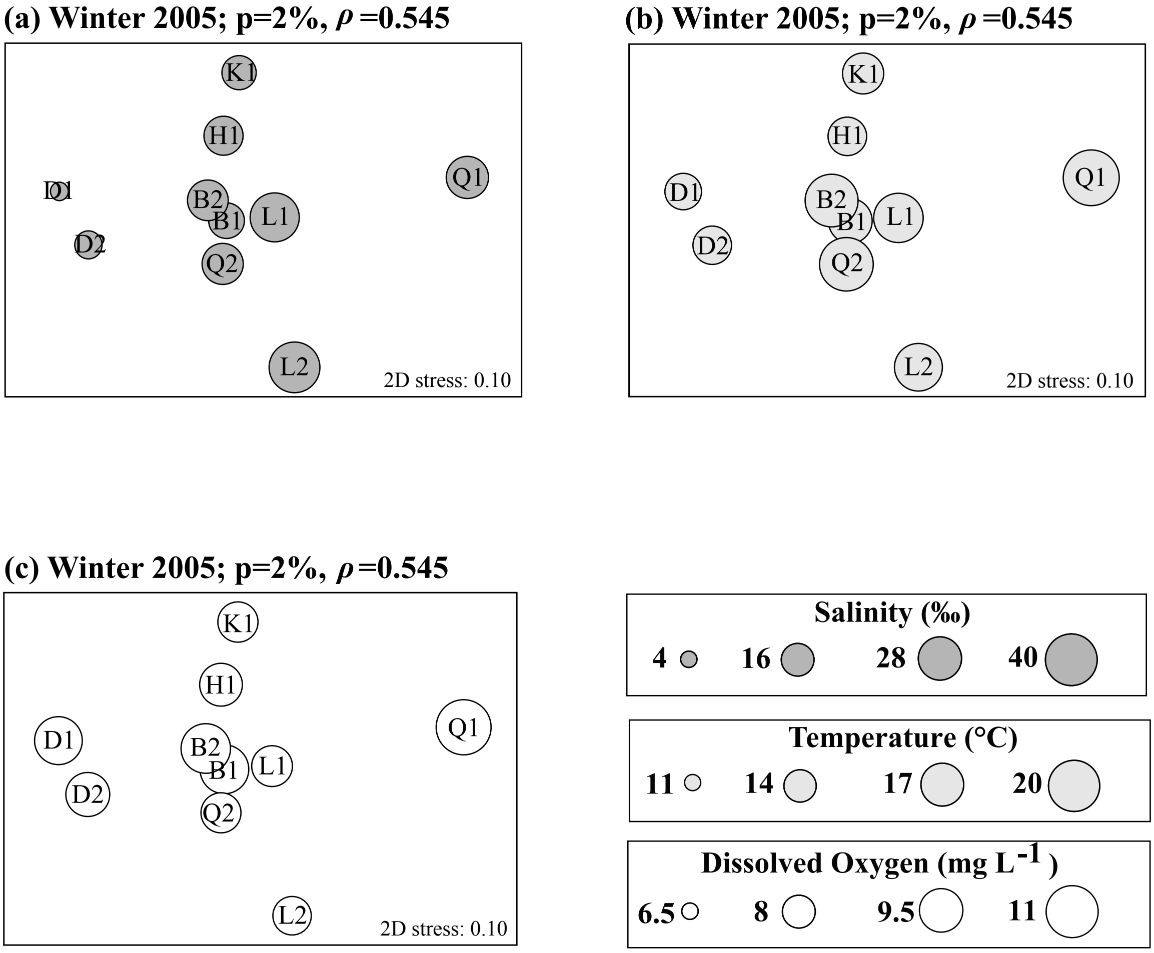
Figure 6.1.3.3: MDS ordination plots constructed from the averages at each habitat type in the Peel-Harvey Estuary of their (a) enduring environmental measurements and (b-c) hyperbenthic faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the hyperbenthic faunal data are also provided for each season.

could not improve the correlation between the hyperbenthic and water quality matrices in winter 2005 and thus selected all three quality water variables, while this procedure did not detect a significant match between the faunal and water quality data in summer 2006.

The relationships between the spatial patterns exhibited by the hyperbenthic assemblages and the magnitude of each of the water quality variables in winter 2005 are illustrated by the MDS and associated bubble plots shown in Fig. 6.1.3.4. During winter 2005, both the sites from the riverine habitat D, which contained faunal compositions that were clearly distinct from those at all other habitats, also had by far the lowest mean salinities (Fig. 6.1.3.4a). Furthermore, the distinct assemblages recorded at site L2 in the channel contained among the greatest salinities. However, the mean salinity at the other site from this channel habitat was just as high, and yet its faunal composition was clearly similar to those at most other sites in the basin. Moreover, the distinct faunal composition recorded at Q1 was not associated with a particularly low or high salinity (Fig. 6.1.3.4a). With respect to water temperature, the lowest mean values were recorded at both sites from habitat D, while the greatest were found at the basin site Q1, and it is thus relevant that the assemblage compositions of sites from the former habitat were the most dissimilar from that at the latter site (Fig. 6.1.3.4b). However, differences in water temperature at the remaining sites were not well correlated with those in faunal composition. Lastly, the distinct faunal assemblages at sites Q1 and L2 were associated with the highest and lowest dissolved oxygen concentrations, respectively (Fig. 6.1.3.4c).

6.1.3.5 Composition of hyperbenthic faunal assemblages among seasons

One-way ANOSIM, carried out separately for the data recorded at each habitat type, showed that the hyperbenthic faunal assemblages differed significantly among seasons in all cases (p=0.1-1.6%) except habitat Q, at which no comparison could be made. The overall extent of those seasonal differences were particularly high at habitat H (Global R=0.976), moderate at K, D and B (Global R=0.439-0.500) and low at habitat L (Global R=0.204). The extents of the seasonal differences in hyperbenthic composition at each habitat are illustrated by the MDS ordination plots and associated global ANOSIM results presented in Fig. 6.1.3.5. These plots showed that the samples from winter 2005 generally formed a discrete group from those representing summer 2006, except for at habitat L, where some overlapping of the two seasons occurred. The degree of dispersion among samples was generally similar for both seasons at all habitats except B, where those representing winter were considerably more dispersed than those from summer, and at D, at which the opposite was true (Fig. 6.1.3.5a and b, respectively).

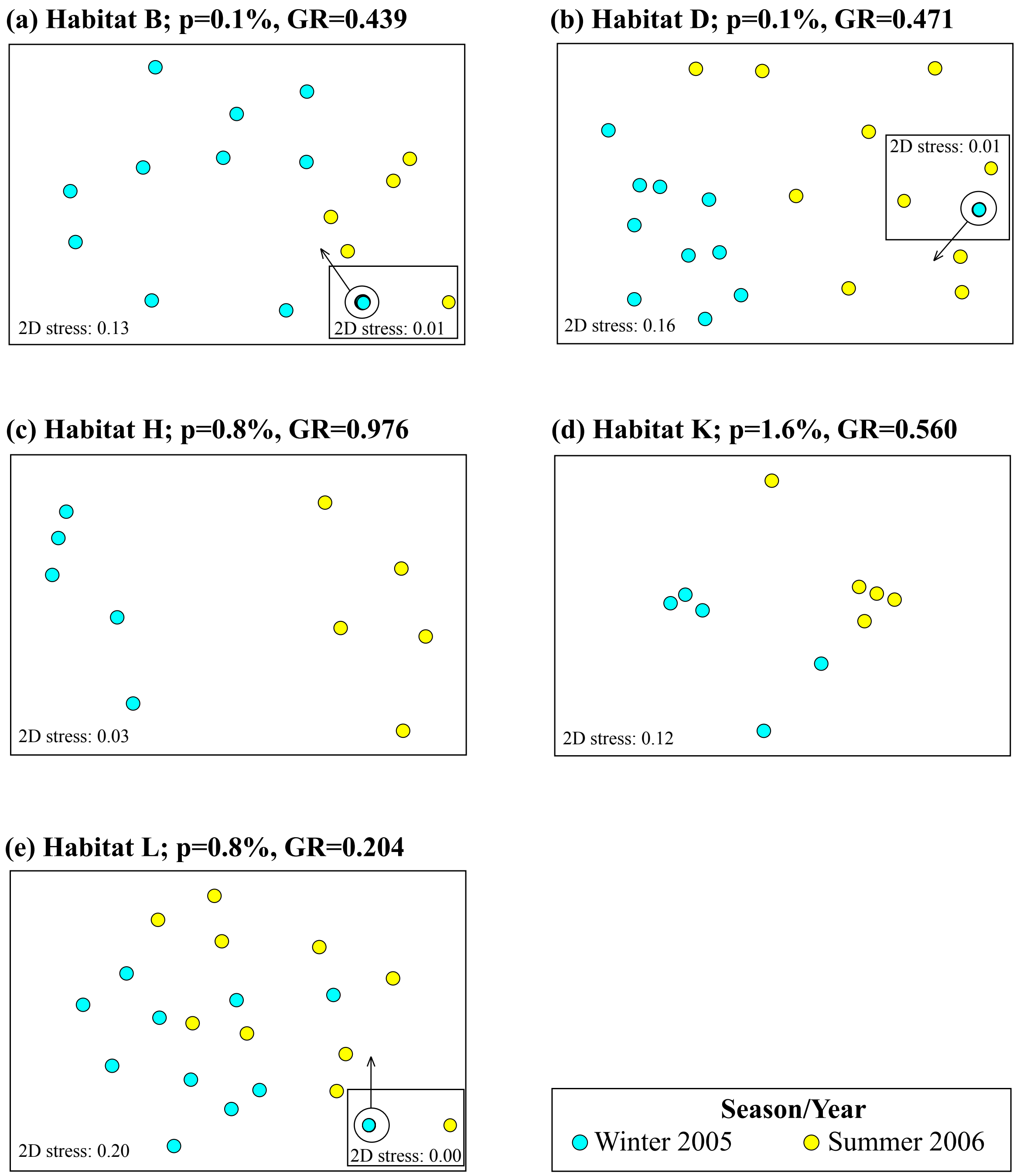


(a) Winter 2005; p=2%, ρ=0.545

(b) Winter 2005; p=2%, ρ=0.545

(c) Winter 2005; p=2%, ρ=0.545

Figure 6.1.3.4: MDS ordination plots derived from the average hyperbenthic faunal composition recorded at each site in the Peel-Harvey Estuary in winter 2005. The magnitude of those water quality variables selected by the BIOENV routine when the matrix constructed from the above faunal data was matched with that constructed from the complementary water quality data are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.



(a) Habitat B; p=0.1%, GR=0.439

(b) Habitat D; p=0.1%, GR=0.471

(c) Habitat H; p=0.8%, GR=0.976

(d) Habitat K; p=1.6%, GR=0.560

(e) Habitat L; p=0.8%, GR=0.204

Figure 6.1.3.5: MDS ordination plots constructed from the hyperbenthic faunal assemblage data recorded in each replicate sample in each sampling season at habitat (a) B, (b) D, (c) H, (d) K and (e) L in the Peel-Harvey Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in the faunal composition among seasons are also provided for each habitat type.

SIMPER showed that the highly pronounced seasonal differences in faunal composition at habitat H were attributable to the fact that the species that characterised the faunas at this habitat in winter included only one that was also prevalent in summer, *i.e.* harpacticoid sp.7. Moreover, whereas the assemblages at this habitat during winter were typified by a small suite of copepod species and ostracod sp.3, that during summer was characterised by a far larger suite of species, such as Spiorbid sp., *P. australis*, *G. sorrentoensis*, *T. dulongii*, caprellid sp.1, Ischyrocerid sp.2 and Hyalid sp.2. Habitat D also contained a substantially different suite of characteristic taxa in winter *vs* summer. Thus, the hyperbenthos in the first of these seasons was characterised mainly by Capitellid sp. calanoid sp.4 and harpacticoid spp. 1 and 7, while that in the latter season was typified largely by cyclopoid spp. 1 and 3 and Hyalid spp. 1 and 2. The greater densities of the first three of the above species in winter were particularly important in distinguishing the hyperbenthic faunas of these two seasons at this habitat. While the hyperbenthos at habitat B was characterised by the commonly occurring harpacticoid spp. 1 and 7 during both winter and summer, the faunas during the first of these seasons were also characterised and/or distinguished by several that were not prevalent in the latter, such as calanoid spp. 2 and 4, Hyalid sp.2 and Tanypodin sp., whereas the opposite was true for cyclopoid sp.3 and *Austrocochlea rudis*. The faunas at habitat K in winter were primarily distinguished from those in summer by the prevalence of ostracod sp.3, harpacticoid sp.1 and Ampithoid sp. in the first of these seasons and of ostracod sp.1, harpacticoid sp.7, *T. dulongii* and Gynodiastylid sp. in the latter, while the greater densities of calanoid sp.2 and harpacticoid sp.1 in winter and harpacticoid sp.7 and *A. semen* in summer were mainly responsible for the small seasonal differences detected at the channel habitat L.

6.2 Discussion

6.2.1 Differences in faunal assemblages among habitats

6.2.1.1 Fish assemblages

The compositions of nearshore fish assemblages throughout the Peel-Harvey Estuary exhibited moderately low to large differences among habitats during each of the six seasons in which they were sampled between winter 2005 and summer 2007. Similarly to the nearshore fish assemblages in the nearby and permanently-open Swan Estuary, the extents of those spatial differences were greatest in summer 2006 and 2007 and least in winter 2005. Furthermore, the compositions of the fish assemblages at one or both of the habitats in the tidal portions of the rivers and in the natural entrance channel of the Peel-Harvey Estuary (*i.e.* habitats D, E and L, M, respectively) were also among the most distinct in several seasons. However, the fish compositions at habitats in these regions of the Peel-Harvey Estuary were not as consistently or as markedly distinct in each season as those in the Swan Estuary, particularly when compared to habitat A in the uppermost reaches of that latter system. Moreover, and also unlike the Swan Estuary, the greatest ichthyofaunal differences in the Peel-Harvey Estuary never occurred between a habitat in the entrance channel and one in the tidal portion of the rivers. Indeed, in autumn 2006, the extents of such differences were among the least detected between those pairs of habitats with significantly different fish assemblage compositions. While the extents of the ichthyofaunal differences between channel and riverine habitats in the Peel-Harvey Estuary were often comparatively large in most of the remaining seasons, the most pronounced almost always involved a habitat located in one of the large basins, such as Q or J in the southern reaches of the Harvey Estuary.

Such contrasts in the relative differences in fish assemblage composition of habitats in comparable regions of the above two permanently-open and closely located estuaries largely reflects major dissimilarities in their overall geomorphology. Thus, the Swan Estuary, a drowned river valley system, has an essentially longitudinal morphology, in which its single entrance channel is located at the opposite end of the system to its major tributaries. In contrast, the Peel-Harvey Estuary is a combination of an interbarrier and basin system, and has two entrance channels and multiple tributaries that are not positioned at opposite ends of a longitudinal axis. Instead, the mouth of the natural entrance channel of this system is located near to its two major tributaries, the Serpentine and Murray rivers, while the second and artificial entrance channel is located a considerable distance away at the junction of its two large basins (see Chapter 3). The unusual geomorphological features of this system are reflected by particular enduring environmental measurements recorded at representatives of its various habitat types. Thus, the fact that the enduring features of habitats L and M in the natural channel of the Peel-Harvey Estuary were among the most similar to those of D and E in the tidal portions of its two main rivers, is attributable to the above similarities in their physical locations and to them all having narrow banks and thus small fetches in all directions, narrow wave shoaling margins and relatively steeply sloping substrates. As discussed below and in the following subsection, the relatively similar enduring environmental characteristics of these channel and riverine habitats were reflected by similarities in the compositions of their fish assemblages in several seasons. This differs from the situation in other south-western Australian estuaries, in which the faunal assemblages in the tidal rivers are the most distinct from those in their entrance channels (*e.g.* Potter and Hyndes 1994, Young *et al.* 1997).

The fish assemblages at the riverine habitats D and E, which were always significantly different and sometimes markedly so, were commonly characterised and distinguished by the estuarine goby *Pseudogobius olorum*, which was particularly prevalent at the latter habitat. This species was also prevalent at habitats C and particularly A in the upper reaches of the Swan Estuary and, while it was recorded at all habitats in this system except two in the entrance channel, it only ever characterised the fish faunas of the two upper estuary habitats (see Chapter 5.1.2). Similar spatial distribution patterns of *P. olorum* have also been recorded in several other estuaries in south-western Australia (*e.g.* Young *et al.* 1997, Hoeksema *et al.* 2006a), which has often been attributed to physiological adaptations or apparent preferences of this small benthic species for environmental conditions that are commonly found in the upper reaches of estuaries, *i.e.* reduced salinities, low dissolved oxygen concentrations, highly sheltered waters, substrates with relatively high proportions of silt and/or clay and a prevalence of fringing and emergent vegetation (Gee and Gee 1991, Neira *et al.* 1992, Gill and Potter 1993). All of the above environmental conditions also characterised habitats D and E in the Peel-Harvey Estuary, several of which were directly or indirectly reflected by their enduring environmental characteristics, *i.e.* very limited fetches in all directions and a relative predominance of reeds and/or samphire in their shallowest waters. Moreover, the mean salinity at E and particularly D was typically lower than that at most other habitats, and dissolved oxygen concentration was always lowest at habitat E. Their substrates also comprised predominantly very fine silt and mud (pers. obs.). However, unlike the situation in several other estuaries in south-western Australia, the other habitat in the Peel-Harvey Estuary at which *P. olorum* regularly characterised the nearshore fish assemblages was L in the entrance channel, where it was prevalent in three of the six sampling seasons and reached greater mean densities than at the riverine habitat D. Although L was also highly sheltered from wave activity, due both to its small fetches and the presence of moderately large areas of seagrass, and had relatively fine sediment (pers. obs.), its mean salinities ranged between 29.4-38.9‰. Furthermore, similar environmental conditions are commonly found in the entrance channels of other permanently-open estuaries in south-western Australia, and yet *P. olorum* does not typically comprise a considerable part of those fish assemblages. Such findings at habitat L in the Peel-Harvey Estuary are thus likely to partly reflect the fact that the natural entrance channel of this unusual system is relatively close to its two major tributaries and, despite the apparent physiological adaptations of *P. olorum* for reduced salinities, the tolerance of this euryhaline estuarine species for more saline conditions (Gill and Potter 1993).

Similarities between the compositions of fish assemblages at habitats in the lower reaches of the rivers and in the entrance channel of the Peel-Harvey Estuary were further enhanced by the fact that several other marine species that are typically found in the lower to middle reaches of south-western Australian estuaries also characterised and/or distinguished the faunas of at least one habitat in both of the above regions (*i.e.* D and/or E and L and/or M) in particular seasons, *e.g. Torquigener pleurogramma, Favonigobius lateralis* and *Atherinomorous ogilbyi*. Both *F. lateralis* and *A. ogilbyi*, which have affinities for greater salinities and, in the case of the first species, also highly sheltered waters (Prince *et al.* 1982, Gill and Potter 1993), characterised and/or distinguished the ichthyofauna of D/E and also L/M during autumn 2006 or summer 2007, and thus at a time of the year when salinities at all of those habitats were the same as or greater than that of full strength seawater, *i.e.* 35.5-41.5‰. However, the marine estuarine-opportunist *T. pleurogramma*, which also apparently has an affinity for higher salinities (Potter *et al.* 1988), characterised habitat D and L/M in all seasons except winter 2006, and thus during periods when salinities at that former habitat fell as low as 6‰. Moreover, in some seasons, it was found more consistently and in greater numbers at D than at many other habitats throughout the system. Such spatial distribution patterns of this marine species in the Peel-Harvey Estuary thus probably reflect, in part, the proximity of the rivers to the natural entrance channel of this system. They most likely also reflect the fact that, while salinities at D fell to low levels in some seasons, they reached *ca* 29-38‰ in other seasons. Other species, such as *Hyperlophus vittatus*, which occur in both the lower and upper reaches of south-western Australian estuaries (Loneragan and Potter 1990, Gaughan *et al.* 1996), also characterised one or both of the above riverine and channel habitats in certain seasons. This marine estuarine-opportunist reached extremely high densities at D and, to a lesser extent, L and M in either spring 2005 or summer 2006, and was primarily responsible for the high mean fish densities detected at these habitats in those seasons. Most of these individuals were 0+ recruits (*i.e.* mean length 31-36 mm), which are known to migrate from nearby marine waters into estuaries around this time of year (Gaughan *et al.* 1990).

Despite the above similarities in the compositions of the ichthyofaunas in the riverine and channel regions of the Peel-Harvey Estuary, the assemblages at habitats in each of these regions were also exclusively characterised and/or distinguished by particular species in some seasons. These included *Afurcagobius suppositus* at D and E in summer 2006, *Leptatherina wallacei* at E and, to a lesser extent D, in all seasons except winter and spring 2005 and *Ammotretis elongata, Stigmatophora argus* and *Gymnapistes marmoratus* at habitat M in spring 2005, summer, autumn and/or winter 2006 and/or summer 2007. The first two of these species, although euryhaline, are commonly found in the upper reaches of south-western Australian estuaries, which has been attributed to their apparent preference for reduced salinities and, in the case of the latter species, also for highly sheltered waters, silty substrates and areas with fringing vegetation (Prince *et al.* 1982, Gill and Potter 1993). The latter three species, all of which are marine estuarine-opportunists or marine stragglers and thus have affinities for the higher salinities consistently recorded at both habitats in the channel, also have morphological and behavioural adaptations for living in the particular submerged vegetation and substrate types recorded at M, *i.e.* marine sands, seagrass beds comprised mainly of *Heterozostera* sp. and often considerable volumes of seagrass and macroalgal wrack washed in from local marine waters. Thus, the flounder *Am. elongata*, which is light in colour, is particularly well camouflaged against the marine sands found predominantly in the entrance channel, as are *S. argus* and *G. marmoratus* among the above vegetation types, which also support valuable food resources for both of these species (Ayvazian and Hyndes 1995, Hyndes *et al.* 2003, Valesini *et al.* 2004, Kendrick and Hyndes 2005). The distinctiveness of the fish assemblages at both channel habitats in the Peel-Harvey Estuary was also attributable to the fact that they contained more than 20 species that were not recorded at any other habitat in the system. These species were mostly the juveniles of marine stragglers and/or those that are typically associated with vegetation.

The fish assemblages at habitats Q and/or J at the southern end of the Harvey Estuary were among the most distinct in nearly all seasons. These habitats contained the lowest total number of species in the estuary, and the mean number of species and taxonomic distinctness (*i.e.* diversity) of their assemblages was notably lower than those at most other habitats in several seasons. Such findings reflect the fact that their ichthyofaunas were only ever distinguished from those of other habitats by *A. elongata, Atherinosoma mugiloides*, *Craterocephalus pauciradiatus* or *Leptatherina presbyteroides*, all of which belong to the same taxonomic group at a relatively low level of the Linnaean tree (*i.e.* the family Atherinidae), and/or the Weeping Toadfish *T. pleurogramma*. Furthermore, the overall mean density of fish at Q was among the lowest in the system, as were the densities of several of its characteristic species in a number of seasons. This was particularly marked in summer 2006, where the pronounced distinctiveness of the ichthyofauna at Q was due to it being characterised only by *A. elongata*, which was always found in greater numbers at other habitats. These findings are probably related to the extremely variable levels of salinity and/or water temperature recorded at habitats Q and J. Thus, these extremely shallow habitats experienced particularly high mean salinities and water temperatures in both summers and/or autumn 2006 (*i.e.* 41.7-47.1‰ and 29.1-31.2°C, respectively), and among the lowest mean salinities of all habitats during one or both winters and/or spring 2005, the latter of which also reflected their proximity to the Harvey River. The fact that the assemblage at Q was characterised only by *A. elongata* in summer 2006 parallels the findings of other workers in the normally-closed Culham Inlet and Wellstead Estuary on the south coast of Australia, in which this atherinid was the sole species comprising the nearshore fish assemblage when the salinities of those systems rose to extremely high levels, *i.e.* >120‰ (Young and Potter 2002, Hoeksema *et al.* 2006a). It is also relevant that most of the fish species that characterised the assemblages at Q and J are particularly euryhaline (Prince *et al.* 1982). In addition to the influence of such seasonally variable salinity and temperature, the low species richness and diversity of the fish assemblages at habitats Q and J also probably reflects the fact that, unlike several other habitats throughout the large basins of the Peel-Harvey Estuary, their substrates comprised almost entirely sand. The greater structural heterogeneity provided by submerged or littoral vegetation has been found by numerous workers in estuaries and coastal waters to be associated with higher fish species richness, diversity and/or density (*e.g.* Jenkins *et al.* 1997, Travers and Potter 2002, Smith *et al.* 2008). Furthermore, the fact that J and Q were located the greatest distance from both entrance channels would considerably reduce the likelihood of marine species occupying either of these habitats.

The ichthyofaunas at habitats in the Peel Inlet and more northern reaches of the Harvey Estuary, *i.e.* B, C, H, I and K, were also commonly distinguished from those in other main regions of the estuary, and from each other, by a prevalence of one or more of the above-mentioned species that distinguished the fish assemblages of J and/or Q. However, various other fish species were also responsible for the compositional differences detected among these habitats. For example, in most seasons, the fish faunas at C, H and I were partly distinguished from those of other habitats by a prevalence of *F. lateralis*, whereas those of K and B were rarely distinguished by this species. Given the affinity of this estuarine and marine goby for higher salinities and particularly sheltered waters (Gill and Potter 1993), such findings are likely to reflect the fact that habitats C, H and I are all located within the vicinity of the artificial entrance channel, and thus had notably higher mean salinities during both winters and spring 2005 than B and K, which are situated near the mouths of the Murray and Serpentine rivers and in the middle reaches of the Harvey Estuary, respectively. Furthermore, unlike the remaining basin habitats sampled during this study, B is highly exposed to southerly and westerly winds that prevail during both winter and summer along the lower west coast of Australia, and thus experiences among the greatest levels of water disturbance throughout the estuary. This habitat also lacked the substantial areas of submerged vegetation that were present at C, H, I and K, and which would thus provide buffering from wave activity.

The ichthyofaunas of each of the above basin habitats were also distinguished from those of many others by various other species in particular seasons. For example, in summer 2007, the estuarine and marine *Apogon rueppellii* and marine estuarine-opportunist *Pelates octolineatus* distinguished the fish assemblage of habitat H and, in the case of the former species, also that of I. The mean length of both of these species at these habitats (*i.e. ca* 30-37 mm and *ca* 20 mm, respectively) indicated they were represented largely by their 0+ recruits, which are known to migrate into the very shallow waters of southern Australian estuaries and coastal areas at this time of year (Chrystal *et al.* 1985, Valesini *et al.* 2003). As both *A. rueppellii* and *P. octolineatus* are typically associated with seagrass (Hyndes *et al.* 2003, Valesini *et al.* 2004), it is thus relevant that habitats I and particularly H contained considerable areas of submerged vegetation. Moreover, as these habitats are located immediately adjacent to the artificial and/or natural entrance channels and on the western shores of the estuary, they are firstly in the direct path of 0+ *A. rueppellii* and *P. octolineatus* migrating into the estuary from nearby marine waters, and secondly are highly sheltered from the westerly and south-westerly winds that prevail during summer afternoons. Such habitats would thus provide ideal nurseries for the juveniles of both of these marine species. Consistent and relatively large numbers of *H. vittatus*, comprising mainly its 0+ juveniles, also partly distinguished the fish assemblage at habitat B in summer 2006. These findings probably reflect the fact that this habitat is located adjacent to both the natural entrance channel and mouths of the Serpentine and Murray rivers, and thus within the path of recruiting juveniles of this clupeid species, which typically migrate from marine waters into estuaries, including their upstream reaches, around this time of year (Gaughan *et al.* 1990, 1996).

Despite the above ichthyofaunal differences at B, C, H, I and K, pairwise comparisons between these basin habitats demonstrated that their fish assemblage compositions were often among the most similar. While this is to be expected to some extent, and was also commonly the case among habitats in the main basin of the Swan Estuary, such findings are also likely to be attributable to the influence of the artificial Dawesville Channel. Thus, Young and Potter (2003a) found that the differences in the composition of the nearshore fish assemblages among various regions of the Peel Inlet and Harvey Estuary were far greater in the early 1980s prior to the construction of this second channel than in 1996-97, two to three years after that channel was opened. Thus, during that earlier period, pronounced ichthyofaunal differences existed between the northern and southern reaches of the Harvey Estuary and western and eastern regions of Peel Inlet, due mainly to the influence of spatial differences in the extent of micro- and macro-algal growth and the highly limited tidal incursion into the Harvey Estuary. However, following channel construction, no such significant differences were detected, except for relatively weak differences between the western Peel Inlet and southern Harvey Estuary. Such findings were attributed to the extreme reductions in both micro- and macro-algal growth throughout the system and the fact that the increased tidal incursion not only led to more homogeneous and marine conditions throughout the basins, but also to a more uniform capacity for marine species to enter both basins (Young and Potter 2003a).

6.2.1.2 Hyperbenthic assemblages

The hyperbenthic faunal composition exhibited relatively small differences among habitats in the Peel-Harvey Estuary during both winter 2005 and summer 2006. The overall extents of these spatial differences were also lower than those detected in the same seasons in the Swan Estuary and, as was the case for the fish assemblages, the relative differences in hyperbenthic composition between habitats from different regions of the Peel-Harvey Estuary varied considerably from those in the Swan. Thus, while the hyperbenthic assemblages at habitats from the entrance channel or tidal portions of the river in the Peel-Harvey were among the most distinct in one or both seasons, they were not as consistently or notably divergent as those at habitats in comparable regions in the Swan Estuary. Indeed, the largest differences typically occurred between habitats located in the two large basins of the Peel-Harvey Estuary and, in summer 2006, the hyperbenthic differences between the riverine habitat D and the channel habitat L were among the lowest detected in that season. As described previously in subsection 6.2.1.1 and discussed further below, these findings are likely to reflect the very different geomorphology of the Swan and Peel-Harvey estuaries, and the influence of the artificial entrance channel in that latter system.

The greatest differences in hyperbenthic faunal composition in both winter 2005 and summer 2006 occurred between habitat B located along the north-eastern shore of Peel Inlet and either H or K, which lay adjacent to each other in the northern and middle reaches of the Harvey Estuary, respectively. Thus, the characteristic assemblages at the first of these habitats contained few species in common with the latter two, and any species they did share were always more prevalent at just one of the habitats. Moreover, the typifying species at each of these habitats often comprised some that did not characterise the assemblages of any other habitat. In addition to these compositional differences, the overall number of species recorded at B was among the lowest of any habitat throughout the estuary, while that at K was equal highest and a conspicuously large mean number of species was found at H in summer 2006. Furthermore, the second greatest overall mean density of hyperbenthos was recorded at the latter habitat.

Such differences in the hyperbenthic characteristics of B compared to those of H or K most likely reflects the substantial differences among those habitats in a suite of environmental attributes. Firstly, they each varied considerably in their proximity to marine and freshwater sources, which not only influenced aspects of their water quality, such as salinity, but also their likelihood of being colonised by marine or fresh water species. Thus, B was positioned directly between the natural entrance channel and mouths of the Serpentine and Murray rivers, H lay adjacent to the artificial entrance channel and a considerable distance from any river, while K was not particularly close to either type of water source. Mean salinities at H were thus the least variable and remained relatively close to those of marine waters, while those of B and K fell to 16.3 and 13.6‰, respectively, in winter and reached *ca* 40‰ in summer. Moreover, the extreme shallowness of B, which was reflected by its exceptionally wide shoaling margin and slight slope of the substrate, also contributed to the seasonal variability in salinity at this habitat. Secondly, habitat B was among the most exposed to waves generated from the strong southerly and south-westerly winds that often prevail during summer afternoons and winter along the lower west coast of Australia, whereas both H and K were far more protected from such wave activity due to their locations on the western shore of the estuary. Lastly, unlike the predominantly bare sand/silt substrate at B, both H and K contained extensive seagrass and macroalgal beds and, in the former habitat, also relatively large quantities of rock.

The hypersaline and extremely shallow waters at B in summer 2006, combined with its relatively high exposure to wave activity and lack of benthic structural heterogeneity, most likely explains the small suite of hyperbenthic taxa that characterised this habitat in this season and its relatively low number of species overall. Furthermore, most of the species that typified B in summer were copepods, *i.e.* harpacticoid spp. 1 and 7 and cyclopoid sp.3, which are tolerant of a broad range of environmental conditions (Bell *et al.* 1987, Mu *et al.* 2002). The first two of these species were particularly widespread throughout the estuary, whereas cyclopoid sp.3 occurred in far greater densities at B and the riverine habitat D than any other habitat throughout the system. This latter species may thus have an affinity for environmental attributes that are typically associated with seasonal river flow, such as reduced salinities, tannin-stained waters or certain planktonic food sources. Moreover, ostracod sp.1, which typified only habitat B in winter 2005 and occurred in the greatest overall densities at this habitat, is particularly well adapted to greater wave activity by possessing a reticulated carapace (www.ucl.ac.uk/GeolSci/micropal/ostracod.html; 15/6/09). In direct contrast to B, the predominant influx of marine waters at H throughout the year, combined with the much more sheltered conditions and structurally complex benthos at both H and K, probably explains the greater number of hyperbenthic species and/or individuals recorded at these latter two habitats (Edgar and Robertson 1992, Cunha *et al.* 1999, Matilla *et al.* 1999), as well as the prevalence of typifying species such as the amphipods caprellid sp.1, Ischyrocerid sp.2*,* and Ampithoid sp. and various other taxa such as Spiorbid sp., *P. australis, G. sorrentoensis* and *T. dulongii*. Thus, most of these species are typically associated with submerged vegetation, which they use as a source of shelter and food, and those such as the above amphipods and *T. dulongii* typically occur in those estuarine waters with salinities that approximate those of marine waters (Mees *et al.* 1993).

The hyperbenthic faunal composition at habitat D in the tidal portion of the rivers was also relatively distinct from that at several other habitats in both seasons, and most notably K and the channel habitat L in winter 2005, and H in summer 2006. The overall mean density of hyperbenthos at D was by far the greatest of any habitat, and the total number of species it contained was the second highest recorded throughout the estuary. The latter finding contrasts with those of various other workers, who have detected the lowest number of hyperbenthic species in estuarine regions that experience salinities close to those of freshwater (Mees and Hamerlynck 1992, Mees *et al.* 1993, Azeiteiro and Marques 1999). Thus, while salinities at this habitat approached those of seawater in summer 2006 (*i.e. ca* 29‰), reflecting its relatively close proximity to the natural entrance channel, they fell as low as *ca* 6‰ in winter 2005. Moreover, the mean number of species, mean density and importance of its characteristic species in distinguishing the hyperbenthic composition of this habitat from that of others, was far greater in winter than summer.

Calanoid sp.4 was one of the most important typifying species at D in winter 2005, comprising over 80% of the total number of individuals and was mainly responsible for the extremely high mean densities of hyperbenthos recorded at this habitat in this season. The only other habitats at which this copepod species was abundant, albeit in much lower numbers, were B and the southern Harvey Estuary habitat Q, the first of which was adjacent to the mouths of the

Serpentine and Murray of rivers, while the latter lay the closest to the mouth of the Harvey River. Moreover, although widely distributed throughout the Swan Estuary, calanoid sp.4 was also particularly abundant in the upper reaches of this system (see Chapter 5.1.5). While the only other habitat in the Swan Estuary at which the densities of calanoid sp.4 reached particularly high levels was in the lower reaches of the system, the general findings from both of these permanently-open estuaries suggest that this copepod has an affinity for environments that receive greater volumes of riverine water. While reduced salinity is unlikely to be the sole factor influencing the spatial distribution of calanoid sp.4, given its prevalence in the lower Swan Estuary and the fact that other habitats in the Peel-Harvey declined to lower levels than at B and Q during winter 2005, the low mean salinities at D in this season indicate that this species is capable of tolerating fresher waters and may thus be able to exploit such niches more readily than other hyperbenthic species. It may also be relevant that D and B lacked permanent submerged vegetation beds and hence shelter, and thus the relatively high densities of calanoid sp.4 at these habitats could reflect a greater tendency for this copepod species to swarm and thereby minimise the chances of being preyed upon (Alldredge and King 1985).

Aside from various ubiquitous copepods, several other species were important in characterising and/or distinguishing the faunas of D in winter, such as the polychaete Capitellid sp., the bivalve *Musculista senhousia* and the Gobiid sp.3. A species of *Capitella* was also abundant in the benthic macroinvertebrate assemblages throughout the Swan Estuary, in which it commonly typified the faunas of various habitats throughout the system (see Chapter 5.1.3). As this widely distributed polychaete species is also a sediment-ingesting deposit feeder (Beesley *et al.* 2000), it would benefit from the abundant detrital accumulations that comprise part of the silty substrate at D (pers. obs.). *Musculista senhousia* was also highly prevalent in the hyperbenthic assemblages of the uppermost habitat in the Swan Estuary, where it reached considerably greater mean densities than at D in the Peel-Harvey Estuary, *i.e.* 9.65 *vs* 3.79 individuals m^{-3}. As described in Chapter 5.2.1.4, this invasive mussel is particularly well adapted at coping with highly reduced and variable salinities and, given its high fecundity, can rapidly exploit niches that may be physiologically stressful for many other hyperbenthic species (NIMPIS 2005). Lastly, the goby *P. olorum* commonly characterised and distinguished the fish assemblages at habitat D in various seasons, including winter 2005 (see subsection 6.1.2) and, given that this species spawns during winter and early spring in the upper reaches of other estuaries in south-western Australia (Neira *et al.* 1992, Gill and Potter 1993), it is probable that the larval Gobiid that consistently occurred in the hyperbenthos at D in this season belonged to this species.

Similar numbers of hyperbenthic species were recorded at D and each of the upper estuary habitats in the Swan Estuary, *i.e.* A and C. However, the mean overall density of hyperbenthos at the former habitat was far higher than at either of the latter two, and particularly the uppermost habitat A, even when the exceptionally abundant calanoid sp.4 (*ca* 992 individuals m^{-3}) was excluded from D, *i.e. ca* 322 *vs* 17-54 individuals m^{-3}. Thus, commonly occurring species such as harpacticoid spp. 1 and 7 and a variety of other taxa, such as nematode spp., the amphipods Ischyrocerid sp.1 and *C. minor,* the polychaetes Capitellid sp. and Serpulid sp. and the mysid *G. sorrentoensis*, occurred in much greater mean densities at D than any other habitat in the Peel-Harvey Estuary and, with respect to those of the above taxa that were also recorded in the upper Swan Estuary, also at habitats A and C in that latter system. The greater densities of hyperbenthos at D than at the remaining habitats in the Peel-Harvey Estuary may reflect more abundant detrital or planktonic food sources in that part of the system or the greater protection from predation provided by its dark tannin-stained waters. However, habitats A and C in the Swan Estuary were also characterised by such environmental attributes, and yet their hyperbenthic densities were much lower than at other habitats in that system. Secondly, the greater hyperbenthic densities at habitat D in the Peel-Harvey Estuary than at habitats in the upper reaches of the Swan Estuary may reflect the fact that the former is far closer to the natural entrance channel of this system, rather than at the opposite end of the estuary, and thus more readily receives larval and juvenile hyperbenthos from marine waters. The connectivity between these two regions of the Peel-Harvey Estuary is supported by the fact that, during summer 2006, the differences in hyperbenthic composition between D and habitat L in the channel were very small.

The hyperbenthic assemblage at the channel habitat L comprised the equal greatest number of species recorded throughout the system, but among the lowest overall number of individuals. Such findings parallel those recorded in various other hyperbenthic studies in estuarine environments (*e.g.* Mees and Hamerlynck 1992, Mees *et al.* 1993, 1995, Azeiteiro and Marques 1999). The relatively speciose hyperbenthic fauna at channel habitats such as L is often attributed to the active or passive movement of a range of marine species into these estuarine waters, the relative stability of various water quality parameters which remain at similar levels to those of the marine environment and/or the presence of considerable beds of submerged vegetation. In contrast, the relatively low hyperbenthic densities at such habitats often reflects the clearer waters and greater tidal currents in this region of the estuary, which lead to greater rates of predation and dispersal of these benthic fauna, respectively. Thus, while the hyperbenthic composition of habitat L exhibited the most notable differences from that at the

Harvey Estuary habitat K and the riverine habitat D in winter 2005, such differences were due largely to the substantially greater number and density of characteristic species at those latter two habitats.

By far the lowest number of hyperbenthic species and mean densities were recorded at habitat Q at the southern end of the Harvey Estuary. Such findings are partly attributable to the extreme shallowness of this habitat, and that it could thus only be sampled following seasonal rainfall during winter 2005. However, they probably also reflect the fact that the mean salinity and temperature at this habitat reached particularly high levels during summer 2006 (*i.e. ca* 44‰ and 27°C, respectively), which would be physiologically stressful for many hyperbenthic fauna, and that its benthic environment comprised only bare sand. Such findings parallel those recorded for the fish assemblages at this habitat (see subsection 6.1.2).

6.2.2 Spatial relationships between the environmental and faunal characteristics of habitats

The spatial pattern in the enduring environmental measurements among the various habitats throughout the Peel-Harvey Estuary was significantly correlated with that exhibited by the fish fauna in each of the six sampling seasons, and with that displayed by the hyperbenthic fauna in winter 2005. The extent of the correlations between the enduring environmental and fish assemblage data was high in winter and spring 2005, moderately high in autumn and winter 2006 and relatively low in both summers. Such trends opposed, in some respects, those exhibited by the overall differences in ichthyofaunal composition among habitats that are described above in subsection 6.2.1.1, in which the greatest differences were detected in both summers. In summer 2006, the reduced spatial correlation between the enduring and ichthyofaunal characteristics of the various habitats was due largely to the marked differences between the fish fauna at Q and those at all other habitats, while that in summer 2007 resulted mainly from the fact that the fish assemblages at the two riverine habitats, and particularly E, were similar to several of those throughout the basins. It should be noted, however, that when the fish assemblage data for the two summers were combined, the resulting spatial correlation between the fish faunal and enduring environmental data improved (*i.e.* $p=0.7\%$, $\rho=0.380$). The spatial correlation between the enduring and hyperbenthic characteristics of the various habitats in winter 2005 was moderate, while the low and insignificant match detected between these two matrices in summer 2006 was due mainly to the particularly distinct assemblages at habitat B and that those at Q could not be sampled, both of which reflected the extreme shallowness of those habitats in that season.

The above findings demonstrate that the spatial interrelationships among habitats that are defined by their enduring environmental characteristics typically provide a reliable surrogate for those exhibited by their fish assemblages and, to a lesser extent, their hyperbenthic assemblages, although there is far less evidence to support the latter. Consequently, the fish species likely to typify any nearshore site in the Peel-Harvey Estuary can be confidently predicted by firstly assigning it to its most appropriate habitat using its enduring environmental measurements and the habitat prediction tool developed in Chapter 3.3.2, and then consulting the list of characteristic species provided for each habitat in any given season. Further sampling of the hyperbenthic assemblages in other seasons should be undertaken to ascertain whether this also likely to be the case for that faunal group.

It is also very important to note that, in each season, the suite of enduring environmental criteria better explained the spatial distribution of the fish assemblages throughout the estuary than the collective suite of measured water quality variables, *i.e.* salinity, temperature and dissolved oxygen. Even when BIOENV was used to identify the particular combination of water quality variables that best matched the spatial pattern exhibited by the fish fauna among habitats, the resulting correlations were still lower, in almost all cases, than those obtained using the suite of enduring criteria. These findings indicate that the other environmental features of the nearshore waters that are encapsulated by the enduring criteria but not by field measurements of the above water quality parameters (*e.g.* the extent of submerged vegetation, wave exposure or aspects of water quality other than those above) are important in discerning the spatial differences in the composition of the fish assemblages in the Peel-Harvey Estuary. They also indicate that the spatial differences in salinity, water temperature and/or dissolved oxygen concentration throughout this system have a relatively small influence on the distribution of the nearshore fish fauna and, with respect to the first of these variables, certainly a lesser influence than that detected in the Swan Estuary (see Chapter 5.1.2). These findings partly reflect the fact that salinities in the tidal portions of the rivers in the Swan Estuary fell to lower levels than those in the same region of the Peel-Harvey and, unlike those in the latter system, were always considerably lower than in all other regions of the estuary. They also reflect the large proportion of the fish assemblage throughout the Peel-Harvey Estuary that comprises particularly euryhaline species, which was well exemplified by the fact that the atherinid *A. elongata* ranked first and represented between 19.5 and 65.9% of the catch at all basin habitats, and ranked either first or second at almost all habitats in the channel and rivers of this system, where it represented *ca* 10-54% of the total number of fish.

Various test sites throughout the Peel-Harvey Estuary were used to examine the extent to which the habitat prediction tool and suite of characteristic fish species established for each habitat in each season could be used to reliably predict the typical ichthyofauna at any nearshore location in the system at a particular time of year. Thus, in each season except winter 2005, the fish assemblages were sampled at four additional sites, two of which were classified as habitat D and the other two as habitat J, on the basis of measurements of their enduring environmental characteristics. ANOSIM demonstrated that only one of the test sites of habitat D contained a significantly different fish fauna from that at just one of the sites primarily chosen to represent this habitat in spring 2005, autumn 2006 and winter 2006. No significant ichthyofaunal differences were detected between either of the test *vs* primary sites of this habitat in summer 2006, while the fish faunas of one of the test sites differed significantly from that of both of the primary sites in summer 2007. These relatively minor ichthyofaunal differences reflected the fact that the species most responsible for characterising the fish assemblages at the primary representatives of D were always among those that typified the faunas at the test sites of this habitat in each season. With respect to the test sites of habitat J, no significant ichthyofaunal differences were detected between either of these sites and the primary representatives of this habitat in summer 2006, autumn 2006 and summer 2007. Furthermore, in spring 2005 and winter 2006, just one of the test sites contained a significantly different fish fauna to those recorded at the primary representatives of this habitat. As with the test sites of habitat D, the species that characterised the fish assemblages at the primary representatives of J were always among those that characterised the ichthyofauna at the test sites of this habitat in each season. Such findings provide further evidence that the habitat and faunal prediction tools developed for the Peel-Harvey Estuary in this study are reliable.

6.2.3 Seasonal differences in faunal assemblage composition among habitats

6.2.3.1 Fish assemblages

The composition of the fish assemblages at each habitat in the Peel-Harvey Estuary differed significantly among seasons, but, as with the Swan Estuary, the overall extents of those differences were generally lower than those detected among habitat types in each of the various seasons. Such findings contrast with those of Young and Potter (2003b), who reported considerably greater seasonal than regional differences in the composition of the nearshore fish fauna throughout the basins and natural entrance channel of the Peel-Harvey Estuary.

Some of the greatest seasonal differences in fish assemblage composition throughout the Peel-Harvey Estuary were detected at habitats D and E in the tidal portion of the rivers. As the salinities at these two habitats, and particularly the former, were the lowest of all or most habitats during several seasons and were among the most variable throughout the year, it would be expected that such temporal differences in their fish assemblage compositions would largely reflect differences in the tolerance or affinities of certain species for higher or lower salinities. However, one of the only species that seemed to reflect such salinity preferences at habitat D was *P. olorum*, which has affinities for lower salinities and was recorded in considerably greater numbers in spring 2005 (followed by winter 2005) than in any other season, and thus at a time of year when salinities at that habitat were at their lowest. However, while *P. olorum* was also most abundant by far during spring 2005 at E, which also experienced its lowest salinities in this season (*i.e.* 5.9‰), this species was also notably more abundant in summer 2006 than in all other seasons at this habitat, and thus at a time of the year when salinities were much greater, *i.e.* 28.6‰. Furthermore, habitat J, which experienced the greatest range in salinity and also water temperature throughout the sampling period (*i.e.* 12.5-46.9‰ and 16.7-31.2°C, respectively), exhibited the lowest overall difference in fish faunal composition among seasons.

Most seasonal differences in the prevalence of particular fish species at both of the above riverine habitats, and also those at several other habitats that experienced notable changes in ichthyofaunal composition throughout the year, seemed to more strongly reflect differences in the reproductive and recruitment patterns of certain marine and/or estuarine species than species preferences for particular salinities or temperatures. For example, the far greater prevalence of *H. vittatus* at habitat D in spring 2005 and summer 2006 reflected the influx of extremely large numbers of its 0+ recruits, which migrate from nearby marine waters into shallow coastal areas and estuaries at that time of year, following the winter spawning period (Gaughan *et al.* 1990, 1996, Valesini *et al.* 2004). It is relevant that the seasons during which the greatest densities of this small clupeid were recorded at habitat D, and also several others such as B, E, L and M, are those in which river flow in this system is declining or close to its minimum, and thus far less likely to preclude the upstream migration of these juvenile fish (Gaughan *et al.* 1990, 1996). Secondly, the greater prevalence of *A. suppositus* at both habitats D and E during summer 2006, which contrasts with the affinities of this estuarine species for reduced salinities, reflected the recruitment of its juveniles following the spring spawning period (Gill and Potter 1993, Hoeksema and Potter 2006). The greater abundances of several other species during particular seasons at various other habitats also reflected the recruitment of their 0+ juveniles, including the marine estuarine-opportunist *Am. elongata* during winter 2005 at the Harvey Estuary habitats H and K (mean length *ca* 28 mm) and the estuarine and marine species *A. rueppellii* in summer 2007 at habitats H, I, L and M (mean length 30-38 mm) and *F. lateralis* in winter and/or spring

2005 at B, C, H, I and Q (mean length 21-34 mm). The recruitment of the juveniles of many of the above species to particular habitats in the Peel-Harvey Estuary during spring and/or summer also contributed substantially to the notably higher ichthyofaunal differences among habitats that were detected in those seasons (see subsection 6.2.1.1), and also the greater mean number of species and densities at most habitats at that time of year.

Although the notable seasonal differences in fish faunal composition at habitat Q reflected, in part, the seasonal recruitment of species such as *F. lateralis*, they were also largely attributable to the particularly low numbers of fish species and densities at this shallow sandy habitat in summer 2006 when salinities and water temperatures reached 44.4‰ and 26.8°C, respectively. The only species that characterised the fish assemblages at this habitat in this season was *A. elongata*, which is particularly euryhaline and able to withstand salinities approximately three times that value (Hoeksema *et al.* 2006a). The remaining seasonal differences in ichthyofaunal composition at this habitat, and also those at the nearby habitat J which were particularly small despite the large temporal variability in salinity and water temperature at this habitat (see above), were mainly attributable to shifts in the prevalence of highly euryhaline atherinid species, such as *L. presbyteroides*, *A. elongata*, *C. pauciradiatus* and *A. mugiloides*. Such seasonal differences in the prevalence of these estuarine species partly reflected the timing of their spawning and thus recruitment (Prince *et al.* 1982), and most likely also their schooling behaviour and thus inconsistent chance of capture.

6.2.3.2 Hyperbenthic assemblages

Moderate to very large differences were detected between winter 2005 and summer 2006 in the composition of the hyperbenthic assemblages and mean number of species at all habitats in the Peel-Harvey Estuary except the channel habitat L. Moreover, pronounced seasonal differences in the mean density of hyperbenthos were detected at all habitats except B and K. However, the seasonal trends in both mean number of species and overall densities varied markedly among habitats. Thus, whereas a far greater mean number of species was recorded in summer 2006 at K and especially H, the opposite was true at B and D. Moreover, the mean density of hyperbenthos at D in winter 2005 was approximately two orders of magnitude higher than in summer 2006, but appreciably more individuals were collected in summer than winter at habitats H and L.

The exceptionally large seasonal differences in hyperbenthic composition at the Harvey Estuary habitat H were attributable not only to a major shift in the suite of species that primarily characterised that assemblage in winter *vs* summer, but also to the considerably greater number of typifying species and their greater densities in that latter season. Thus, whereas the hyperbenthos at this habitat in winter was mainly characterised by a restricted suite of commonly occurring copepods, that in summer was typified and regularly distinguished by various amphipod species such as Hyalid sp.2, Ischyrocerid sp.2 and caprellid sp.1, and other taxa such as the mysid *G. sorrentoensis*, polychaete Spiorbid sp., decapod *P. australis* and tanaid *T. dulongii*, several of which exclusively characterised this habitat in this season. Such large differences in the characteristics of the hyperbenthos at H between winter and summer are inconsistent with the fact that it experienced one of the smallest seasonal differences in salinity due to its proximity to the artificial entrance channel. However, as many of the above species that characterised H in summer are typically associated with vegetation, which they use as a source of food and/or shelter, their greater prevalence in this season may reflect the increase in biomass of *Halophila ovalis*, the predominant seagrass at this habitat, and macroalgae that occurs around this time of year (Hillman *et al.* 1995, Astill and Lavery 2004). It may also reflect the reproductive patterns of these taxa and the recruitment of their juveniles during seasons when water temperatures, and thus conditions for growth, are at their maxima. Indeed, the abundance of Hyalid sp. has been shown by other workers to be positively related to water temperature (Hiwatari and Kajihara 1984).

The moderately high seasonal differences in hyperbenthic composition at the riverine habitat D and habitat B near the mouth of the Murray and Serpentine rivers partly reflected their greater suites and/or abundances of typifying species in winter 2005, which were considerably more important in distinguishing the faunas of these habitats than during summer 2006, particularly in the case of D. Thus, whereas the assemblages of B and D were only distinguished from those of other habitats by particular harpacticoid and/or cyclopoid species in summer, they were distinguished by a variety of other taxa in winter, such as Hyalid sp.2 and *Tanypodin* sp. at B and calanoid sp.4 and the polychaetes Capitellid sp. and Serpulid sp. at D. Such seasonal changes in the characteristics of the hyperbenthos at B are most likely related to the pronounced changes in water level and salinity that occurred at this habitat between summer and winter. Thus, the extremely shallow and hypersaline waters at B in summer presumably explain the dominance of its assemblage by a small suite of highly tolerant copepods in this season. Moreover, due to its location along the north-eastern shore of Peel Inlet, habitat B commonly received large accumulations of unattached floating macroalgae that were swept across that wide basin by prevailing south-westerly winds (pers. obs.). Such algal accumulations would provide a rich source of food and shelter for many hyperbenthic taxa and, combined with the higher water levels and moderate salinities at B in winter, most likely account for the increase in the mean number of species and relatively large suite of characteristic taxa at this habitat and time of year. The far greater hyperbenthic densities at the riverine habitat D in winter reflected the extraordinarily large numbers of calanoid sp.4, which was also important in distinguishing the faunas of this habitat in this season. As discussed in subsection 6.2.1.2, the prevalence of this species at D during winter may reflect its affinity for particular environmental conditions that result from increased freshwater flow, such as reduced salinity, greater turbidity or increases in particular food sources. Moreover, the greater occurrence of various polychaete species at D in winter may reflect the influence of greater sediment disturbance from increased river flow in this season. However, other workers have also shown that the presence of one of the polychaete species that characterised D in winter, namely Serpulid sp., often leads to localised increases in the number of other benthic species, as it provides a valuable microhabitat both between and on the calcareous tubes it builds (Haines and Maurer 1980).

7. Relationships between habitat types and faunal assemblages in the Broke Inlet

7.1 Results

7.1.1 Water quality parameters

The average values for salinity, water temperature and dissolved oxygen concentration, which were recorded at replicate sites representing each of the 11 habitats sampled seasonally throughout Broke Inlet between spring 2007 and winter 2008, were subjected to PERMANOVA to ascertain the extent to which they differed among habitats and seasons. These tests demonstrated that mean salinity and dissolved oxygen concentration differed significantly among both main effects and the interaction term ($p=0.001$), whereas mean water temperature exhibited only significant season and habitat x season effects ($p=0.001$; Table 7.1.1.1). For all three of these dependent variables, the relative importance of season was considerably greater than that of any other term, followed by that for the habitat x season interaction (Table 7.1.1.1).

Mean salinity was the least during winter 2008 at every habitat and, in most cases, the difference between these salinities and the next lowest value was considerable, *i.e. ca* 6-14‰ (Fig. 7.1.1.1a). Salinities were often greatest in summer or autumn 2008, and such differences in the rank order of seasons among habitats contributed to the significant interaction effect that was detected for this dependent variable. The interaction was also attributable to the considerable variability in the extent of seasonal differences in mean salinity among habitats. For example, whereas values ranged only between *ca* 24 and 31‰ at habitat G, with values for spring 2007, summer 2008 and autumn 2008 all being very similar, those at habitat E ranged between *ca* 6 and 31‰, with values in most seasons being considerably different. In general, consistently higher salinities were often recorded at the channel habitats B, G and H (Fig. 7.1.1.1a).

The mean water temperature was greatest in spring 2007, followed by summer 2008, at every habitat (Fig. 7.1.1.1b). Mean temperatures in autumn and winter 2008 were very similar, both to each other and among habitats, but with values in the latter season typically being lower. The significant habitat x season interaction was due mainly to variability in the extent of seasonal differences among habitats. For example, whereas a 7.3°C difference was detected between spring 2007 and summer 2008 at habitat D, the difference between this pair of seasons at habitat E was only 1°C (Fig. 7.1.1.1b).

Table 7.1.1.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on the data for salinity, water temperature and dissolved oxygen concentration throughout the Broke Inlet during spring 2007 and summer, autumn and winter 2008. df = degrees of freedom. Significant results are highlighted in bold.

		Salinity				**Temperature**				**Dissolved Oxygen**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Habitat	10	**180.070**	**16.789**	**3.379**	**0.001**	2.361	1.747	0.261	0.084	**8.759**	**11.999**	**0.736**	**0.001**
Season	3	**2394.900**	**223.290**	**7.716**	**0.001**	**671.090**	**496.740**	**4.090**	**0.001**	**183.880**	**251.920**	**2.139**	**0.001**
Two-way Interaction													
Habitat * Season	28	**61.896**	**5.771**	**3.622**	**0.001**	**5.016**	**3.713**	**0.969**	**0.001**	**4.279**	**5.863**	**0.954**	**0.001**
Residual	122	10.725		3.275		1.351		1.162		0.730		0.854	

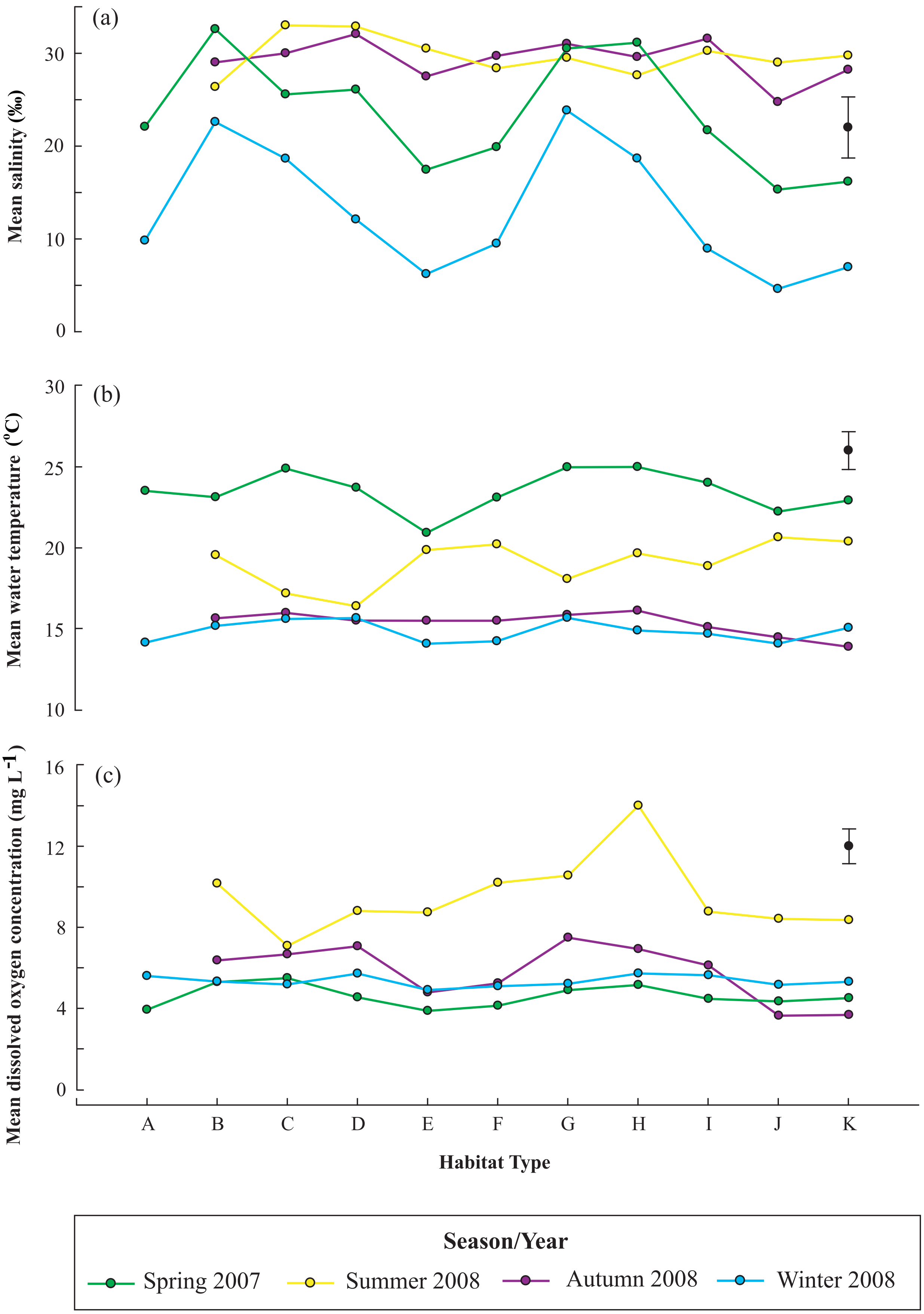


Figure 7.1.1.1: Mean (a) salinity, (b) water temperature and (c) dissolved oxygen concentration at each habitat type in the Broke Inlet between spring 2007 and winter 2008. For the sake of clarity, the average ±95% confidence intervals have been presented for each of these plots.

The mean dissolved oxygen concentration was greatest in summer 2008 at every habitat in Broke Inlet (Fig. 7.1.1.1c). However, this dependent variable also exhibited the most pronounced spatial differences during this season, which contributed to the substantial variability among habitats in the extent of the difference between summer 2008 values and the next highest value, *e.g.* 0.4 *vs* 7.1 mg L^{-1} at habitats C and H, respectively (Fig. 7.1.1.1c). These differences, in addition to the variability in the order of the remaining seasons among habitats, contributed to the significant habitat x season interaction that was detected for this water quality variable. Despite this, the lowest dissolved oxygen values were often found in spring 2007. Trends among habitats were less clear, but consistently low values were recorded at habitat C (5.2-7.1 mg L^{-1}) and, with the exception of summer 2008, habitats E, F, J and K (3.7-5.3 mg L^{-1}; Fig. 7.1.1.1c).

7.1.2 Fish assemblages

7.1.2.1 Species mean density and length characteristics at each habitat type

A total of 21 fish species and 48 247 individuals (*i.e.* after the number of fish in each sample was adjusted to that in 100 m^2 and summed) were recorded from the 11 nearshore habitats sampled throughout Broke Inlet during the four sampling seasons between spring 2007 and winter 2008 (Table 7.1.2.1). The most speciose habitat was H in the upper reaches of the channel (16), followed by habitats C (13) and B (12) on the southern shore of the basin and lower channel, respectively. The lowest number of species (5) was recorded at habitat A, located on the eastern shore of the basin near the mouth of the Inlet River. However, it should be noted that, due to the extremely large and shallow sand banks that surrounded this habitat, it could only be accessed during two of the four sampling seasons. Relatively low numbers of species, *i.e.* 6-8, were also recorded at each of the remaining habitats. As with number of species, the mean density of fish was greatest by far at habitat H, followed by that at the other channel habitat, B (*i.e.* 518 and 308 fish 100 m^{-2}, respectively), while the lowest was recorded at habitat A (*i.e.* 19 fish 100 m^{-2}). Average densities of approximately 150 fish 100 m^{-2} were recorded at habitats C and G, while those of 52-75 fish 100 m^{-2} were recorded at the remaining habitats (Table 7.1.2.1).

Atherinosoma elongata, *Leptatherina wallacei*, *L. presbyteroides* and *Afurcagobius suppositus,* all of which can complete their life cycles within the estuarine environment, ranked within the top four most abundant species at every habitat except B and I, at which the last species ranked fifth. The former species ranked first at all habitats, again with the exception of B, at which it ranked second, and comprised between *ca* 38 and 68% of the overall catch. The percentage contributions of *A. elongata* were greatest at habitats I, G, D and F (*i.e.* 64.4-68.3% of the total number of fish), but were not necessarily those at which the greatest mean densities

Table 7.1.2.1: Mean density (M), standard deviation (^{SD}), percentage contribution to the overall catch (%), rank by density (R) and length range and median length (L^{Med}) of each fish species recorded at each habitat type in the Broke Inlet between spring 2007 and winter 2008. Abundant species (*i.e.* those that contribute >5% to the catch) are highlighted in grey. The life-history category of each species is also provided (^{E}=estuarine, ^{EM}=estuarine and marine, ^{O}=marine estuarine-opportunist, ^{S}=marine straggler). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of fish in each sample had been adjusted to that in 100 m^2 and summed) are given for each habitat type.

Species name	Habitat type A				Habitat type B				Habitat type C				Habitat type D			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$10.88^{9.16}$	56.42	1	$17\text{-}87^{36}$	$116.51^{101.64}$	37.79	2	$17\text{-}90^{43}$	$79.98^{111.50}$	54.03	1	$16\text{-}95^{40}$	$33.38^{37.13}$	64.43	1	$16\text{-}104^{46}$
Leptatherina wallacei ^{E}	$7.54^{4.87}$	39.11	2	$18\text{-}73^{33}$	$30.52^{31.80}$	9.90	3	$20\text{-}67^{38}$	$27.88^{41.62}$	18.84	3	$20\text{-}77^{40}$	$7.89^{7.23}$	15.24	2	$22\text{-}71^{45}$
Leptatherina presbyteroides ^{EM}	$0.54^{1.05}$	2.79	3	$31\text{-}60^{38}$	$150.59^{225.16}$	48.85	1	$18\text{-}70^{36}$	$28.42^{75.42}$	19.20	2	$23\text{-}69^{44}$	$2.10^{4.50}$	4.06	4	$19\text{-}58^{42}$
Afurcagobius suppositus ^{E}	$0.27^{0.39}$	1.40	4	$30\text{-}37^{32}$	$3.39^{4.65}$	1.10	5	$17\text{-}96^{34}$	$7.54^{5.62}$	5.10	4	$20\text{-}93^{43}$	$6.63^{7.33}$	12.79	3	$22\text{-}73^{35}$
Favonigobius lateralis ^{EM}	$0.05^{0.15}$	0.28	5	35	$4.80^{5.80}$	1.56	4	$16\text{-}77^{35}$	$1.75^{2.23}$	1.18	5	$17\text{-}64^{45}$	$0.89^{1.73}$	1.72	5	$28\text{-}65^{46}$
Pseudogobius olorum ^{E}					$1.62^{5.14}$	0.52	6	$22\text{-}46^{34}$	$1.35^{3.03}$	0.91	6	$20\text{-}47^{28}$	$0.48^{1.03}$	0.94	6	$31\text{-}52^{35}$
Ammotretis rostratus ^{O}					$0.51^{0.69}$	0.17	7	$24\text{-}88^{59}$	$0.03^{0.11}$	0.02	9	41				
Engraulis australis ^{EM}					$0.22^{0.75}$	0.07	8	$59\text{-}86^{70}$								
Platycephalus speculator ^{EM}					$0.05^{0.22}$	0.02	9	$133\text{-}146^{140}$								
Pseudolabrus parilus ^{S}					$0.03^{0.11}$	0.01	10	89	$0.03^{0.11}$	0.02	9	74				
Achoerodus gouldii ^{S}					$0.03^{0.11}$	0.01	10	51								
Pseudorhombus jenynsii ^{O}					$0.03^{0.11}$	0.01	10	$36\text{-}195^{116}$								
Hyporhamphus melanochir ^{EM}									$0.92^{2.59}$	0.62	7	$59\text{-}214^{103}$	$0.03^{0.11}$	0.05	8	97
Enoplosus armatus ^{S}									$0.05^{0.15}$	0.04	8	$26\text{-}33^{30}$				
Urocampus carinirostris ^{EM}									$0.03^{0.11}$	0.02	9	52				
Pseudocaranx dentex ^{S}									$0.03^{0.11}$	0.02	9	44				
Neoodax balteatus ^{S}									$0.03^{0.11}$	0.02	9	109				
Aldrichetta forsteri ^{O}													$0.40^{1.62}$	0.78	7	$154\text{-}191^{174}$
Number of species	**5**				**12**				**13**				**8**			
Total mean density	**19**				**308**				**148**				**52**			
Number of samples	**16**				**32**				**32**				**32**			
Total number of fish	**309**				**9 866**				**4 737**				**1 658**			

Species name	Habitat type E				Habitat type F				Habitat type G				Habitat type H			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$38.66^{41.17}$	58.93	1	$16\text{-}110^{38}$	$42.16^{52.10}$	64.43	1	$17\text{-}90^{44}$	$103.10^{80.13}$	66.79	1	$15\text{-}108^{43}$	$210.21^{160.92}$	40.58	1	$15\text{-}97^{46}$
Leptatherina wallacei ^{E}	$19.61^{20.74}$	29.90	2	$16\text{-}76^{40}$	$16.38^{21.37}$	25.03	2	$21\text{-}79^{41}$	$28.85^{50.92}$	18.69	2	$20\text{-}66^{35}$	$122.93^{138.35}$	23.73	3	$19\text{-}85^{38}$
Leptatherina presbyteroides ^{EM}	$0.70^{1.81}$	1.07	4	$17\text{-}57^{30}$	$1.40^{2.46}$	2.14	4	$26\text{-}68^{43}$	$9.62^{13.15}$	6.23	3	$20\text{-}62^{38}$	$158.03^{266.49}$	30.50	2	$16\text{-}76^{34}$
Afurcagobius suppositus ^{E}	$6.03^{6.54}$	9.20	3	$20\text{-}78^{38}$	$3.99^{3.00}$	6.09	3	$21\text{-}81^{40}$	$7.92^{6.14}$	5.13	4	$17\text{-}90^{38}$	$14.68^{11.40}$	2.83	4	$15\text{-}93^{42}$
Favonigobius lateralis ^{EM}	$0.27^{0.56}$	0.41	6	$42\text{-}61^{50}$	$0.46^{0.94}$	0.70	6	$26\text{-}52^{42}$	$0.57^{0.93}$	0.37	6	$31\text{-}65^{48}$	$3.37^{6.71}$	0.65	6	$25\text{-}84^{53}$
Pseudogobius olorum ^{E}	$0.30^{0.66}$	0.45	5	$22\text{-}64^{26}$	$0.97^{2.34}$	1.48	5	$23\text{-}44^{33}$	$4.31^{6.32}$	2.79	5	$16\text{-}52^{29}$	$5.82^{9.24}$	1.12	5	$19\text{-}62^{30}$
Ammotretis rostratus ^{O}													$0.05^{0.15}$	0.01	11	$160\text{-}207^{184}$
Engraulis australis ^{EM}													$1.45^{4.00}$	0.28	7	$61\text{-}92^{78}$
Platycephalus speculator ^{EM}																
Pseudolabrus parilus ^{S}													$0.38^{0.75}$	0.07	10	$41\text{-}100^{85}$
Achoerodus gouldii ^{S}													$0.40^{1.19}$	0.08	9	$69\text{-}101^{89}$
Pseudorhombus jenynsii ^{O}																
Hyporhamphus melanochir ^{EM}	$0.03^{0.11}$	0.04	7	104	$0.03^{0.11}$	0.04	7	124					$0.54^{1.32}$	0.10	8	$60\text{-}257^{167}$
Enoplosus armatus ^{S}					$0.03^{0.11}$	0.04	7	24					$0.03^{0.11}$	0.01	16	31
Urocampus carinirostris ^{EM}																
Pseudocaranx dentex ^{S}																
Neoodax balteatus ^{S}																
Aldrichetta forsteri ^{O}													$0.03^{0.11}$	0.01	15	46
Girella zebra ^{S}													$0.05^{0.22}$	0.01	11	116
Mugil cephalus ^{O}													$0.05^{0.22}$	0.01	11	$24\text{-}29^{27}$
Haletta semifasciata ^{S}													$0.05^{0.22}$	0.01	11	95
Number of species		**7**				**8**				**6**				**16**		
Total mean density		**66**				**65**				**154**				**518**		
Number of samples		**32**				**32**				**32**				**32**		
Total number of fish		**2 099**				**2 094**				**4 940**				**16 578**		

Species name	Habitat type I				Habitat type J				Habitat type K			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	45.23$^{44.64}$	68.34	1	14-89^{38}	34.27$^{25.65}$	56.92	1	15-108^{32}	35.99$^{48.50}$	47.92	1	17-119^{36}
Leptatherina wallacei ^{E}	15.11$^{19.78}$	22.83	2	19-82^{37}	16.70$^{18.56}$	27.74	2	15-95^{31}	16.78$^{22.60}$	22.35	3	18-68^{32}
Leptatherina presbyteroides ^{EM}	2.77$^{4.87}$	4.19	3	16-57^{38}	0.68$^{1.44}$	1.13	4	22-36^{27}	20.99$^{76.62}$	27.94	2	20-67^{40}
Afurcagobius suppositus ^{E}	1.13$^{1.52}$	1.71	5	21-64^{33}	7.65$^{10.62}$	12.71	3	18-53^{32}	1.02$^{1.53}$	1.36	4	20-72^{37}
Favonigobius lateralis ^{EM}	1.78$^{1.93}$	2.69	4	23-63^{40}	0.43$^{0.86}$	0.72	6	26-54^{42}	0.19$^{0.35}$	0.25	5	28-57^{34}
Pseudogobius olorum ^{E}	0.13$^{0.30}$	0.20	6	25-43^{29}	0.47$^{0.95}$	0.78	5	18-50^{27}	0.05$^{0.15}$	0.07	6	34-40^{37}
Ammotretis rostratus ^{O}	0.03$^{0.11}$	0.04	7	110								
Engraulis australis ^{EM}									0.03$^{0.11}$	0.04	8	57
Platycephalus speculator ^{EM}												
Pseudolabrus parilus ^{S}												
Achoerodus gouldii ^{S}												
Pseudorhombus jenynsii ^{O}												
Hyporhamphus melanochir ^{EM}									0.05$^{0.22}$	0.07	7	141-152^{147}
Enoplosus armatus ^{S}												
Urocampus carinirostris ^{EM}												
Pseudocaranx dentex ^{S}												
Neoodax balteatus ^{S}												
Aldrichetta forsteri ^{O}												
Girella zebra ^{S}												
Mugil cephalus ^{O}												
Haletta semifasciata ^{S}												
Number of species		**7**				**6**				**8**		
Total mean density		**66**				**60**				**75**		
Number of samples		**32**				**24**				**32**		
Total number of fish		**2 118**				**1 445**				**2 403**		

of this species were recorded. Likewise, although the overall proportions of *L. wallacei* were greatest at habitats A, E and J (*i.e.* 27.7-39.1%), considerably higher mean densities were recorded at other habitats (Table 7.1.2.1). The estuarine and marine species *L. presbyteroides* made the greatest contribution, both in terms of its proportional and actual contribution, to the ichthyofauna at the channel habitats B and H and, to a lesser extent, to those at habitats K and C on the north-western and southern shores of the basin, respectively. By far the greatest percentage contributions of *A. suppositus* were recorded at habitats D, J and E (*i.e.* 9.2-12.8%), and these habitats included those at which some of the higher mean densities of this species were recorded (Table 7.1.2.1).

Several species, most of which were marine estuarine-opportunists or marine stragglers, *i.e. Platycephalus speculator, Achoerodus gouldii, Pseudorhombus jenynsii, Girella zebra, Mugil cephalus* and *Haletta semifasciata*, were recorded only at one or both of the channel habitats. Several species were also unique to habitat C, such as *Urocampus carinirostris, Pseudocaranx dentex* and *Neoodax balteatus* (Table 7.1.2.1).

7.1.2.2 Spatial and temporal differences in mean species richness, density and taxonomic distinctness

PERMANOVA demonstrated that the mean number of species, density and taxonomic distinctness of the fish assemblages in Broke Inlet each differed significantly among the 11 habitats and four sampling seasons, and that there was a significant habitat x season interaction in each case (p=0.001-0.028; Table 7.1.2.2). Based on the components of variation associated with each term in the above tests, differences among habitat types explained most of the variability in the case of the first two of these dependent variables, while the influence of the interaction term, followed closely by that of habitat type, was most important for the last dependent variable. The habitat x season interaction and the season main effect had the next greatest influence on the mean number of species and density, respectively (Table 7.1.2.2).

The mean number of species was typically higher at habitats B, C and H (4.25-6.5 species), and particularly during summer 2008 at the latter habitat type (8.75 species), and lower at habitats A, D, F and K (2.5-4.5 species; Fig. 7.1.2.1a). The significant habitat x season interaction detected for this dependent variable was due to the fact that the particular rank order of the seasons and the extent of seasonal differences varied considerably among habitats. For example, the greatest mean number of species was recorded during spring at habitats C and D, whereas the lowest values were recorded in this season at most of the remaining habitats. Moreover, while a considerable seasonal range in the mean number of species was found at

Table 7.1.2.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on the number of species, density and quantitative taxonomic distinctness of fish assemblages throughout the Broke Inlet during spring 2007 and summer, autumn and winter 2008. df = degrees of freedom. Significant results are highlighted in bold.

		Number of Species				**Density**				**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Habitat	10	**14.758**	**15.725**	**0.965**	**0.001**	**10.096**	**14.360**	**0.796**	**0.001**	**357.750**	**6.715**	**4.531**	**0.001**
Season	3	**6.046**	**6.442**	**0.357**	**0.003**	**11.446**	**16.280**	**0.518**	**0.001**	**336.830**	**6.323**	**2.661**	**0.002**
Two-way Interaction													
Habitat * Season	28	**1.758**	**1.873**	**0.458**	**0.012**	**1.163**	**1.654**	**0.343**	**0.028**	**163.920**	**3.077**	**5.326**	**0.001**
Residual	122	0.939		0.969		0.703		0.839		53.275		7.299	

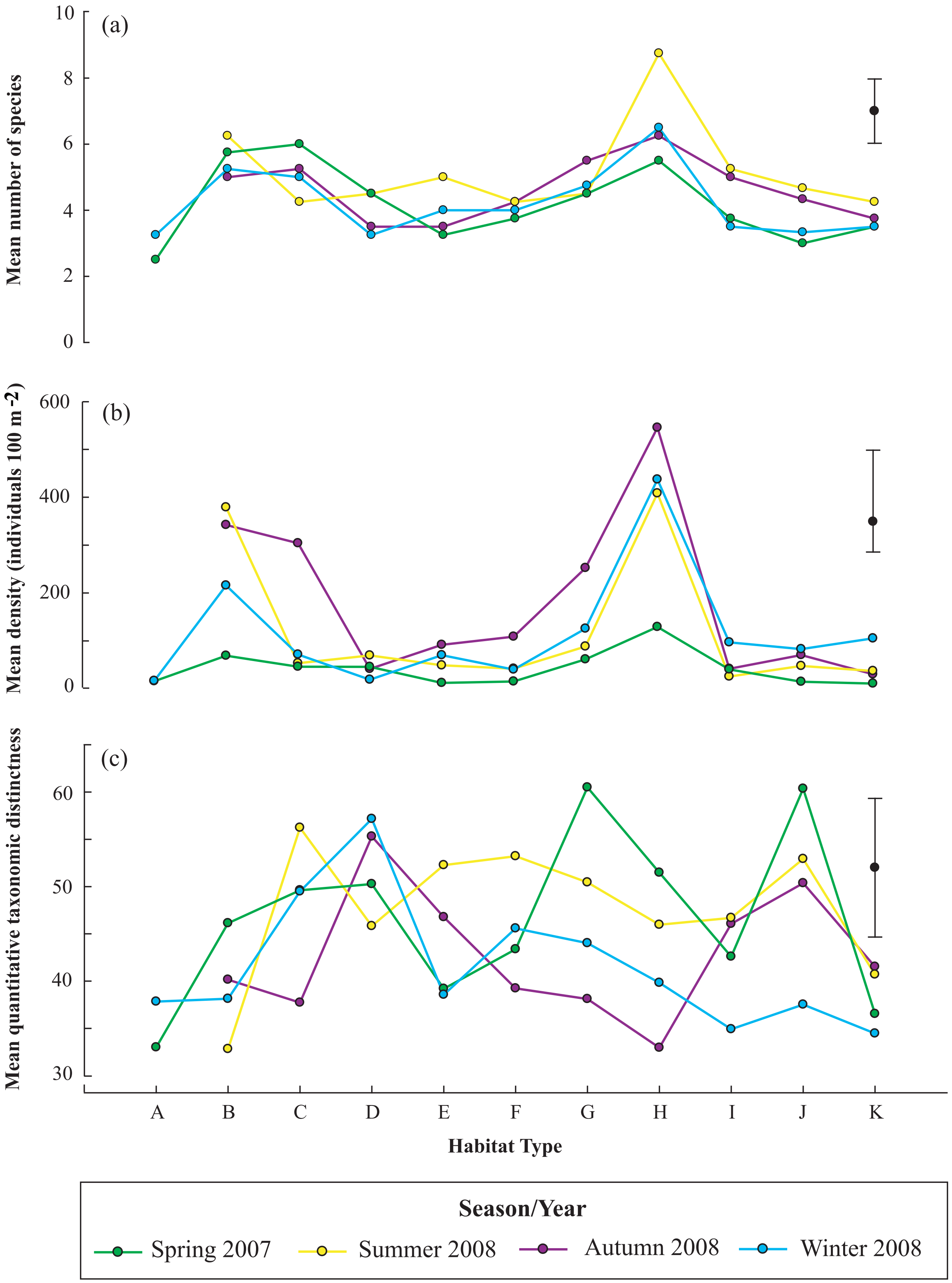


Figure 7.1.2.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the fish assemblages recorded at each habitat type in the Broke Inlet between spring 2007 and winter 2008. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

habitat H (5.5-8.75), it varied little at habitats such as F (3.75-4.25). Despite these interaction effects, the lowest number of species was recorded in winter or spring and the greatest in summer at most habitats (Fig. 7.1.2.1a).

In every season, the greatest mean density of fish was recorded at habitat H (*ca* 129-546 fish 100 m^{-2}), while the second greatest was recorded at the other channel habitat, B (*ca* 69-379 fish 100 m^{-2}). These trends were particularly marked in all seasons except spring 2007, during which spatial differences in this dependent variable were relatively small (Fig. 7.1.2.1b). Comparatively high mean densities were also recorded at habitats C and G in autumn, *i.e. ca* 304 and 252 fish 100 m^{-2}, respectively. With respect to seasonal trends, the greatest, or close to the greatest, mean density of fish was recorded during autumn at most habitats, while the lowest densities were often recorded in spring. Variability in the pattern and extent of seasonal differences in this dependent variable among habitats was mainly responsible for the significant habitat x season interaction. Thus, whereas marked seasonal differences were detected at the two channel habitats (see above) and, to lesser extents, at C and G, relatively minor seasonal differences were found at the remaining habitats, *i.e.* 11-109 fish 100 m^{-2} (Fig. 7.1.2.1b).

The plot of mean taxonomic distinctness of the fish assemblage at each habitat in each season demonstrated that there was considerable and erratic variability in the magnitude of this dependent variable, both spatially and temporally (Fig. 7.1.2.1c). Such variability explained the relative importance of the interaction term detected by PERMANOVA. Despite this, comparatively low values were found in most seasons at habitats A and K, while higher values were consistently found at habitat D. Clear seasonal trends among the various habitats were more difficult to discern, but more diverse assemblages were typically found in spring or summer, while the faunas were often least diverse in autumn or winter (Fig. 7.1.2.1c).

7.1.2.3 Composition of fish assemblages among habitats

Two-way crossed PERMANOVA demonstrated that the mean composition of the fish assemblages recorded at replicate sites representing each habitat throughout Broke Inlet in each season between spring 2007 and winter 2008 differed significantly among habitats and seasons, and that there was a significant interaction between these main effects (p=0.001). Moreover, the influence of habitat type was shown to be approximately twice as strong as that for both season and the habitat x season interaction. However, in view of the significant season and interaction terms, the following analyses to ascertain the nature and extent of ichthyofaunal differences among habitats were carried out separately for each season.

One-way ANOSIM tests, performed separately for the data collected in each season, showed that the composition of the fish assemblages differed significantly among habitats in each case (p=0.1%), but that the overall extents of those differences were only moderate. The greatest seasonal differences were detected in spring 2007 (Global R=0.502), while those in the remaining seasons were similar (Global R=0.320-0.381; Table 7.1.2.3). In each case, numerous comparisons between pairs of habitats were not significant, and several were not significant in any season, *e.g.* F *vs* A, C, D, G, J and K. However, those comparisons that were significant often had relatively large R-statistics, *i.e.* R >0.600 (Table 7.1.2.3).

During spring 2007, the fish fauna at the very shallow unvegetated habitat A was particularly distinct, as reflected by the high pairwise R-statistics for comparisons involving this habitat, *i.e.* often >0.800, and the fact that its representative samples formed a tight group on one side of the MDS plot constructed from the data recorded in this season (Table 7.1.2.3a, Fig. 7.1.2.2a). Its distinctiveness was largely attributable to its relatively depauperate fish fauna. Thus, while the fish assemblages at this habitat type were typified by the atherinids *A. elongata* and *L. wallacei*, the abundance of the first of these species was almost always greater at other habitats (Table 7.1.2.4a). The fish faunas at habitats B and I and, to a lesser extent, E and K, were also notably distinct in spring 2007, *i.e.* R often >0.700 (Table 7.1.2.3a). Three of the four samples representing the average fish composition at each replicate site of B formed a tight and discrete group that lay to one side of the MDS plot, while samples from habitat I generally lay between those for A and B. Samples from habitats E and K formed slightly more dispersed and intermingled groups, some of which also intermingled with those from A. Samples from habitats C, D, G and H formed overlapping groups, while those for F were highly dispersed throughout the MDS plot (Fig. 7.1.2.2a). The unvegetated channel habitat B was characterised by a relatively large and, in some cases, unique suite of species in this season, including *Favonigobius lateralis, A. elongata, Ammotretis rostratus, L. presbyteroides* and *L. wallacei*. With the exception of *L. wallacei*, each of these species were always more abundant at this habitat than at all other habitats with a significantly different ichthyofauna (Table 7.1.2.4a). This was also commonly the case for the species that characterised the fish assemblages at the unvegetated habitat I located on the northern shore of the basin, particularly with respect to *F. lateralis* and *L. wallacei*. Habitat K, which, like A, was located near a river mouth and was shallow and unvegetated, shared several ichthyofaunal similarities with that latter habitat in that its assemblages were also characterised by *A. elongata* and *L. wallacei* which were almost always more abundant at other habitats. The fish faunas at E in this season were also typified by

Table 7.1.2.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal composition among habitat types in the Broke Inlet during (a) spring 2007, (b) summer 2008, (c) autumn 2008 and (d) winter 2008. Insignificant pairwise comparisons are highlighted in grey.

(a) Spring 2007; p=0.1%, Global R=0.502

	A	B	C	D	E	F	G	H	I	J
B	0.844									
C	0.948	0.292								
D	0.938	0.625	-0.010							
E	0.229	0.792	0.625	0.521						
F	0.146	0.729	0.208	0.260	-0.104					
G	1.000	0.719	0.115	0.094	0.802	0.375				
H	0.979	0.573	0.083	0.104	0.792	0.469	0.104			
I	0.729	0.375	0.510	0.510	0.792	0.573	0.979	0.844		
J	0.833	0.759	0.426	0.296	0.222	0.093	0.389	0.630	0.981	
K	0.063	0.729	0.813	0.500	-0.177	-0.198	0.948	0.969	0.719	0.370

(b) Summer 2008; p=0.1%, Global R=0.381

	B	C	D	E	F	G	H	I	J
C	0.958								
D	0.990	0.000							
E	1.000	-0.094	0.063						
F	0.990	-0.083	0.115	-0.021					
G	0.865	-0.177	0.094	0.052	0.000				
H	0.594	0.604	0.688	0.667	0.792	0.510			
I	0.969	0.417	0.688	0.385	0.250	0.292	0.875		
J	0.944	-0.111	0.222	0.074	-0.093	-0.204	0.574	-0.056	
K	1.000	0.177	0.156	0.167	0.135	0.042	0.927	0.031	-0.093

(c) Autumn 2008; p=0.1%, Global R=0.320

	B	C	D	E	F	G	H	I	J
C	-0.125								
D	0.531	0.542							
E	0.375	0.552	-0.042						
F	0.344	0.344	0.354	-0.156					
G	0.177	0.156	0.688	0.323	0.281				
H	0.125	0.000	0.948	0.885	0.781	0.240			
I	0.302	0.323	0.177	0.448	0.208	0.625	0.844		
J	0.296	0.519	0.000	-0.130	-0.111	0.500	0.852	0.222	
K	0.188	0.333	0.406	0.250	0.115	0.406	0.490	0.219	-0.037

(d) Winter 2008; p=0.1%, Global R=0.348

	A	B	C	D	E	F	G	H	I	J
B	0.604									
C	0.896	0.271								
D	0.385	0.406	0.635							
E	0.250	0.375	0.292	0.458						
F	0.073	0.208	0.177	0.052	0.000					
G	0.708	-0.073	0.156	0.656	0.302	0.146				
H	1.000	-0.146	0.469	0.896	0.802	0.646	0.208			
I	0.438	0.479	0.667	0.521	-0.125	0.156	0.510	0.979		
J	0.370	0.204	0.241	0.519	-0.222	-0.037	0.352	0.815	-0.204	
K	0.469	0.479	0.625	0.604	-0.177	0.125	0.427	0.917	-0.240	-0.278

Table 7.1.2.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each habitat in the Broke Inlet during (a) spring 2007, (b) summer 2008, (c) autumn 2008 and (d) winter 2008, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Spring 2007

	A	B	C	D	E	F	G	H	I	J	K
A	*A. elongata* *L. wallacei*										
B	*F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *L. presbyteroides*^{B} *L. wallacei*^{A}	*F. lateralis* *A. elongata* *A. rostratus* *L. presbyteroides* *L. wallacei*									
C	*A. suppositus*^{C} *E. armatus*^{C} *P. olorum*^{C} *F. lateralis*^{C} *A. elongata*^{C} *L. wallacei*^{A}	▨	*A. elongata* *A. suppositus* *L. wallacei* *P. olorum*								
D	*A. suppositus*^{D} *P. olorum*^{D} *A. elongata*^{D} *F. lateralis*^{D} *L. wallacei*^{D}	*F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *A. suppositus*^{D} *P. olorum*^{D} *L. presbyteroides*^{B} *L. wallacei*^{D}	▨	*A. suppositus* *A. elongata* *L. wallacei* *P. olorum*							
E	▨	*F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *L. presbyteroides*^{B} *A. suppositus*^{E}	*A. suppositus*^{C} *E. armatus*^{C} *P. olorum*^{C} *F. lateralis*^{C} *A. elongata*^{C} *L. wallacei*^{C}	*A. elongata*^{D} *P. olorum*^{D} *A. suppositus*^{D} *F. lateralis*^{D} *L. wallacei*^{D}	*L. wallacei* *A. elongata* *A. suppositus*						
F	▨	*F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *A. suppositus*^{F} *L. presbyteroides*^{B}	▨	▨	*A. suppositus*^{F} *P. olorum*^{F} *A. elongata*^{E} *L. wallacei*^{E}	*L. wallacei* *A. elongata*					
G	*A. suppositus*^{G} *P. olorum*^{G} *A. elongata*^{G} *L. wallacei*^{A} *F. lateralis*^{G}	*A. suppositus*^{G} *P. olorum*^{G} *F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *L. presbyteroides*^{B} *L. wallacei*^{B}	▨	▨	*P. olorum*^{G} *A. suppositus*^{G} *A. elongata*^{G} *L. wallacei*^{E} *F. lateralis*^{G}	▨	*A. suppositus* *A. elongata* *P. olorum*				

	A	B	C	D	E	F	G	H	I	J	K
H	*A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H}	*F. lateralis*^{B} *A. suppositus*^{H} *A. rostratus*^{B} *P. olorum*^{H} *A. elongata*^{H} *L. presbyteroides*^{B}			*A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H}	*A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H}		*A. elongata* *P. olorum* *L. wallacei* *A. suppositus*			
I	*F. lateralis*^{I} *L. wallacei*^{I} *A. elongata*^{I} *L. presbyteroides*^{I}		*A. suppositus*^{C} *F. lateralis*^{I} *E. armatus*^{C} *P. olorum*^{C} *L. wallacei*^{I} *A. elongata*^{I}	*A. suppositus*^{D} *F. lateralis*^{I} *A. elongata*^{D} *P. olorum*^{D} *L. wallacei*^{I}	*F. lateralis*^{I} *A. elongata*^{I} *L. wallacei*^{I} *A. suppositus*^{E}	*F. lateralis*^{I} *A. elongata*^{I} *A. suppositus*^{F} *L. wallacei*^{I} *P. olorum*^{F}	*A. suppositus*^{G} *P. olorum*^{G} *F. lateralis*^{I} *L. wallacei*^{I} *A. elongata*^{G}	*A. suppositus*^{H} *A. elongata*^{H} *F. lateralis*^{I} *P. olorum*^{H}	*F. lateralis* *A. elongata* *L. wallacei*		
J	*A. suppositus*^{J} *L. wallacei*^{A} *A. elongata*^{A}	*F. lateralis*^{B} *A. rostratus*^{B} *A. suppositus*^{J} *A. elongata*^{B} *L. presbyteroides*^{B} *L. wallacei*^{B}						*A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H} *L. wallacei*^{H}	*F. lateralis*^{I} *A. suppositus*^{J} *L. wallacei*^{I} *A. elongata*^{I}	*A. suppositus* *A. elongata*	
K		*F. lateralis*^{B} *A. rostratus*^{B} *A. elongata*^{B} *L. presbyteroides*^{B}	*A. suppositus*^{C} *E. armatus*^{C} *A. elongata*^{C} *P. olorum*^{C} *F. lateralis*^{C} *L. wallacei*^{C}	*A. elongata*^{D} *A. suppositus*^{D} *P. olorum*^{D} *F. lateralis*^{D} *L. wallacei*^{D}			*A. suppositus*^{G} *P. olorum*^{G} *A. elongata*^{G} *L. wallacei*^{K} *F. lateralis*^{G}	*A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H} *F. lateralis*^{H}	*F. lateralis*^{I} *A. elongata*^{I} *L. wallacei*^{I} *L. presbyteroides*^{I}		*L. wallacei* *A. elongata*

(b) Summer 2008

	B	C	D	E	F	G	H	I	J	K
B	*L. presbyteroides* *L. wallacei* *A. elongata* *F. lateralis* *A. rostratus*									
C	*L. presbyteroides*^{B} *F. lateralis*^{B} *L. wallacei*^{B} *A. suppositus*^{C} *A. elongata*^{B} *A. rostratus*^{B}	*A. suppositus* *A. elongata*								
D	*F. lateralis*^{B} *L. presbyteroides*^{B} *A. suppositus*^{D} *L. wallacei*^{B} *A. elongata*^{B} *A. rostratus*^{B}		*A. suppositus* *A. elongata* *L. wallacei*							
E	*L. presbyteroides*^{B} *F. lateralis*^{B} *A. suppositus*^{E} *L. wallacei*^{B} *A. elongata*^{B} *A. rostratus*^{B}			*A. suppositus* *A. elongata* *L. wallacei*						
F	*L. presbyteroides*^{B} *F. lateralis*^{B} *A. suppositus*^{F} *L. wallacei*^{B} *A. elongata*^{B} *A. rostratus*^{B}				*A. suppositus* *L. wallacei* *A. elongata* *F. lateralis*					
G	*L. presbyteroides*^{B} *F. lateralis*^{B} *L. wallacei*^{B} *A. suppositus*^{G} *A. rostratus*^{B} *A. elongata*^{B}					*A. suppositus* *A. elongata*				
H	*A. suppositus*^{H} *F. lateralis*^{B} *L. wallacei*^{H} *P. parilus*^{H} *A. elongata*^{H} *L. presbyteroides*^{B} *A. gouldii*^{H} *E. australis*^{H} *A. rostratus*^{B} *H. melanochir*^{H}	*L. wallacei*^{H} *A. elongata*^{H} *F. lateralis*^{H} *A. suppositus*^{H} *A. gouldii*^{H} *P. parilus*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*A. elongata*^{H} *L. wallacei*^{H} *F. lateralis*^{H} *A. suppositus*^{H} *P. parilus*^{H} *A. gouldii*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*A. elongata*^{H} *L. wallacei*^{H} *F. lateralis*^{H} *P. parilus*^{H} *A. suppositus*^{H} *A. gouldii*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*A. elongata*^{H} *L. wallacei*^{H} *A. suppositus*^{H} *P. parilus*^{H} *F. lateralis*^{H} *A. gouldii*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*L. wallacei*^{H} *A. suppositus*^{H} *A. elongata*^{H} *P. olorum*^{H} *P. parilus*^{H} *F. lateralis*^{H} *A. gouldii*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*A. suppositus* *A. elongata* *L. wallacei* *L. presbyteroides*			

	B	C	D	E	F	G	H	I	J	K
I	*L. presbyteroides*^{B} *F. lateralis*^{B} *L. wallacei*^{B} *A. elongata*^{B} *A. rostratus*^{B} *A. suppositus*^{I}	*A. suppositus*^{C} *F. lateralis*^{I} *P. olorum*^{C} *A. elongata*^{C} *L. wallacei*^{I}	*A. suppositus*^{D} *F. lateralis*^{I} *L. wallacei*^{D} *A. elongata*^{D} *L. presbyteroides*^{D}	*A. suppositus*^{E} *F. lateralis*^{I} *L. wallacei*^{E} *P. olorum*^{E} *A. elongata*^{E}		*A. suppositus*^{G} *A. elongata*^{G} *F. lateralis*^{I} *P. olorum*^{G} *L. wallacei*^{I}	*A. suppositus*^{H} *A. elongata*^{H} *L. wallacei*^{H} *P. parilus*^{H} *A. gouldii*^{H} *F. lateralis*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}	*F. lateralis* *A. elongata* *L. wallacei* *A. suppositus*		
J	*L. presbyteroides*^{B} *F. lateralis*^{B} *L. wallacei*^{B} *A. suppositus*^{J} *A. elongata*^{B} *A. rostratus*^{B}								*A. elongata* *A. suppositus* *F. lateralis* *L. wallacei*	
K	*L. presbyteroides*^{B} *F. lateralis*^{B} *L. wallacei*^{B} *A. elongata*^{B} *A. rostratus*^{B} *A. suppositus*^{K}	*A. suppositus*^{C} *F. lateralis*^{C} *P. olorum*^{C} *L. wallacei*^{K} *A. elongata*^{C}					*A. suppositus*^{H} *A. elongata*^{H} *L. wallacei*^{H} *P. parilus*^{H} *F. lateralis*^{H} *A. gouldii*^{H} *L. presbyteroides*^{H} *H. melanochir*^{H}			*A. elongata* *L. wallacei* *A. suppositus* *L. presbyteroides*

(c) Autumn 2008

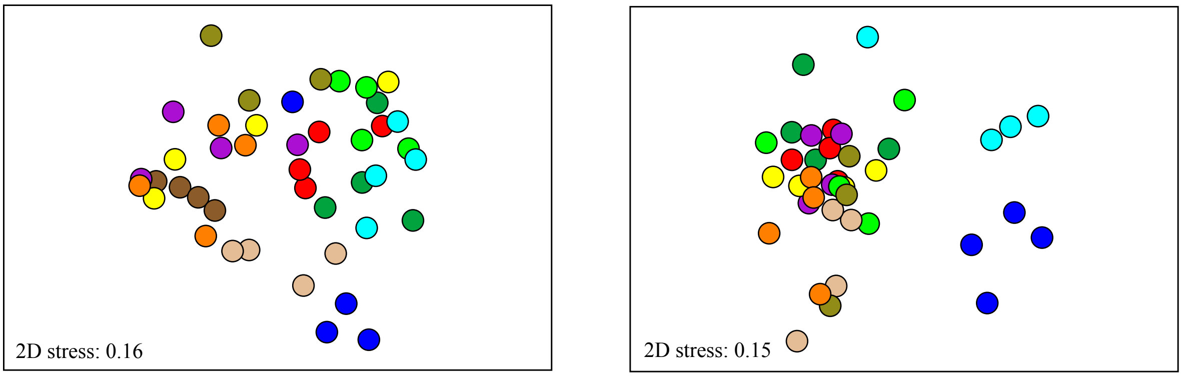
	B	C	D	E	F	G	H	I	J	K
B	*L. presbyteroides* *A. elongata* *F. lateralis* *L. wallacei* *A. suppositus*									
C		*A. elongata* *L. wallacei* *F. lateralis* *A. suppositus* *L. presbyteroides*								
D	*L. presbyteroides*^{B} *A. elongata*^{B} *A. suppositus*^{D} *L. wallacei*^{B} *F. lateralis*^{B}	*L. wallacei*^{C} *A. elongata*^{C} *L. presbyteroides*^{C} *A. suppositus*^{D} *F. lateralis*^{C}	*A. suppositus* *A. elongata* *L. wallacei*							
E	*L. presbyteroides*^{B} *A. elongata*^{B} *A. suppositus*^{E} *F. lateralis*^{B} *L. wallacei*^{B}	*F. lateralis*^{C} *L. wallacei*^{C} *L. presbyteroides*^{C} *A. elongata*^{C} *A. suppositus*^{E}		*A. suppositus* *L. wallacei* *A. elongata*						
F	*L. presbyteroides*^{B} *A. elongata*^{B} *L. wallacei*^{F} *F. lateralis*^{B} *A. suppositus*^{F}				*A. elongata* *L. wallacei* *A. suppositus*					
G			*L. wallacei*^{G} *A. elongata*^{G} *F. lateralis*^{D} *P. olorum*^{G} *A. suppositus*^{D} *L. presbyteroides*^{G}			*L. wallacei* *A. elongata* *A. suppositus* *L. presbyteroides*				
H			*L. wallacei*^{H} *A. elongata*^{H} *L. presbyteroides*^{H} *F. lateralis*^{H} *A. suppositus*^{D} *P. olorum*^{H}	*L. wallacei*^{H} *L. presbyteroides*^{H} *F. lateralis*^{H} *A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H}	*L. wallacei*^{H} *L. presbyteroides*^{H} *F. lateralis*^{H} *A. elongata*^{H} *A. suppositus*^{H} *P. olorum*^{H}		*L. wallacei* *A. elongata* *A. suppositus* *L. presbyteroides* *F. lateralis*			
I	*L. presbyteroides*^{B} *A. elongata*^{B} *L. wallacei*^{B} *A. suppositus*^{B} *F. lateralis*^{B}					*L. wallacei*^{G} *A. elongata*^{G} *A. suppositus*^{G} *F. lateralis*^{I} *P. olorum*^{G}	*L. wallacei*^{H} *A. elongata*^{H} *L. presbyteroides*^{H} *A. suppositus*^{H} *F. lateralis*^{H} *P. olorum*^{H}	*A. elongata* *A. suppositus* *L. wallacei* *F. lateralis* *L. presbyteroides*		

	B	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
J						*L. wallacei*^{G} *A. elongata*^{G} *A. suppositus*^{J} *P. olorum*^{G} *F. lateralis*^{G}	*L. wallacei*^{H} *L. presbyteroides*^{H} *A. elongata*^{H} *F. lateralis*^{H} *A. suppositus*^{J} *P. olorum*^{H}		*A. suppositus* *A. elongata* *L. wallacei*	
K		*L. wallacei*^{C} *A. elongata*^{C} *F. lateralis*^{C} *L. presbyteroides*^{C} *A. suppositus*^{C}	*A. suppositus*^{D} *F. lateralis*^{D} *A. elongata*^{K} *L. presbyteroides*^{K} *L. wallacei*^{K}	*A. suppositus*^{E} *A. elongata*^{E} *L. wallacei*^{E} *L. presbyteroides*^{K}		*L. wallacei*^{G} *A. elongata*^{G} *A. suppositus*^{G} *L. presbyteroides*^{K} *P. olorum*^{G} *F. lateralis*^{G}	*L. wallacei*^{H} *A. elongata*^{H} *A. suppositus*^{H} *L. presbyteroides*^{H} *F. lateralis*^{H} *P. olorum*^{H}			*A. elongata* *L. wallacei*

(d) Winter 2008

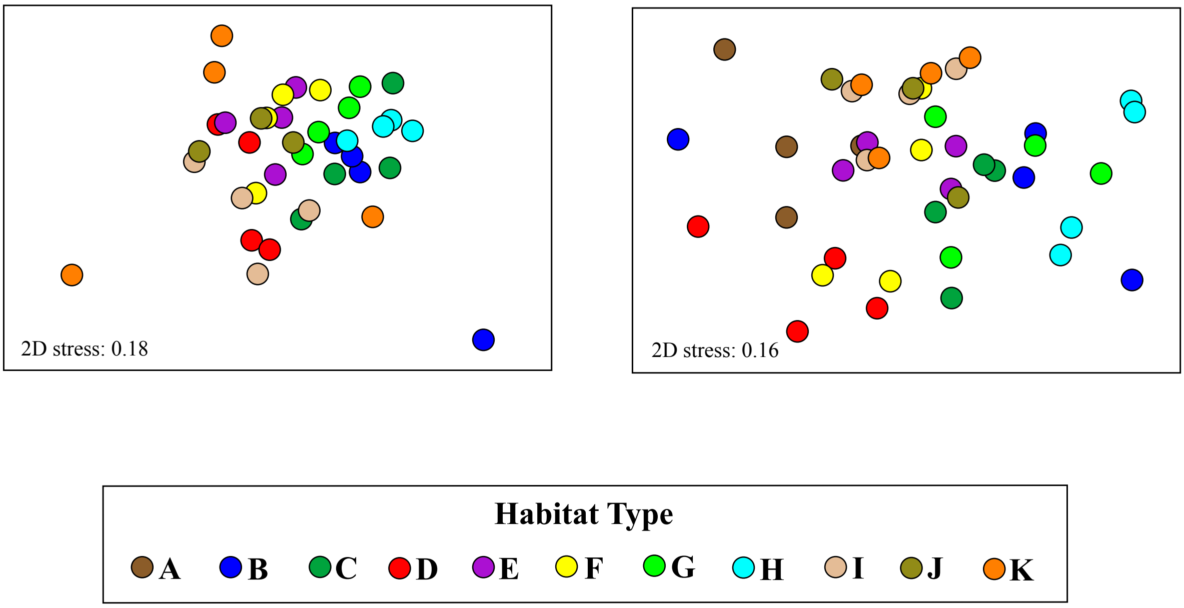
	A	B	C	D	E	F	G	H	I	J	K
A	*L. wallacei* *A. elongata* *A. suppositus*										
B		*L. presbyteroides* *A. elongata* *A. suppositus* *L. wallacei*									
C	*A. suppositus*^{C} *A. elongata*^{C} *F. lateralis*^{C} *L. wallacei*^{C} *P. olorum*^{C}	*L. presbyteroides*^{B} *A. suppositus*^{C} *L. wallacei*^{C} *A. elongata*^{B} *P. olorum*^{B} *F. lateralis*^{B}	*A. suppositus* *L. wallacei* *A. elongata* *P. olorum*								
D	*L. wallacei*^{A} *A. suppositus*^{D} *F. lateralis*^{D} *A. elongata*^{D} *A. forsteri*^{D}	*L. presbyteroides*^{B} *A. suppositus*^{B} *L. wallacei*^{B} *P. olorum*^{B} *A. elongata*^{B} *F. lateralis*^{B}	*A. suppositus*^{C} *L. wallacei*^{C} *A. elongata*^{C} *F. lateralis*^{C} *P. olorum*^{C}	*A. elongata* *A. suppositus* *F. lateralis*							
E	*L. wallacei*^{E} *A. elongata*^{E} *A. suppositus*^{E} *F. lateralis*^{E}	*L. presbyteroides*^{B} *L. wallacei*^{E} *A. suppositus*^{B} *P. olorum*^{B} *A. elongata*^{B}		*L. wallacei*^{E} *A. suppositus*^{E} *A. elongata*^{E} *F. lateralis*^{D} *A. forsteri*^{D}	*L. wallacei* *A. elongata* *A. suppositus*						
F						*A. suppositus* *L. wallacei* *A. elongata*					
G	*A. elongata*^{G} *A. suppositus*^{G} *P. olorum*^{G} *L. wallacei*^{G} *L. presbyteroides*^{G}			*A. suppositus*^{G} *A. elongata*^{G} *P. olorum*^{G} *L. wallacei*^{G} *L. presbyteroides*^{G} *F. lateralis*^{D}			*A. elongata* *A. suppositus* *P. olorum* *L. wallacei*				
H	*L. presbyteroides*^{H} *A. suppositus*^{H} *P. olorum*^{H} *A. elongata*^{H} *L. wallacei*^{H} *F. lateralis*^{H}		*L. presbyteroides*^{H} *L. wallacei*^{H} *A. elongata*^{H} *P. olorum*^{H} *A. suppositus*^{H}	*L. presbyteroides*^{H} *L. wallacei*^{H} *P. olorum*^{H} *A. suppositus*^{H} *A. elongata*^{H} *F. lateralis*^{H}	*L. presbyteroides*^{H} *P. olorum*^{H} *A. suppositus*^{H} *L. wallacei*^{H} *A. elongata*^{H} *F. lateralis*^{H}	*L. presbyteroides*^{H} *L. wallacei*^{H} *P. olorum*^{H} *A. elongata*^{H} *A. suppositus*^{H} *F. lateralis*^{H}		*A. suppositus* *L. wallacei* *A. elongata* *L. presbyteroides* *P. olorum*			
I	*A. elongata*^{I} *L. wallacei*^{I} *A. suppositus*^{I} *F. lateralis*^{I}	*L. presbyteroides*^{B} *A. suppositus*^{B} *L. wallacei*^{I} *A. elongata*^{I} *P. olorum*^{B}	*A. suppositus*^{C} *A. elongata*^{I} *F. lateralis*^{C} *L. wallacei*^{I} *P. olorum*^{C}	*L. wallacei*^{I} *A. elongata*^{I} *A. suppositus*^{D} *F. lateralis*^{D} *A. forsteri*^{D}			*A. suppositus*^{G} *L. wallacei*^{I} *A. elongata*^{G} *P. olorum*^{G} *L. presbyteroides*^{G}	*L. presbyteroides*^{H} *A. suppositus*^{H} *P. olorum*^{H} *L. wallacei*^{H} *A. elongata*^{H} *F. lateralis*^{H}	*L. wallacei* *A. elongata*		

	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
J				*L. wallacei*^{J} *A. suppositus*^{J} *A. elongata*^{J} *F. lateralis*^{D}				*L. presbyteroides*^{H} *A. suppositus*^{H} *P. olorum*^{H} *L. wallacei*^{H} *A. elongata*^{H} *F. lateralis*^{H}		*L. wallacei* *A. elongata*	
K	*A. elongata*^{K} *L. wallacei*^{K}	*L. presbyteroides*^{B} *L. wallacei*^{K} *A. suppositus*^{B} *A. elongata*^{K} *P. olorum*^{B}	*A. suppositus*^{C} *A. elongata*^{K} *L. wallacei*^{K} *F. lateralis*^{C}	*L. wallacei*^{K} *A. elongata*^{K} *A. suppositus*^{D} *F. lateralis*^{D}			*A. suppositus*^{G} *L. wallacei*^{K} *A. elongata*^{G} *P. olorum*^{G} *L. presbyteroides*^{G}	*L. presbyteroides*^{H} *A. suppositus*^{H} *P. olorum*^{H} *L. wallacei*^{H} *A. elongata*^{H} *F. lateralis*^{H}			*L. wallacei* *A. elongata*



(a) Spring 2007

(b) Summer 2008



(c) Autumn 2008

(d) Winter 2008

Figure 7.1.2.2: MDS ordination plots constructed from the fish assemblage data recorded at each replicate site representing each habitat type in the Broke Inlet during (a) spring 2007, (b) summer 2008, (c) autumn 2008 and (d) winter 2008.

the same two atherinid species, as well as *A. suppositus*. Moreover, each of these species were occasionally found in greater densities at E than other habitats (Table 7.1.2.4a).

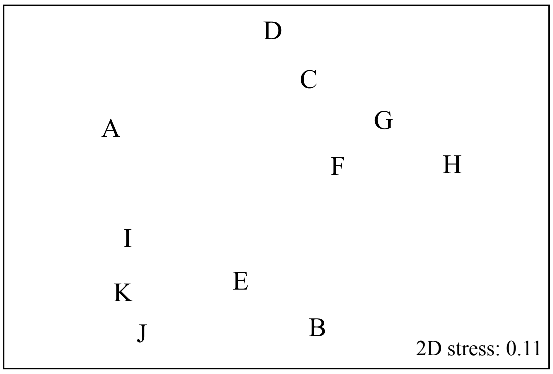
The fish faunal composition at B was particularly distinct in summer 2008, as reflected by the very high pairwise R-statistics for this habitat (*i.e.* >0.900 in almost all cases; Table 7.1.2.3b) and the fact that each of its representative samples formed a relatively tight and entirely discrete group that lay a considerable distance from those for all other habitats on the MDS plot shown in Fig. 7.1.2.2b. The fish assemblage at B was most similar to that at H (R=0.594), which was also located in the channel but was highly vegetated. The ichthyofauna at this latter habitat type was also distinct, as indicated by the relatively high R values for many pairwise comparisons involving this habitat (*i.e.* often >0.600) and the fact that most of its samples formed a discrete group that was located a considerable distance from those for all others (Table 7.1.2.3b, Fig. 7.1.2.2b). SIMPER showed that the fish assemblage at habitat B in summer 2008 was characterised by the same suite of species as in spring 2007, with the exception that the relative importance of those species differed, *i.e. cf* listed order in Table 7.1.2.4a *vs* b. All of these species were always more prevalent at B than at any other habitat, apart from *A. elongata* and *L. wallacei* at H. The ichthyofauna at habitat H was characterised by A. *suppositus, A. elongata, L. wallacei* and *L. presbyteroides*, which were each nearly always most prevalent at this habitat, and was also consistently distinguished by the marine stragglers *A. gouldii* and *Pseudolabrus parilus* and the estuarine and marine species *Hyporhamphus melanochir* and *F. lateralis* (Table 7.1.2.4b). Apart from habitat I, the fish faunal compositions of all basin habitats were largely similar to each other in summer 2008 (Table 7.1.2.3b, Fig. 7.1.2.2b).

Habitat H contained the most distinct fish assemblages in both autumn and winter 2008, as demonstrated by the fact that the relevant pairwise R values were often greater than 0.800 and its representative samples formed a group, that was particularly tight in the first of these cases, that lay on one side of the MDS plots constructed from the data recorded in each of these seasons (Table 7.1.2.3c and d and Fig. 7.1.2.2c and d). The ichthyofaunas at habitat D were also relatively distinct from those at several other habitats in both of these seasons (*i.e.* R often >0.500), and particularly in winter 2008. In both cases, samples from D tended to form a group towards the opposite side of the MDS plot from those representing H. High pairwise R-statistic values were also recorded for several comparisons involving habitat A in winter 2008, during which its representative samples formed a group above those for D (Table 7.1.2.3d, Fig. 7.1.2.2d). In general, the groups of samples representing the various habitats in winter 2008 were considerably more dispersed than in other seasons (*cf* Fig. 7.1.2.2d and a, b and c). The fish fauna at habitat H was characterised by a similar suite of species in both of the above seasons, except that *F. lateralis* and *P. olorum* were more prevalent in autumn and winter, respectively, and that the relative importance of the remaining species differed (*cf* Table 7.1.2.4c and d). In almost all cases in both seasons, each of these species were more abundant at H than any other habitat. During autumn 2008, the fish fauna at the middle basin habitat D was typified by *A. suppositus, A. elongata* and *L. wallacei*, but only the first of these species was regularly more prevalent at this habitat than others from which it differed significantly (Table 7.1.2.4c). The first two of the above species and *F. lateralis* characterised habitat D in winter 2008, but only the two goby species were occasionally more abundant at this than other habitats in this season (Table 7.1.2.4d).

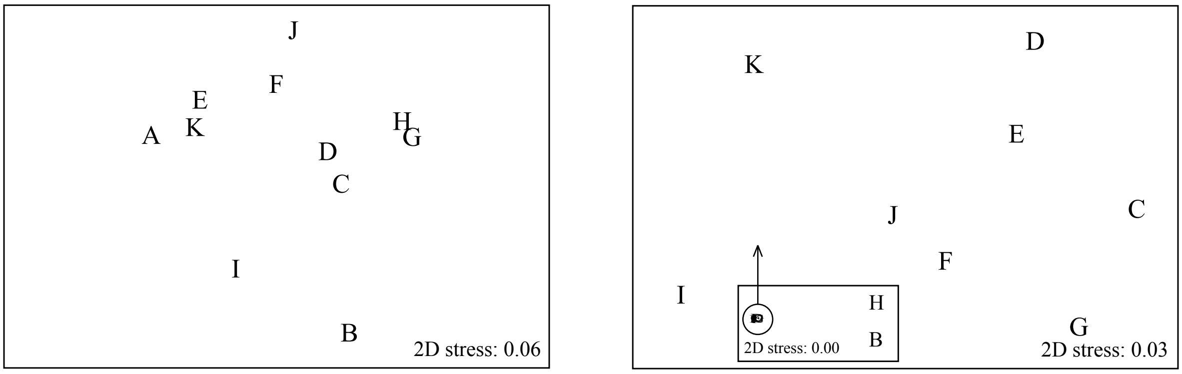
7.1.2.4 Matching spatial patterns between the environmental and fish assemblage characteristics of habitats

RELATE demonstrated that, in each of the four seasons, the spatial pattern among habitats exhibited by the suite of enduring environmental characteristics significantly matched that defined by the composition of their fish faunas (p=0.2-2.9%). However, the extent of that correlation was moderate to low, *i.e.* ρ=0.376 (winter 2008) - 0.282 (summer 2008). These results are reflected by the modest degree of similarity in the overall spatial distribution of samples between the MDS plot shown in Fig. 7.1.2.3a, which was constructed from the averages of the enduring environmental characteristics at each habitat, and those shown in Fig. 7.1.2.3b-e, which were constructed from the average fish faunal composition at each habitat in a particular season.

In spring 2007, the spatial pattern displayed by the average fish assemblage compositions at habitats A, B, C, D, G, H and I was similar to that exhibited by the complementary enduring environmental data (*cf* Fig. 7.1.2.3b and a). However, whereas similar enduring environmental measurements were recorded at habitats I, J and K, which were all unvegetated and located close to river mouths in the north-western corner of the basin, their average fish compositions differed considerably. Moreover, the ichthyofaunal characteristics of E were very similar to those of A and K in this season, whereas the enduring features of particularly A and E were conspicuously different (*cf* Fig. 7.1.2.3b and a). In summer 2008, the fish faunal assemblages at the channel habitats were exceptionally distinct from those for all basin habitats (see inset for Fig. 7.1.2.3c), and the MDS plot of the remaining data again demonstrated that the ichthyofaunal compositions of habitats I, J and K were all considerably different (Fig. 7.1.2.3c). The spatial patterns exhibited by the average fish compositions during autumn 2008 at habitats B, D, F, K and, to a

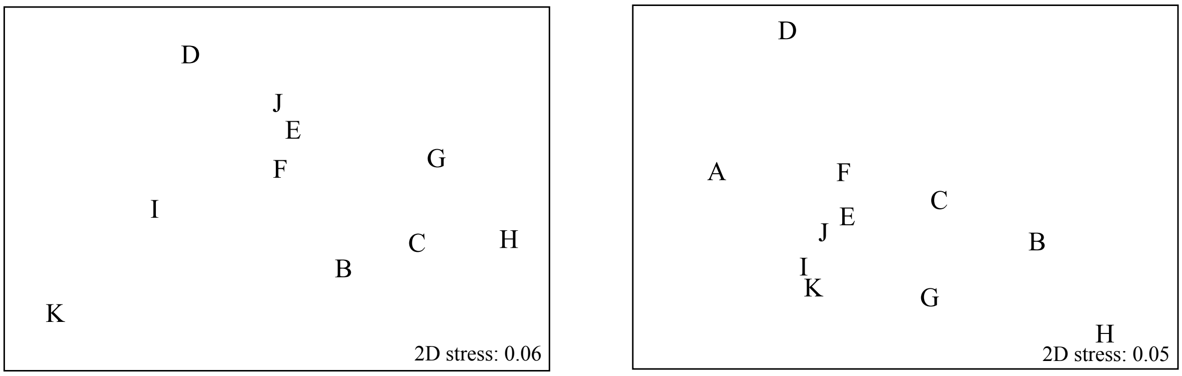


(a) Enduring environmental data



(b) Spring 2007; p=2.9%, ρ=0.285

(c) Summer 2008; p=1%, ρ=0.282



(d) Autumn 2008; p=1.6%, ρ=0.338

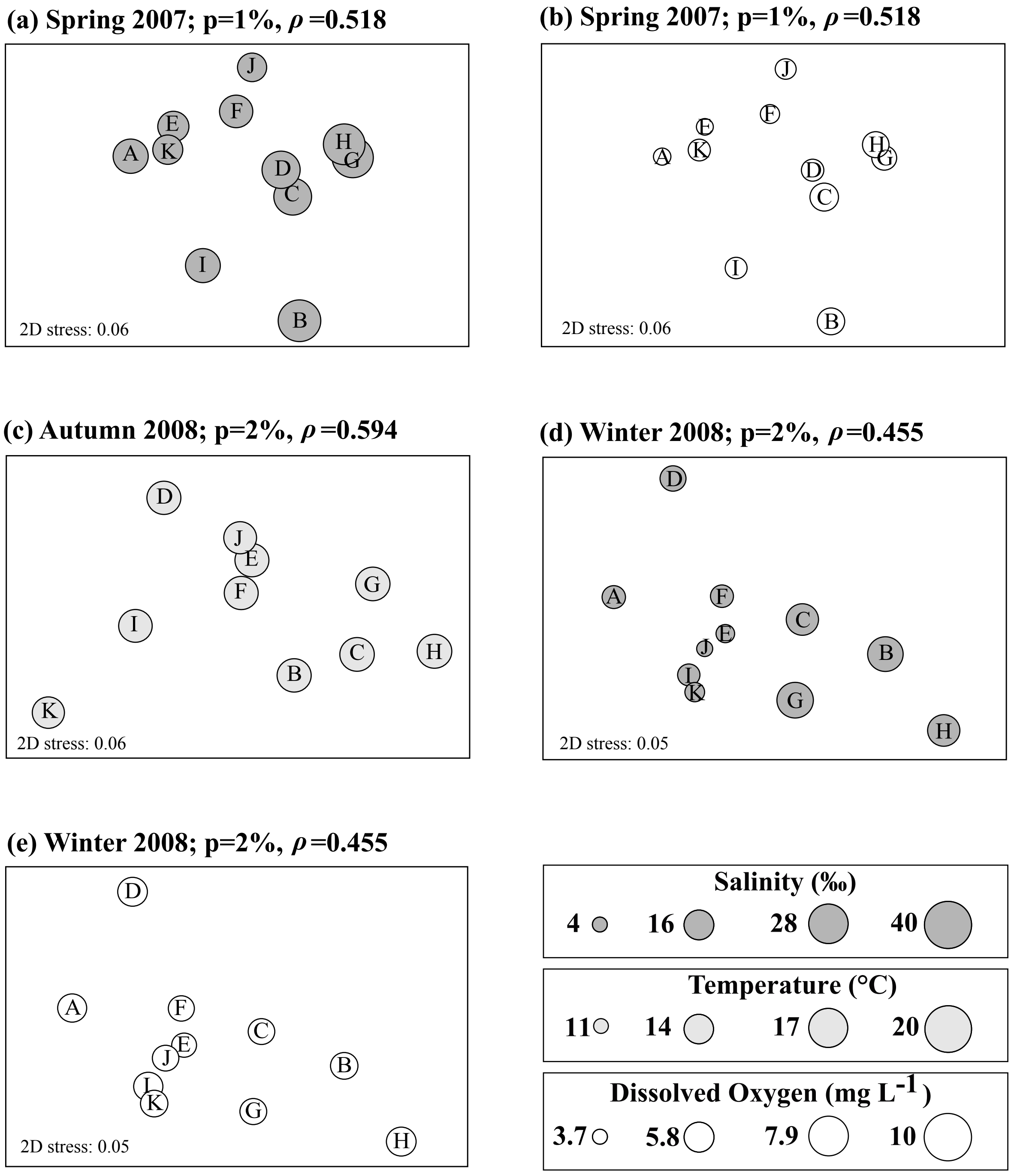
(e) Winter 2008; p=0.2%, ρ=0.376

Figure 7.1.2.3: MDS ordination plots constructed from the averages at each habitat type in the Broke Inlet of their (a) enduring environmental measurements and (b-e) fish faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the fish faunal data are also provided for each season.

lesser extent, G and H, were similar to those of the complementary enduring environmental data. Again, however, notable differences in ichthyofaunal composition among habitats I, J and K, and unexpected similarities in that between habitats E and F and also B and C, contributed to the relatively low correlation obtained in this season (*cf* Fig. 7.1.2.3d and a). Winter 2008 was the only season during which the spatial patterns exhibited by the average fish compositions at habitats I, J and K were similar to those of the complementary enduring environmental data. Furthermore, the spatial arrangement of habitats A, B, D and, to a lesser extent, H, were broadly similar between these two data sets. However, the ichthyofaunal similarities between habitats E, F, I, J and K and the relatively pronounced differences between habitats D and C were not mirrored by the environmental data (*cf* Fig. 7.1.2.3e and a).

Significant results were obtained for only spring 2007 and winter 2008 when each of the matrices constructed from the averages of the fish assemblage data at each habitat were matched, separately for each season, with the complementary matrices constructed from the suite of water quality data, *i.e.* salinity, temperature and dissolved oxygen (p=0.3-0.5%). However, in both cases, the extent of the correlation was slightly higher than that obtained when the fish data recorded in the above seasons was matched to the enduring environmental data, *i.e.* ρ=0.484 and 0.453, respectively. The subsequent use of BIOENV demonstrated that, in all seasons except summer 2008, a significant and greater correlation between the complementary fish and water quality matrices could be obtained by using only data for particular subsets of water quality variables. However, in both spring 2007 and winter 2008, this improvement was only marginal (*i.e.* p=1 and 2%, ρ=0.518 and 0.455, respectively), and was achieved when just dissolved oxygen concentration and salinity were employed. In autumn 2008, a notably greater match with the fish faunal data was obtained by using only water temperature, *i.e.* p=2%, ρ=0.594.

The relationships between the spatial patterns exhibited by the ichthyofaunal composition and the magnitude of the water quality parameter(s) selected by BIOENV are illustrated, for each season during which significant results were obtained, by the MDS and associated bubble plots shown in Fig. 7.1.2.4. These results demonstrated that, in spring 2007, habitats A, E, F, J and K, which shared relatively similar fish compositions and thus tended to occupy one side of the MDS plot, mainly had lower salinities and dissolved oxygen concentrations than those at the remaining habitats (Fig. 7.1.2.4a and b). During autumn 2008, the lowest and highest mean water temperatures were recorded at habitats K and H, respectively, which corresponded with their fish faunal compositions being the most dissimilar in this season (Fig. 7.1.2.4c). As in spring 2007, a range of basin habitats that had comparatively similar fish compositions all had relatively low salinities in winter 2008. Samples representing these habitats tended to occupy the opposite side



(a) Spring 2007; p=1%, ρ=0.518

(b) Spring 2007; p=1%, ρ=0.518

(c) Autumn 2008; p=2%, ρ=0.594

(d) Winter 2008; p=2%, ρ=0.455

(e) Winter 2008; p=2%, ρ=0.455

Figure 7.1.2.4: MDS ordination plots derived from the average fish faunal composition recorded at each habitat in the Broke Inlet in a particular sampling season. The magnitude of those water quality variables selected by the BIOENV routine when one of those matrices constructed from the above faunal data was matched with that constructed from the complementary water quality data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

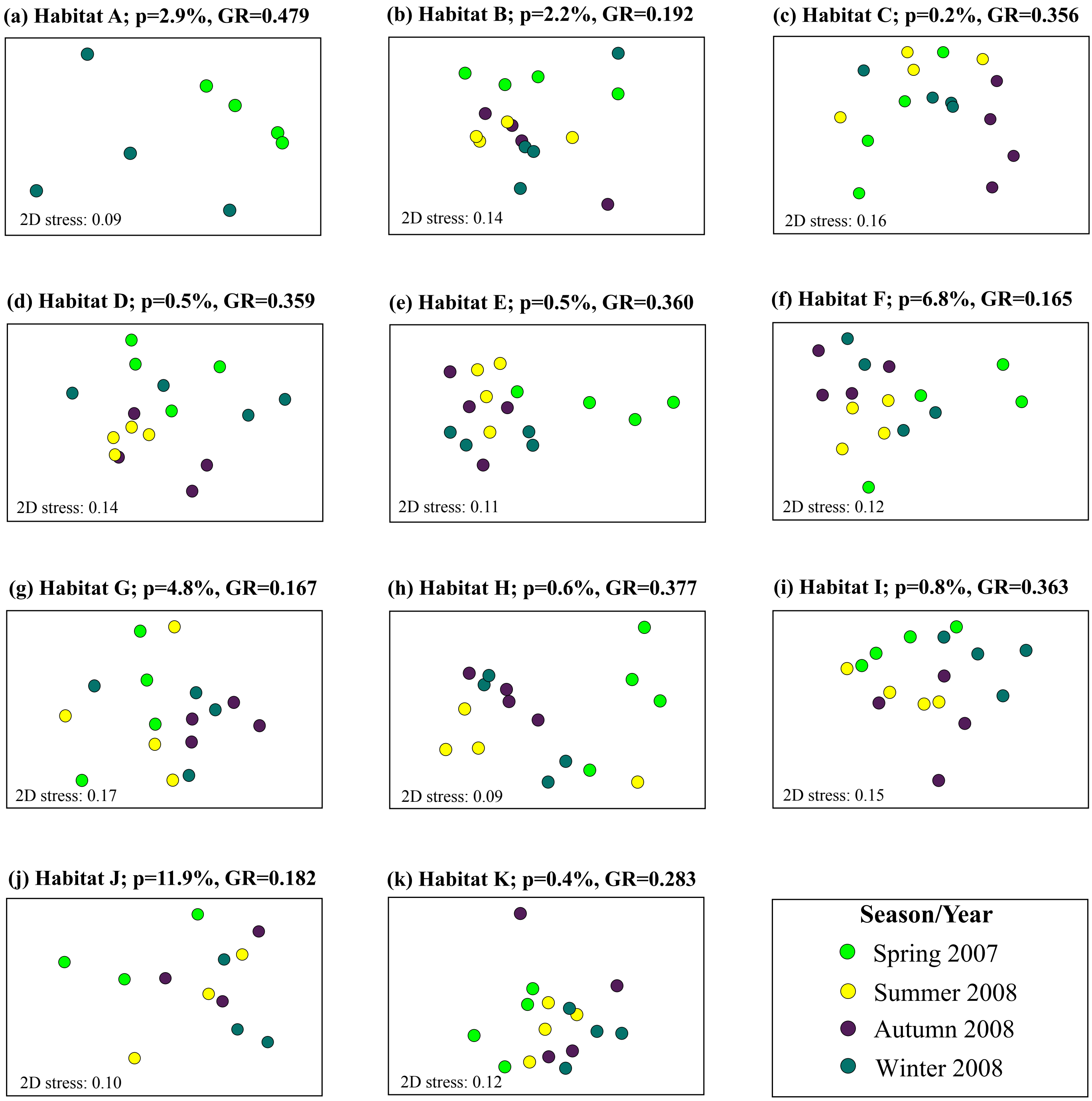
of the MDS plot, and were thus notably different in fish composition, from those representing habitats in the channel and lower reaches of the basin, at which much greater salinities were recorded (Fig. 7.1.2.4d). The relationship between the spatial patterns of the fish assemblages and dissolved oxygen concentration in winter 2008 demonstrated that habitats A, D and H, which each had relatively distinct ichthyofaunal compositions, also had the greatest mean dissolved oxygen concentrations. However, whereas habitat I also contained a relatively large dissolved oxygen concentration, its ichthyofaunal composition was very similar to that of the remaining habitats where the dissolved oxygen concentrations were lower (Fig. 7.1.2.4e).

7.1.2.5 Composition of fish assemblages among seasons

The composition of the ichthyofauna in Broke Inlet differed significantly among seasons at each habitat (p=0.2-4.8%), except for at F and J (p=6.8 and 11.9%, respectively). However, the extents of those significant differences were low to moderate and, in several cases, were lower than those detected among habitats, *i.e.* Global R=0.167-0.479 *vs* 0.320-0.502. The global one-way ANOSIM results and MDS plots, calculated separately for each habitat type using the average ichthyofaunal data recorded at representative sites in each season, are provided in Fig. 7.1.2.5. The mainly small temporal differences in ichthyofaunal composition are illustrated on these plots by the fact that, at many habitats, samples from each of the different seasons often did not tend to form discrete groups.

The greatest seasonal differences were detected at A (Global R=0.479), at which fish could only be sampled in spring 2007 and winter 2008 due to the extreme shallowness of the extensive sandy shoals that surrounded this habitat in the remaining seasons. The fish composition in the latter of those seasons was relatively variable, as reflected by the high dispersion of its representative samples on the MDS plot shown in Fig. 7.1.2.5a. However, consistently greater abundances of *A. suppositus* and *L. wallacei* in winter and of *A. elongata* in spring best distinguished the ichthyofaunas in these seasons.

The overall extent of the seasonal differences at habitats C, D, E, H and I was similar, *i.e.* Global R=0.356-0.377, but there was considerable variability in the patterns and main causes of those differences. Such variability was demonstrated by the following pairwise ANOSIM and SIMPER results, and also by differences in the relative spatial arrangement of samples representing each season and/or the extent of their group dispersion on the MDS plots shown in Fig. 7.1.2.5c, d, e, h and i, respectively. Thus, at the lower basin habitat C, significant differences were detected between all seasons except spring and summer, with the greatest differences occurring between autumn and all other seasons (R=0.510-0.583). SIMPER showed that the fish


(a) Habitat A; p=2.9%, GR=0.479

(b) Habitat B; p=2.2%, GR=0.192

(c) Habitat C; p=0.2%, GR=0.356

(d) Habitat D; p=0.5%, GR=0.359

(e) Habitat E; p=0.5%, GR=0.360

(f) Habitat F; p=6.8%, GR=0.165

(g) Habitat G; p=4.8%, GR=0.167

(h) Habitat H; p=0.6%, GR=0.377

(i) Habitat I; p=0.8%, GR=0.363

(j) Habitat J; p=11.9%, GR=0.182

(k) Habitat K; p=0.4%, GR=0.283

Figure 7.1.2.5: MDS ordination plots constructed from the fish assemblage data recorded at each replicate site in each sampling season at habitat (a) A, (b) B, (c) C, (d) D, (e) E, (f) F, (g) G, (h) H, (i) I, (j) J and (k) K in the Broke Inlet. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

faunas in autumn were distinguished from those in all other seasons by greater abundances of *L. wallacei, L. presbyteroides*, *F. lateralis* and *A. elongata*. In contrast, significant differences were detected only for summer *vs* spring and winter and for autumn *vs* spring (R=0.448-0.552) at habitat D, while at E, significant and similar differences (R=0.427-0.604) were found between all seasons except autumn *vs* summer and winter, which did not differ significantly. At the first of these habitats, greater catches of *A. suppositus* in summer than spring and winter were mainly responsible for distinguishing the ichthyofaunas of these seasons, and this species was also more prevalent in autumn than spring. *Atherinosoma elongata* and *L. wallacei* were also more abundant in summer than winter, while *P. olorum* was consistently more abundant in spring than summer. At habitat E, the summer and winter fish assemblages were mainly distinguished from those recorded in all other significantly different seasons by greater catches of *A. suppositus* and *L. wallacei*, respectively, while the ichthyofauna in autumn was best separated from that in spring, which was relatively depauperate, by greater abundances of both of the above species. Fish assemblage composition differed between all pairs of seasons except for winter *vs* summer and autumn at the channel habitat H, with the greatest differences by far occurring between spring and autumn (R=0.854), followed by spring *vs* winter and summer (R=0.583-0.698). These differences were primarily due to a lower prevalence of *L. wallacei, L. presbyteroides, A. suppositus* and *A. elongata* in spring than in each of the other seasons and, in the case of the latter comparison, also to greater catches of *F. lateralis, A. gouldii, P. parilus* and *H. melanochir* in summer. Significant differences were only detected between winter and all other seasons at habitat I, with the greatest of these occurring between summer and winter (R=0.740). The fish faunas in winter were best set apart from those recorded in all other seasons by their greater abundances of *L. wallacei* and *A. elongata*. In contrast, *L. presbyteroides* was more prevalent in autumn than winter, while the same applied to *F. lateralis* in spring and summer.

Overall seasonal differences in fish faunal composition were minimal at the lower channel habitat B, habitat G at the top of the channel/lower reaches of the basin and habitat K near the mouth of the Forth River (Global R=0.167-0.283; Fig. 7.1.2.5b, g and k, respectively). At the first of these habitats, significant differences were detected only for summer *vs* spring and winter (R=0.323-0.427), which was due mainly to more consistent and abundant catches of *L. wallacei, L. presbyteroides, F. lateralis* and *A. elongata* in summer than spring, and of *F. lateralis* and *A. rostratus* in summer than winter. Significant ichthyofaunal differences were detected only for autumn *vs* spring and summer at habitat G (R=0.281-0.594), which were driven mainly by the greater prevalence in the first of these seasons of *L. wallacei, A. elongata* and *L. presbyteroides* than in spring, and of *L. wallacei* and *P. olorum* than in summer. Finally, significant differences were detected only for winter *vs* summer and spring at habitat K, and the extent of those differences were much higher for the latter comparison, *i.e.* R=0.365 and 0.750, respectively. This was due mainly to the far greater and more consistent catches of *L. wallacei* and *A. elongata* in winter than in spring.

7.2 Discussion

7.2.1 Differences in fish assemblages among habitats

Significant differences in fish assemblage composition were detected among the various nearshore habitats throughout the seasonally-open and near pristine Broke Inlet in each of the four seasons between spring 2007 and winter 2008. However, the overall extents of those spatial differences were moderate to moderately low, and thus typically less than those detected in the permanently-open and highly modified Swan and Peel-Harvey estuaries on the lower west coast, particularly with respect to the former system. Moreover, the total number of fish species recorded throughout the nearshore waters of Broke Inlet was far lower than that found in the Swan and Peel-Harvey estuaries (*i.e.* 21 *vs* 60 and 71, respectively) and, unlike those two west coast systems, all of the abundant species at every habitat comprised *Atherinosoma elongata, Leptatherina wallacei, L. presbyteroides* and/or *Afurcagobius suppositus*, which are each able to complete their life cycle within the estuary. Moreover, with the exception of habitats in the entrance channel and the lowermost reaches of the basin, the faunas at almost all of the remaining habitats in Broke Inlet only contained one or two other species that were represented by more than one individual, *i.e.* the estuarine *Pseudogobius olorum* and the estuarine and marine *Favonigobius lateralis*. As discussed below and in the following subsections, such findings largely reflect (i) the seasonal closure of Broke Inlet to the sea, (ii) differences in the overall geomorphology of the above lower west coast systems *vs* this south coast system, (iii) the wide environmental tolerances of most of the species that dominate the nearshore fish assemblages within Broke Inlet, (iv) the higher wave energy in the nearshore marine waters adjacent to Broke Inlet than that outside the lower west coast estuaries, and thus less hospitable environment for the 0+ juveniles of marine species that migrate inshore, (v) limitations in the geographical range of particular fish species (Potter *et al.* 1990), (vi) the less diverse benthic structural heterogeneity throughout this estuary and/or (vii) the inability to sample the nearshore fish faunas in the tidal portions of the rivers of Broke Inlet (*i.e.* using a comparable method to that in the rest of the system and the four other estuaries examined in this study) due to their very steep banks and numerous snags.

In every season, some of the most distinct ichthyofaunal compositions were found at one or both of the habitats located in the entrance channel, *i.e.* B and H. Both of these habitats, but particularly the former, contained a notably distinct fish assemblage in spring and summer, while only that of H was also conspicuously different from those at most other habitats in the remaining seasons. Moreover, the fish compositions of these two channel habitats were conspicuously different in the first two of the above seasons. Such ichthyofaunal differences were typically reflected by the enduring environmental characteristics of these habitats. Thus, while several enduring features distinguished both of these channel habitats from the remainder in the wide basin of this system, *i.e.* their location, limited fetches in all directions and narrow wave shoaling margins, others clearly differentiated between these two habitats, such as the substantial submerged vegetation beds and steep slope of the substrate at H but not B.

The distinctness of the fish faunas at habitats B and H compared to those in the basins during the above-mentioned seasons was attributable, firstly, to the far greater densities of most species that characterised the former two habitats, even though most were also typical of the assemblages at many other habitats and, secondly, to other species that exclusively typified these channel habitats at particular times of year. For example, *A. elongata*, which was prevalent at most habitats throughout the year, always occurred in greater densities at B and H during each of the seasons in which their ichthyofaunas were markedly distinct. The same was almost always true of the widely distributed *L. wallacei, A. suppositus* and *P. olorum* at habitat H. Such findings were also reflected by the far greater overall mean density of fish recorded at these two channel habitats, and particularly H, than any of those in the basin. Moreover, the ichthyofauna at B was exclusively typified and regularly distinguished by the marine estuarine-opportunist *Ammotretis rostratus* in both spring and summer and, with one minor exception, also by the estuarine and marine species *F. lateralis* and *L. presbyteroides* in the first of these seasons. The marine stragglers *Pseudolabrus parilus* and *Achoerodus gouldii* and the estuarine marine *Hyporhamphus melanochir* also typified and distinguished the ichthyofauna of only habitat H during spring 2007.

The persistently greater densities of ubiquitous species such as *A. elongata* at B and H may partly reflect an affinity of this atherinid for the greater and less variable salinities recorded at these channel habitats throughout the year. Thus, while this estuarine species is extremely euryhaline and can tolerate salinities from *ca* 5-135‰ (Prince *et al.* 1982, Hoeksema *et al.* 2006a), it has typically been found in the greatest numbers at salinities of 20-36‰ in other south-western Australian estuaries (Prince *et al.* 1982). It may thus be relevant that, while the salinities at all habitats in Broke Inlet reached 29-33‰ throughout the year, they fell only to *ca* 19‰ at both channel habitats, but were as low as 4.6‰ in the basin. However, although the other three common atherinid and goby species (*i.e. L. wallacei*, *A. suppositus* and *P. olorum*) are also euryhaline, they are typically found in reduced salinities (Prince *et al.* 1982, Gill and Potter 1993). Their prevalence at H must thus be related to other factors, and most likely the greater shelter and/or food it provides. For example, the narrow banks and thus far smaller fetches in the channel of Broke Inlet are primarily responsible for the much lower levels of wave activity in this region than in the wide basin. Furthermore, the extensive and dense beds of the seagrass *Ruppia megacarpa* at habitat H provide further buffering of water disturbance, protection from piscivores and also a variety of food sources. The last feature is reflected by the greater densities of benthic macroinvertebrates, and primarily polychaetes, that typically occur at H compared to other habitats in the basin of Broke Inlet, and which provide a major food source for many fish species (Tweedley and Valesini 2008). Given that *A. suppositus* and *P. olorum* are typically associated with highly sheltered areas that have silty substrates, and that *A. suppositus* and *L. wallacei* feed mainly on polychaetes and/or planktonic crustaceans while *P. olorum* feeds largely on algae, detritus and mats of bacteria/fungi (Prince *et al.* 1982, Gill and Potter 1993, Humphries and Potter 1993), their notably greater densities at this habitat is thus presumably related to the additional shelter, detrital accumulations and food sources provided by the extensive beds of seagrass it contains. Each of the above three species was also relatively abundant at habitat G in the uppermost reaches of the channel and south-western corner of the basin and, in the case of *L. wallacei* and *A. suppositus*, also at habitat C along the south coast of the basin. Given the apparent environmental preferences of the above species, it is thus relevant that both of these habitats were relatively protected from wave activity due either to their fetches being limited in all directions (*i.e.* G) or their aspect (*i.e.* C, which was protected from the prevailing south-easterly winds). Furthermore, both C and G contained *R. megacarpa* beds, which were particularly extensive at the latter habitat.

Several of the above findings parallel those of Humphries and Potter (1993) in the nearby Wilson Inlet, another seasonally-closed basin estuary, in which the densities of *P. olorum, A. suppositus*, *L. wallacei* and *A. elongata* were greatest in areas containing patchy or dense *R. megacarpa* as opposed to bare sand. However, the spatial distribution patterns of the former three species in Broke Inlet differ, in some respects, from those recorded in various other estuaries in south-western Australia, including those in the current study of the Swan Estuary, in which these species are predominant in the fresher upper reaches and least prevalent in the more saline lower reaches (*e.g.* Prince *et al.* 1982, Loneragan and Potter 1990, Gill and Potter 1993, Young *et al.* 1997, Hoeksema *et al.* 2006a). The common occurrence of *P. olorum, A. suppositus* and *L. wallacei* throughout the basin of Broke Inlet probably partly reflects the fact that salinities at several habitats in that region of the estuary fell to <10‰ during winter 2008 (*cf* a minimum of *ca* 17‰ in the main basin of the Swan Estuary during this study) and, at habitats such as D and F, the presence of considerable beds of *R. megacarpa*. However, the greater densities of these three species at the channel habitat H, even during winter and spring when the mouth of Broke Inlet was open and thus the potential for these estuarine species to be flushed out to sea was greatest, presumably reflects the much greater protection from wave activity at that fetch-limited location and/or more abundant food sources. Moreover, it is possible that *P. olorum, A. suppositus* and *L. wallacei* may have been even more abundant in the tidal portions of the rivers of Broke Inlet, which could not be sampled. However, the latter seems less likely, given that the mean densities of these three species at habitat J, located immediately at the mouth of the Shannon River, were far less than those recorded at H.

The prevalence of *L. presbyteroides* and *F. lateralis* in the entrance channel, and particularly at habitat B at which the substrate consisted almost entirely of relatively coarse marine sand (J. Tweedley, unpublished data), parallels the findings of several other workers in south-western Australian estuaries. Thus, both of these species, which can complete their life cycle in marine and estuarine waters, have an affinity for higher salinities and are thus typically in their greatest numbers in the lower reaches of estuaries (Prince *et al.* 1982, Gill and Potter 1993). Moreover, the latter small benthic species is also known to prefer highly sheltered waters and sandy substrates comprising coarser grains (Gill and Potter 1993, Humphries and Potter 1993). Although these species occasionally typified the faunas of some habitats in the basins, they were rarely important in distinguishing the assemblages of those habitats. The only exception in some seasons was habitat I located on the northern shore of the basin, which had an entirely sandy substrate and extensive shallow wave shoaling margins. However, the densities of *F. lateralis* at this habitat were often notably lower than in the channel.

The consistent occurrence of the marine estuarine-opportunist *A. rostratus* only at habitat B and the marine stragglers *P. parilus* and *A. gouldii* only at H in particular seasons, which were each represented largely by their 0+ juveniles, reflected the recruitment of these species from nearby marine waters at a time of year when the bar to the estuary was open (*i.e.* spring 2007), or had closed recently before sampling was undertaken (*i.e.* summer 2008). The higher salinities and proximity to the sea of these channel habitats, as well as the greater camouflage provided for their juveniles against the marine sands at B in the case of the light-coloured flounder *A. rostratus* and seagrass at H in the case of the latter two species, were likely to be the predominant environmental factors influencing their spatial distribution in Broke Inlet during the above seasons. Several other marine species were also found exclusively at these channel habitats, namely *Platycephalus speculator* and *Pseudorhombus jenynsii* at B, both of which are well adapted for resting against a sandy substrate, and *Girella zebra, Mugil cephalus* and *Haletta semifasciata* at H, each of which are well camouflaged amongst and/or seek food from seagrass.

However, the numbers of marine estuarine-opportunist and marine straggler species recorded at these channel habitats were far lower than in the same region of the permanently-open Swan and Peel-Harvey estuaries. Such findings are likely to reflect not only the seasonal closure of Broke Inlet from the sea, but also various other factors such as the higher coastal wave energy immediately outside this system and thus greater potential for deleterious impacts on the 0+ juveniles of marine species that migrate inshore (Potter and Hyndes 1999), limitations in the geographical range of species such as *Apogon rueppellii, Amniataba caudavittatus* and *Atherinosoma mugiloides* to estuaries on the lower west coast (Potter *et al.* 1990), and the lower structural heterogeneity of the monospecific seagrass beds and homogeneous substrates that occur throughout much of Broke Inlet.

Aside from the habitats in the channel, relatively distinct ichthyofaunas were also detected at a small number of basin habitats in some seasons. Thus, the fish assemblage at A, which could only be sampled during spring and winter due to the extreme shallowness of the extensive sandy shoals that surrounded this habitat throughout the rest of the year, was distinct in both of those seasons but particularly the former, due largely to its depauperate composition. Thus, of the two commonly occurring atherinid species that typified the fish fauna at A in spring, only *L. wallacei* was occasionally found in greater abundances at this habitat. Moreover, habitat A contained the lowest overall number of species and taxonomic diversity and by far the lowest mean density of fish. Such findings reflected not only the particularly shallow waters at this habitat, but also the lack of structural complexity of its sandy substrate, both of which were indicated by several of its enduring environmental characteristics, *i.e.* wide wave shoaling margin, shallow slope and a substrate comprised solely of sand. The fish assemblages at habitat D, which was located on the northern shore of the basin and contained extensive beds of seagrass, also contained a comparatively distinct fish fauna in seasons such as autumn and winter 2008, which was attributable largely to the relatively consistent catches of *A. suppositus* and/or *F. lateralis*. However, aside from the notable differences in some seasons of the ichthyofaunas at other basin habitats such as C, G and I that were mentioned above, those of several others in this region of Broke Inlet did not differ significantly from each other in most seasons, reflecting their dominance by a common suite of atherinid or goby species that were present in similar densities. Thus, even basin habitats such as D and E, which differed markedly in their exposure to wave activity, location within the basin and extent of submerged vegetation, did not contain significantly different fish faunas in summer and autumn 2008. Moreover, the moderate ichthyofaunal differences that were detected between these habitats in spring 2007 and winter 2008, which were driven largely by dissimilarities in the abundance of the common species

A. elongata, L. wallacei, P. olorum, A. suppositus and/or *F. lateralis*, were not consistent between those two seasons. Such findings presumably reflect the wide environmental tolerances of several of these species, and also the relatively limited number of species that comprise the fish assemblages throughout the basin of Broke Inlet. They most likely also reflect less pronounced environmental gradients throughout the middle reaches of a basin system such as Broke Inlet than in the same region of a drowned river valley system such as the Swan Estuary.

7.2.2 Spatial relationships between the environmental and faunal characteristics of habitats

The spatial pattern among habitats, as defined by their enduring environmental characteristics, was significantly correlated that exhibited by their ichthyofaunal composition in each season, thus demonstrating statistically the potential for the former data to provide a surrogate for predicting differences in the latter. However, the extents of those correlations were moderate to low in each season, thereby indicating that the relative extent of the differences in the enduring environmental characteristics of habitats did not mirror those of the fish assemblage particularly well. Thus, while the average ichthyofaunal compositions at the channel habitats B and H were typically distinct from most of those in the basin and from each other, as was reflected by their enduring environmental measurements, the spatial patterns exhibited by the fish assemblages of most basin habitats were not well matched with those of their enduring characteristics. This was sometimes attributable to the lack of differentiation in average fish faunal composition among many basin habitats, while, in other cases, it was due to relatively pronounced differences in the ichthyofauna of basin habitats that had similar enduring environmental characteristics. For example, whereas the enduring characteristics of habitats I and K were alike, *i.e.* reflecting their similar locations, exposure to wave activity and bare sandy substrates, their average fish faunas in spring differed markedly from each other due mainly to greater catches of *F. lateralis, A. elongata* and *L. wallacei* at the former habitat. As the latter two species are highly schooling and widely distributed, it is possible that such ichthyofaunal differences between environmentally similar habitats result more from the chance of encountering these schools, rather than any affinity that those species may have for a particular habitat. The potential effects of randomly intercepting schools of such species on the pattern of fish assemblage differences among habitats are amplified in Broke Inlet, given that the fish fauna is heavily dominated by a small suite of ubiquitous species, several of which exhibit pronounced schooling activity.

The spatial pattern exhibited by the suite of water quality variables recorded at every habitat in each season did not significantly match that of the fish fauna in both summer and autumn 2008, thus indicating that these data were not useful in "explaining" spatial differences in fish composition. In addition to the relatively small ichthyofaunal differences among several habitats in summer and autumn, such findings also reflect the small variation throughout the estuary in the magnitude of water quality variables such as salinity in both of these seasons, *i.e. ca* 25-33‰. However, in all seasons except summer 2008, moderate correlations with the spatial pattern exhibited by the fish assemblages were achieved only when particular water quality variables were employed. Although the pattern of differences in salinity among habitats partially matched that displayed by the fish assemblages in spring 2007 and winter 2008 when the mouth of the estuary was open, the extent of that match was considerably lower than that obtained between this water quality variable and the ichthyofauna in the permanently-open and longitudinal Swan Estuary (see Chapter 5.1.2.4).

Despite the relatively low correlations in spatial pattern between the enduring environmental and fish assemblage matrices, it is still likely that the habitat prediction tool developed for Broke Inlet in Chapter 3.3.2 and the list of species that characterise each habitat in any given season, can be used to reasonably predict those species likely to typify the fish fauna at any nearshore site in this system throughout the year. Thus, as the relative distinctiveness of the enduring characteristics of the channel habitats were well reflected by that of their fish fauna, and that a main cause of the low correlations between the enduring environmental and fish matrices was typically a lack of significant ichthyofaunal differences among basin habitats, it is unlikely that the results of the habitat and fish prediction procedures will produce misleading results.

7.2.3 Seasonal differences in fish assemblage composition among habitats

The extents of the differences in ichthyofaunal composition among seasons were often less than those detected among habitats in Broke Inlet and, in some cases, were not significant. Such findings are surprising, given that the bar to this system was open in two of the four sampling seasons (*i.e.* spring 2007 and winter 2008), and thus contributed not only to the pronounced spatio-temporal differences in the hydrology of the estuary during those periods (*e.g.* salinity, water temperature and force of tidal flow), but also provided an opportunity for marine species to enter the estuary.

The extent of seasonal differences in fish composition were among the lowest at habitats J and F in the main basin, despite the fact that both experienced large changes in salinity throughout the year and particularly the former, due mainly to its location just next to the mouth of the Shannon River, *i.e.* 4.6-29‰. Thus, in every season, the faunas at these habitats were typified by two or more of the atherinid or goby species *A. elongata, L. wallacei, A. suppositus* and *F. lateralis,* with the former two representing at least 85% of the total catch. Given the osmoregulatory potential of each of these estuarine species, and the fact that the former two have protracted spawning periods over spring and summer (Prince and Potter 1983), it is not surprising that the ichthyofaunas of these basin habitats exhibited very small or insignificant seasonal differences. However, it is relatively unusual that the fish faunas of habitat J, or indeed any other basin habitat whose salinities approached those of freshwater during winter, did not contain any freshwater species. Although the overall extent of the seasonal differences in fish faunal composition at most of the remaining basin habitats was larger than that detected at J and F, they were always attributable to differences in the prevalence of several of the above species and/or *L. presbyteroides* and *F. lateralis*. Few consistent seasonal trends in the abundance of each of the above atherinid or goby species could be detected among the various basin habitats, but it was often true that the prevalence of *L. wallacei* was greater in winter, which may reflect the affinity of this euryhaline species for reduced salinities (Prince *et al.* 1982).

While several marine species such as *A. gouldii, P. parilus* and/or *A. rostratus* characterised the faunas at the channel habitats H and, to a lesser extent, B, in late spring 2007 and/or late summer 2008 when the bar to Broke Inlet was open or had recently closed, they did not invoke particularly large seasonal differences in ichthyofaunal composition at these habitats. Indeed the overall extent of such differences at B was among the lowest recorded throughout the estuary. Moreover, although the seasonal differences in fish composition at H were among the highest recorded throughout the system, they were mainly attributable to the relatively low catches of the commonly occurring estuarine species *L. wallacei, L. presbyteroides, A. suppositus* and *A. elongata* in spring than any other season. Similar findings were also detected at habitat B in the lowermost reaches of the channel, and it is thus possible that they reflected the flushing of these small atherinid and goby species out to sea on outflowing tides during this season. The low recruitment of marine species into Broke Inlet during those periods of the year in which the bar is open presumably reflects either the deleterious impact of the relatively high wave energy along the coast near this system, the transport of their eggs and larvae to other coastal locations by local and/or offshore currents, or that those times of year during which the bar is open do not coincide with the spawning periods of the various marine species that recruit into nearshore areas and estuaries. However, given the winter to spring spawning periods of several marine species that commonly occur along the south coast of Western Australia (*e.g. Aldrichetta forsteri, Mugil cephalus* and *Sillaginodes punctatus*; Chubb *et al.* 1981, Hyndes *et al.* 1998), the latter is less likely.

8. Relationships between habitat types and faunal assemblages in the Wilson Inlet

8.1 Results

8.1.1 Water quality parameters

Preliminary three-way PERMANOVA tests were used to determine whether habitats or their representative sites were most appropriate for examining spatial differences in the salinity, water temperature and dissolved oxygen concentration recorded seasonally throughout the Wilson Inlet between winter 2006 and summer 2008. Since each of these tests demonstrated that there were no significant differences between sites assigned to the same habitat, and that the site x season interaction was never significant, the replicate data for each of these water quality variables was subsequently subjected to a habitat x season PERMANOVA to more thoroughly elucidate the nature of extent of their spatial and temporal differences (Table 8.1.1.1).

Salinity and water temperature differed significantly among both habitats and seasons, and the interaction between these main effects was also significant for the first of these dependent variables (p=0.001). Significant habitat effects were not detected in the case of dissolved oxygen, but season and the interaction term were significant (p=0.001-0.007; Table 8.1.1.1). Based on the relative values of the components of variation of each term in the model, season was by far the greatest influence on the magnitude of salinity and temperature. The habitat x season interaction exerted the next greatest influence on salinity, with that of habitat being relatively minor in comparison. Season and the habitat x season interaction were almost equally important with respect to their influence on dissolved oxygen (Table 8.1.1.1).

The lowest mean salinities were always recorded during summer 2008 (17.7-18.4‰), with the exception of habitat F (located, in part, near the mouth of the Denmark River), at which the salinities in spring 2006 were slightly lower (17.4‰), and habitat O (located near the mouths of the Hay and Sleeman rivers), at which salinities during winter 2006 were far lower (11.5‰; Fig. 8.1.1.1a). Salinities in spring 2006 were often only slightly greater than those in summer 2008, typically followed by those for the winters of 2006 and 2007. The greatest mean salinities were usually recorded during autumn 2007 (25.4-26.5‰), with those for summer 2007 often being *ca* 2-3‰ lower. The significant interaction detected for this dependent variable was attributable to the typically small differences in the rank order and extent of seasonal differences at each habitat type, the most pronounced of which occurred at habitat O. Differences among

Table 8.1.1.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for habitat x season PERMANOVAs on the data for salinity, water temperature and dissolved oxygen concentration recorded throughout the Wilson Inlet during winter and spring 2006, summer, autumn and winter 2007 and summer 2008. df = degrees of freedom. Significant results are highlighted in bold.

		Salinity				**Temperature**				**Dissolved Oxygen**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Habitat	7	**0.208**	**3.739**	**0.086**	**0.001**	**7.784**	**5.472**	**0.556**	**0.001**	3.750	0.982	-0.058	0.445
Season	5	**2.839**	**51.011**	**0.320**	**0.001**	**682.300**	**479.630**	**5.003**	**0.001**	**30.824**	**8.074**	**0.996**	**0.001**
Two-way Interaction													
Habitat * Season	29	**0.165**	**2.971**	**0.166**	**0.001**	2.213	1.556	0.445	0.061	**7.778**	**2.037**	**0.995**	**0.007**
Residual	126	0.056		0.236		1.423		1.193		3.818		1.954	

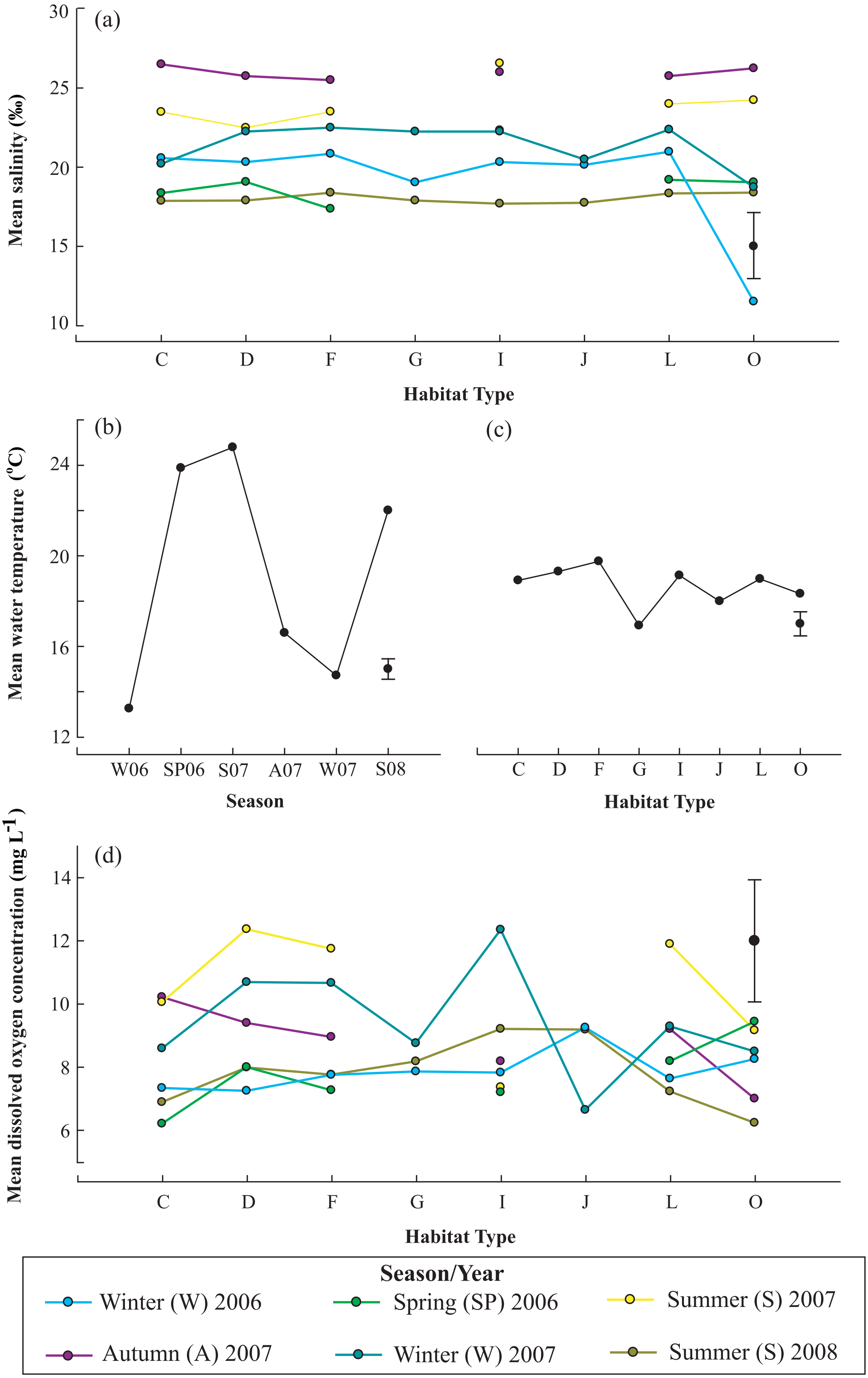


Figure 8.1.1.1: Mean (a) salinity, (b-c) water temperature and (d) dissolved oxygen concentration at each habitat type/season sampled in the Wilson Inlet between winter 2006 and summer 2008. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

habitats were minimal, with the exception of habitat O, at which mean salinities during both winters, and particularly winter 2006, were notably lower than those at all other habitats (Fig. 8.1.1.1a).

Mean water temperature was significantly higher in summer 2007 and spring 2006 than in all other seasons (23.8-24.8°C). Temperatures in summer 2008 (22°C) were also far higher than those in the remaining seasons, and particularly winter 2006 (13.3-16.6°C; Fig. 8.1.1.1b). Habitat differences in this dependent variable were relatively small, with the lowest mean value being recorded at habitat G (16.9°C) and the highest at habitats F and D (19.3-19.8°C; Fig. 8.1.1.1c).

The seasonal trends in mean dissolved oxygen concentration varied markedly among habitats, thus explaining the significant interaction detected between these two main effects. For example, whereas the highest or second highest values were recorded in summer or winter 2007 at most habitats, the lowest values, or those close to the lowest, were recorded in the first of these seasons at habitat I and in the latter season at habitat J (Fig. 8.1.1.1d). Moreover, the extent of the seasonal differences in dissolved oxygen concentration varied considerably among habitats. Thus, whereas concentrations ranged between 7.4 and 12.4 mg L^{-1} at I, they ranged only between 6.2 and 9.4 mg L^{-1} at O. Furthermore, a large confidence interval was associated with each mean, which was also reflected by the fact that the residual components of variation in the above PERMANOVA test was approximately twice that for each of the significant terms (Table 8.1.1.1).

8.1.2 Fish assemblages

8.1.2.1 Species mean density and length characteristics at each habitat type

A total of 23 fish species and 112 937 individuals (*i.e.* after the number of fish in each sample was adjusted to that in 100 m^2 and summed) were recorded at the eight nearshore habitat types sampled throughout the Wilson Inlet between winter 2006 and summer 2008 (Table 8.1.2.1). By far the greatest number of species (18) was recorded at habitat F, which was located on the western shore of Wilson Inlet between the mouth of the Denmark River and the top of the entrance channel, while the least were recorded at habitats J and G (7), which were located on the western shore of the entrance channel and interspersed among habitat F, respectively. The greatest mean density of fish were also recorded at habitat F (535 fish 100 m^{-2}), followed relatively closely by that at habitat I, which was located on the eastern shore of the channel, and the other channel habitat, J, *i.e.* 451-496 fish 100 m^{-2}. By far the lowest mean density of fish was recorded at habitat G, *i.e.* 140 fish 100 m^{-2}.

Table 8.1.2.1: Mean density (M), standard deviation (^{SD}), percentage contribution to the overall catch (%), rank by density (R) and length range and median length (L^{Med}) of each fish species recorded at each habitat type in the Wilson Inlet between winter 2006 and summer 2008. Abundant species (*i.e.* those that contribute >5% to the catch) are highlighted in grey. The life-history category of each species is also provided (^{E}=estuarine, ^{EM}=estuarine and marine, ^{O}=marine estuarine-opportunist, ^{S}=marine straggler). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of fish in each sample had been adjusted to that in 100 m^2 and summed) are given for each habitat type.

	Habitat type C				**Habitat type D**				**Habitat type F**			
Species name	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**	**M^{SD}**	**%**	**R**	**L^{Med}**
Atherinosoma elongata ^{E}	$226.04^{271.84}$	65.05	1	$17\text{-}95^{34}$	$108.96^{181.95}$	47.47	1	$17\text{-}104^{40}$	$330.42^{423.19}$	61.8	1	$15\text{-}98^{40}$
Leptatherina wallacei ^{E}	$75.59^{124.04}$	21.75	2	$17\text{-}70^{31}$	$79.15^{114.94}$	34.48	2	$21\text{-}62^{37}$	$59.43^{81.77}$	11.12	3	$20\text{-}67^{39}$
Pseudogobius olorum ^{E}	$28.34^{95.68}$	8.16	3	$12\text{-}59^{30}$	$21.43^{40.81}$	9.33	3	$19\text{-}51^{26}$	$111.15^{209.37}$	20.79	2	$14\text{-}55^{29}$
Favonigobius lateralis ^{EM}	$8.42^{29.36}$	2.42	4	$20\text{-}73^{38}$	$1.19^{2.73}$	0.52	6	$18\text{-}79^{51}$	$3.84^{6.69}$	0.72	6	$23\text{-}70^{50}$
Afurcagobius suppositus ^{E}	$4.51^{10.47}$	1.30	5	$20\text{-}91^{34}$	$11.14^{26.16}$	4.85	4	$19\text{-}82^{34}$	$11.42^{15.22}$	2.14	5	$20\text{-}78^{31}$
Leptatherina presbyteroides ^{EM}	$3.83^{11.19}$	1.10	6	$22\text{-}62^{35}$	$6.38^{18.58}$	2.78	5	$22\text{-}68^{50}$	$15.14^{33.93}$	2.83	4	$21\text{-}72^{37}$
Urocampus carinirostris ^{EM}	$0.36^{1.27}$	0.10	7	$52\text{-}69^{58}$	$0.56^{2.04}$	0.24	7	$47\text{-}73^{62}$	$0.16^{0.68}$	0.03	11	$55\text{-}68^{62}$
Aldrichetta forsteri ^{O}	$0.22^{1.10}$	0.06	8	$36\text{-}99^{99}$	$0.02^{0.12}$	0.01	13	206	$0.72^{4.98}$	0.13	8	$136\text{-}178^{165}$
Pugnaso curtirostris ^{S}	$0.11^{0.46}$	0.03	9	$93\text{-}132^{126}$	$0.22^{1.49}$	0.09	9	$132\text{-}142^{134}$	$0.02^{0.12}$	<0.01	14	151
Engraulis australis ^{EM}	$0.07^{0.30}$	0.02	10	$86\text{-}101^{94}$	$0.11^{0.75}$	0.05	10	$85\text{-}100^{99}$	$0.25^{1.74}$	0.05	10	$88\text{-}102^{98}$
Hyporhamphus melanochir ^{EM}	$0.02^{0.12}$	0.01	11	115	$0.32^{1.51}$	0.14	8	$77\text{-}173^{113}$	$1.40^{6.66}$	0.26	7	$99\text{-}154^{123}$
Cnidoglanis macrocephalus ^{EM}					$0.07^{0.30}$	0.03	11	$83\text{-}149^{127}$				
Pseudolabrus parilus ^{S}					$0.04^{0.17}$	0.02	12	125	$0.02^{0.12}$	<0.01	14	159
Mugil cephalus ^{O}									$0.50^{1.88}$	0.09	9	$36\text{-}166^{142}$
Sillaginodes punctata ^{O}									$0.05^{0.28}$	0.01	12	$81\text{-}97^{96}$
Platycephalus speculator ^{EM}									$0.04^{0.25}$	0.01	13	$181\text{-}190^{186}$
Pelates octolineatus ^{O}									$0.02^{0.12}$	<0.01	14	308
Arenigobius bifrenatus ^{EM}									$0.02^{0.12}$	<0.01	14	92
Pseudorhombus jenynsii ^{O}									$0.02^{0.12}$	<0.01	14	291
Number of species			**11**				**13**				**18**	
Total mean density			**348**				**230**				**535**	
Number of samples			**48**				**48**				**48**	
Total number of fish			**16 680**				**11 019**				**25 662**	

Species name	Habitat type G				Habitat type I				Habitat type J			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$62.41^{74.94}$	44.66	1	$19\text{-}85^{44}$	$268.84^{523.17}$	54.16	1	$14\text{-}95^{39}$	$296.20^{291.33}$	65.69	1	$16\text{-}90^{34}$
Leptatherina wallacei ^{E}	$51.24^{128.00}$	36.67	2	$21\text{-}59^{32}$	$179.04^{401.91}$	36.07	2	$17\text{-}73^{35}$	$116.77^{127.93}$	25.90	2	$19\text{-}68^{31}$
Pseudogobius olorum ^{E}	$11.02^{18.98}$	7.89	3	$19\text{-}44^{27}$	$28.47^{62.07}$	5.74	3	$16\text{-}53^{29}$	$25.59^{55.89}$	5.67	3	$15\text{-}43^{25}$
Favonigobius lateralis ^{EM}	$0.37^{0.68}$	0.27	6	$22\text{-}62^{36}$	$6.29^{16.85}$	1.27	5	$17\text{-}75^{40}$	$7.13^{19.33}$	1.58	4	$15\text{-}64^{31}$
Afurcagobius suppositus ^{E}	$4.87^{9.49}$	3.49	5	$21\text{-}62^{34}$	$4.26^{6.27}$	0.86	6	$21\text{-}82^{37}$	$1.18^{2.46}$	0.26	6	$26\text{-}60^{41}$
Leptatherina presbyteroides ^{EM}	$9.71^{25.21}$	6.95	4	$21\text{-}65^{35}$	$7.53^{20.60}$	1.52	4	$21\text{-}64^{35}$	$4.00^{7.61}$	0.89	5	$19\text{-}46^{31}$
Urocampus carinirostris ^{EM}					$0.11^{0.55}$	0.02	11	$50\text{-}64^{57}$				
Aldrichetta forsteri ^{O}					$0.11^{0.75}$	0.02	10	$176\text{-}190^{188}$				
Pugnaso curtirostris ^{S}					$0.09^{0.51}$	0.02	12	$147\text{-}171^{151}$				
Engraulis australis ^{EM}												
Hyporhamphus melanochir ^{EM}	$0.11^{0.54}$	0.08	7	$103\text{-}105^{104}$	$0.66^{2.60}$	0.13	8	$97\text{-}179^{127}$	$0.04^{0.18}$	0.01	7	100
Cnidoglanis macrocephalus ^{EM}					$0.05^{0.28}$	0.01	13	$100\text{-}247^{151}$				
Pseudolabrus parilus ^{S}												
Mugil cephalus ^{O}					$0.79^{4.98}$	0.16	7	$26\text{-}32^{31}$				
Sillaginodes punctata ^{O}					$0.13^{0.75}$	0.03	9	$89\text{-}103^{100}$				
Number of species		**7**				**13**				**7**		
Total mean density		**140**				**496**				**451**		
Number of samples		**23**				**48**				**22**		
Total number of fish		**3 214**				**23 825**				**9 920**		

Species name	Habitat type L				Habitat type O			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$165.91^{234.79}$	69.40	1	$17\text{-}82^{39}$	$198.24^{262.50}$	85.40	1	$14\text{-}87^{38}$
Leptatherina wallacei ^{E}	$19.74^{33.56}$	8.26	4	$17\text{-}67^{38}$	$28.54^{45.71}$	12.29	2	$18\text{-}64^{30}$
Pseudogobius olorum ^{E}	$21.03^{59.95}$	8.80	2	$17\text{-}54^{30}$	$0.86^{1.21}$	0.37	5	$19\text{-}53^{34}$
Favonigobius lateralis ^{EM}	$19.88^{32.68}$	8.32	3	$19\text{-}74^{37}$	$2.10^{5.65}$	0.91	3	$19\text{-}67^{44}$
Afurcagobius suppositus ^{E}	$9.79^{28.70}$	4.09	5	$22\text{-}86^{50}$	$1.38^{2.53}$	0.60	4	$18\text{-}75^{33}$
Leptatherina presbyteroides ^{EM}	$1.72^{6.52}$	0.72	6	$19\text{-}70^{44}$	$0.70^{2.12}$	0.30	6	$25\text{-}66^{50}$
Urocampus carinirostris ^{EM}	$0.25^{0.75}$	0.11	9	$36\text{-}62^{58}$	$0.05^{0.37}$	0.02	9	$59\text{-}65^{64}$
Aldrichetta forsteri ^{O}								
Pugnaso curtirostris ^{S}	$0.05^{0.28}$	0.02	10	$95\text{-}117^{106}$	$0.02^{0.12}$	0.01	11	112
Engraulis australis ^{EM}								
Hyporhamphus melanochir ^{EM}					$0.13^{0.44}$	0.05	7	$101\text{-}131^{106}$
Cnidoglanis macrocephalus ^{EM}	$0.34^{2.00}$	0.14	7	$47\text{-}400^{70}$	$0.04^{0.17}$	0.02	10	$35\text{-}401^{218}$
Pseudolabrus parilus ^{S}								
Mugil cephalus ^{O}								
Sillaginodes punctata ^{O}								
Platycephalus speculator ^{EM}								
Pelates octolineatus ^{O}								
Arenigobius bifrenatus ^{EM}								
Pseudorhombus jenynsii ^{O}								
Parablennius tasmanicus ^{S}	$0.29^{1.99}$	0.12	8	$53\text{-}72^{62.5}$				
Ammotretis rostratus ^{O}	$0.04^{0.17}$	0.02	11	$109\text{-}139^{124}$				
Blenniidae sp.	$0.02^{0.12}$	0.01	12	25				
Platycephalidae sp.					$0.07^{0.50}$	0.03	8	16
Number of species		**12**				**11**		
Total mean density		**239**				**232**		
Number of samples		**48**				**48**		
Total number of fish		**11 475**				**11 142**		

The first, second and third most abundant species at all habitats, with minor exceptions at F, L and O, were the estuarine species *Atherinosoma elongata, Leptatherina wallacei* and *Pseudogobious olorum*, which together comprised between 89 and 97% of the total catch (Table 8.1.2.1). The percentage contributions of *A. elongata* were generally lower (*ca* 45-54%) and those of *L. wallacei* higher (*ca* 34-37%) at habitats D, G and I than at the other habitats, *i.e. ca* 62-85% and 8-26%, respectively. Furthermore, the contribution of *P. olorum* was substantially higher at habitat F, *i.e. ca* 21% *cf* 0.4-9.3%. The only other species that were abundant at particular habitats were *Leptatherina presbyteroides* at G (*ca* 7%) and *Favonigobius lateralis* at L (*ca* 8%), both of which were estuarine and marine species and ranked within the top six at all habitats (Table 8.1.2.1).

Several species, which were either estuarine and marine or marine estuarine-opportunists, were found only habitat F, *i.e. Platycephalus speculator, Pelates octolineatus, Arenigobius bifrenatus* and *Pseudorhombus jenynsii*. Furthermore, other marine species were found only at habitats L and O, *i.e. Parablennius tasmanicus, Ammotretis rostratus,* Blenniidae sp. and Platycephalidae sp.

8.1.2.2 Spatial and temporal differences in mean species richness, density and taxonomic distinctness

Replicate data for the number of fish species, total density and taxonomic distinctness of the fish assemblage, which were recorded at each site representing the eight habitat types sampled seasonally throughout Wilson Inlet between winter 2006 and summer 2008, were each subjected to a preliminary three-way PERMANOVA test to ascertain whether their spatial differences were most appropriately analysed at the habitat or site level. The first two of these dependent variables exhibited significant site and/or site x season effects, while no such significant effects were detected for the latter. In view of these results, the number of fish species and total density were then subjected to a site x season PERMANOVA and that for taxonomic distinctness to a habitat x season PERMANOVA to better elucidate the nature and extent of their spatio-temporal differences.

Both the mean number of fish species and density differed significantly among sites and seasons, and the interaction between these main effects was also significant (p=0.001; Table 8.1.2.2). For both of these dependent variables, the relative importance of season was greatest, followed by that for site in the case of number of species and the interaction term in the case of density. The plot of the mean number of species at the various sites in each season demonstrated that the cause of the significant interaction was the considerable variability among

Table 8.1.2.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for site x season PERMANOVAs on the number of species and density and a habitat x season PERMANOVA on the quantitative taxonomic distinctness of the fish assemblages recorded throughout the Wilson Inlet during winter and spring 2006, summer, autumn and winter 2007 and summer 2008. df = degrees of freedom. Significant results are highlighted in bold.

	Number of Species					**Density**				**Quantitative Taxonomic Distinctness**				
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p
Main Effects														
Habitat										7	**839.490**	**5.762**	**4.129**	**0.001**
Season	5	**37.120**	**35.380**	**0.818**	**0.001**	**41.869**	**44.855**	**0.872**	**0.001**	5	**1404.500**	**9.640**	**4.832**	**0.001**
Site	15	**6.554**	**6.246**	**0.517**	**0.001**	**8.546**	**9.155**	**0.608**	**0.001**					
Two-way Interactions														
Habitat * Season										29	**339.270**	**2.329**	**4.939**	**0.001**
Season * Site	63	**1.988**	**1.895**	**0.487**	**0.001**	**3.196**	**3.424**	**0.755**	**0.001**					
Residual	249	1.049		1.024		0.933		0.966		291	145.700		12.070	

sites in the extent of seasonal differences and, to a lesser extent, their rank order (Fig. 8.1.2.1a). For example, whereas there was little difference among seasons in the mean number of species at C1 (4-4.75 species), there were relatively large seasonal differences at F2 (3.5-7.25 species). Moreover, whereas the mean number of species was lowest during autumn at L2, it was among the highest in this season at O2. However, the lowest number of species were recorded either during winter 2006 or 2007 at almost all sites, while the greatest were always recorded in either summer 2007 or 2008 (Fig. 8.1.2.1a). Spatial trends in the mean number of species were less clear, but lower values were often recorded at sites representing habitat O in several seasons, while higher values were frequently recorded at sites representing F.

The mean density of fish also varied considerably among sites in the extent and rank order of seasonal differences, thus explaining the relative importance of the interaction term (Fig. 8.1.2.1b). Seasonal trends in this dependent variable were similar in several respects to those displayed by the mean number of species. Thus, the lowest densities of fish were typically recorded during winter 2007, while the greatest were often recorded in summer 2007 or 2008. Unlike mean number of species however, the mean densities recorded in winter 2006 exhibited considerably more variability, and fluctuated from being the highest, or among the highest, at several sites, to the lowest. Again, clear spatial trends were difficult to discern, but lower densities were more often recorded at sites representing habitats G, D and O (Fig. 8.1.2.1b).

Taxonomic distinctness differed significantly among habitats and seasons, and the interaction between these two main effects was also significant (p=0.001; Table 8.1.2.2). Each of these terms had very similar components of variation, and were thus equally important in explaining the overall variation in this diversity measure. However, the components of variation attributable to the residual was approximately three times that for any of the above terms (Table 8.1.2.2). This was also reflected by the large confidence interval associated with the mean taxonomic distinctness values plotted in Fig. 8.1.2.1c. Seasonal differences in taxonomic distinctness were more pronounced at F and J than the remaining habitats, and the seasonal rank order of this dependent variable differed considerably among habitats, both of which contributed to the significant habitat x season interaction. However, the lowest values were often recorded in winter 2007, while the highest or close to the highest values were typically found in either summer 2008 or winter 2006. Moreover, the lowest taxonomic distinctness was recorded at habitat O in several seasons (Fig. 8.1.2.1c).

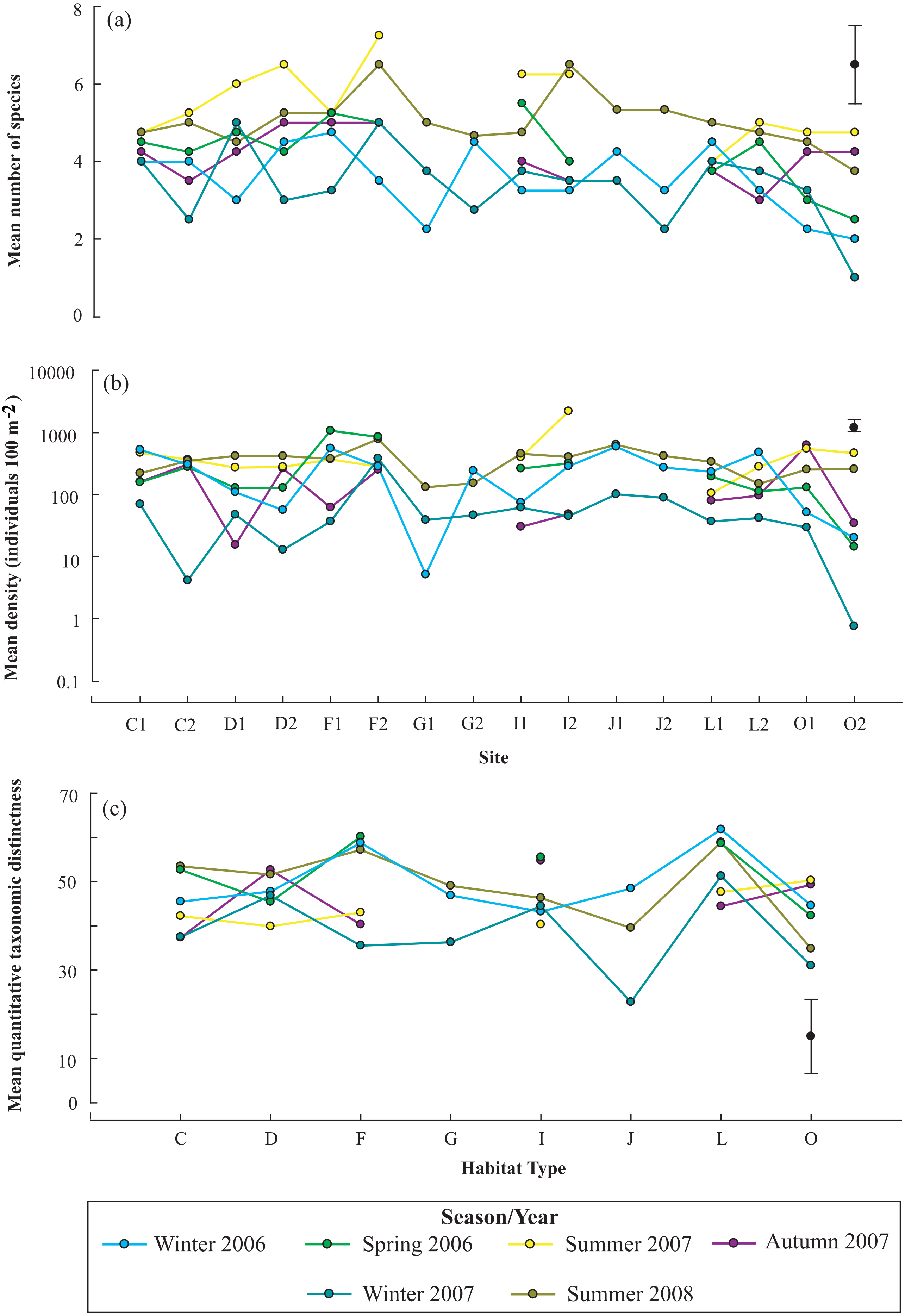


Figure 8.1.2.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the fish assemblages recorded at each site/habitat in the Wilson Inlet between winter 2006 and summer 2008. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

8.1.2.3 Composition of fish assemblages among habitats

An initial three-way PERMANOVA was used to test, firstly, whether spatial differences in the fish assemblage data recorded in replicate samples from each site representing each habitat during each of the six sampling seasons was most appropriately analysed at the site or broader habitat level. Secondly, this test was also used to determine whether the above spatial differences should be examined separately for each season. This test demonstrated that all main effects and interactions were significant (p=0.001-0.002), and that the relative importance of differences among sites and habitats was approximately equal. However, one-way ANOSIM tests for site, carried out separately for data collected in each sampling season in view of the above significant season main effect and interactions, demonstrated that the majority of the significant differences between sites assigned to the same habitat occurred in spring 2006 and, to a lesser extent, summer 2007, *i.e.* out of the six pairwise comparisons between sites in the same habitat, five and three, respectively, were significant. Given that the majority of significant intra-habitat differences were largely restricted to just two seasons, the following analyses were carried out at the habitat rather than site level.

One-way ANOSIM tests, performed separately for the replicate data collected in each season, showed that, while the composition of the fish assemblages differed significantly among habitats in each case (p=0.1%), the overall extents of those differences were low to moderate, *i.e.* Global R=0.155-0.409 (Table 8.1.2.3). The greatest differences occurred in spring 2006 and summer 2008 (Global R=0.409), while the least occurred in winter and autumn 2007 (Global R=0.155 and 0.211, respectively).

During spring 2006 and summer 2008, the majority of the pairwise comparisons between habitats were significant. In the first of these seasons, the most pronounced differences were typically detected between habitat F, located on the western shore of the basin, and most other habitats (Table 8.1.2.3b). The ichthyofaunal composition at F was particularly distinct from that at habitats L and D (R=0.894 and 0.835, respectively), which were located on the northern and southern shores of the basin, respectively. Relatively high differences were also detected between those latter two habitats in this season (R=0.646; Table 8.1.2.3b). These ANOSIM results were reflected by the MDS plot constructed from the spring 2006 fish faunal data (Fig. 8.1.2.2b). Thus, samples from habitat F formed a tight group on one side of the plot, while those from habitats D and L each formed slightly more dispersed but discrete groups that were positioned similar distances from that representing F. The majority of the samples from habitat O formed a comparatively tight group between those for D and L, but two samples from this habitat were highly dissimilar and thus distant from the remainder and each other. Samples from the

Table 8.1.2.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal composition among habitat types in the Wilson Inlet during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2006; p=0.1%, Global R=0.344

	C	D	F	G	I	J	L
D	0.397						
F	0.448	0.716					
G	0.240	0.078	0.439				
I	0.343	-0.036	0.777	0.062			
J	0.145	0.393	0.423	0.243	0.263		
L	0.439	0.522	0.179	0.323	0.566	0.354	
O	0.579	0.098	0.826	0.088	0.148	0.569	0.617

(b) Spring 2006; p=0.1%, Global R=0.409

	C	D	F	I	L
D	0.383				
F	0.428	0.835			
I	-0.109	0.369	0.323		
L	0.150	0.646	0.894	0.142	
O	0.283	0.364	0.666	0.313	0.247

(c) Summer 2007; p=0.1%, Global R=0.294

	C	D	F	I	L
D	0.172				
F	-0.072	-0.070			
I	-0.003	0.319	0.017		
L	0.040	0.157	0.121	0.317	
O	0.538	0.747	0.682	0.751	0.397

(d) Autumn 2007; p=0.1%, Global R=0.211

	C	D	F	I	L
D	0.282				
F	0.196	0.298			
I	0.304	0.114	0.030		
L	0.392	0.287	0.196	0.200	
O	0.357	0.377	0.072	0.030	0.071

(e) Winter 2007; p=0.1%, Global R=0.155

	C	D	F	G	I	J	L
D	-0.015						
F	0.109	0.231					
G	0.129	0.326	0.196				
I	-0.015	0.037	0.024	-0.006			
J	0.099	0.310	0.010	0.199	0.005		
L	0.003	0.065	0.228	0.314	0.111	0.142	
O	0.092	0.296	0.411	0.320	0.307	0.357	0.257

(f) Summer 2008; p=0.1%, Global R=0.409

	C	D	F	G	I	J	L
D	0.421						
F	0.217	0.196					
G	0.356	0.068	0.261				
I	0.276	0.085	0.171	0.013			
J	0.297	0.426	0.319	0.426	-0.036		
L	0.199	0.670	0.332	0.635	0.571	0.298	
O	0.691	0.840	0.694	0.658	0.475	0.494	0.738

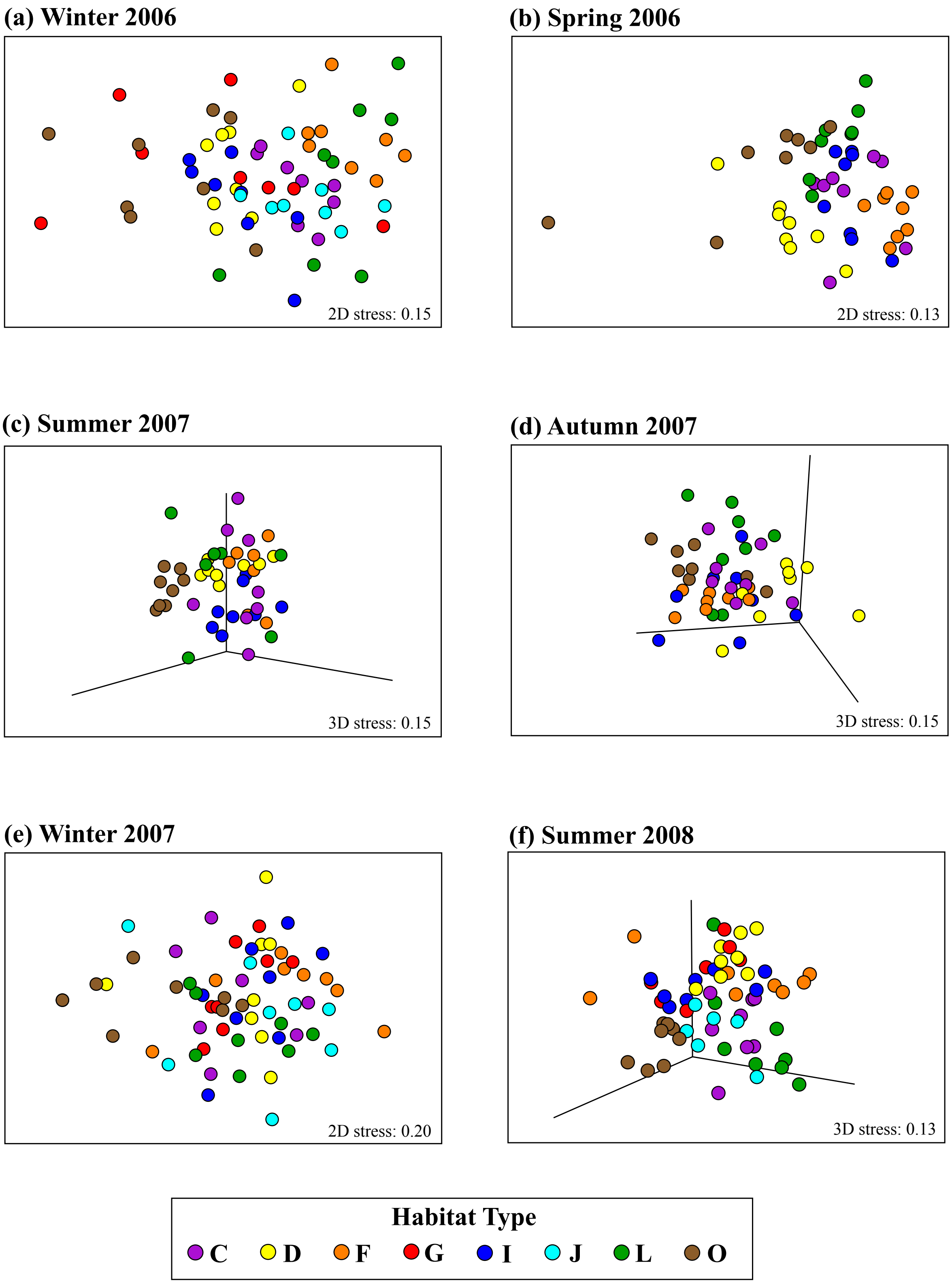


Figure 8.1.2.2: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample at each habitat type in the Wilson Inlet during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008.

remaining habitats formed groups between those for F and D, L and O (Fig. 8.1.2.2b). SIMPER showed that the ichthyofauna at habitat F in this season was consistently distinguished from those at habitats D and L by greater abundances of *P. olorum, A. elongata* and *Afurcagobius suppositus*. *Favonigobius lateralis* and *L. wallacei* were also more prevalent at F than D and L, respectively (Table 8.1.2.4b). Habitats D and L were best distinguished from each by the greater abundances of *L. wallacei* and *A. suppositus* at the former habitat and of *F. lateralis*, *P. olorum* and *A. elongata* at the latter. In contrast, a greater prevalence of all of the above species at habitat F best separated its fish assemblage from that at O (Table 8.1.2.4b).

During summer 2008, those habitats with the most distinct fish faunas were L and particularly O, as reflected by the pairwise ANOSIM comparisons involving one of these habitats often exceeding 0.500 (Table 8.1.2.3f). The largest differences occurred for O *vs* D and L (R=0.738-0.840). The MDS ordination plot constructed from the replicate data collected in this season showed that samples from habitat O formed the tightest group to one side of the plot, which was essentially discrete from those representing all other habitat types (Fig. 8.1.2.2f). Samples from habitat D also formed a compact group that was located relatively far from that for habitat O and, although relatively dispersed, most samples from L were located on the opposite side of the MDS plot from those representing O. Samples from habitats G, I and J formed reasonably distinct groups, whereas those representing F were relatively dispersed (Fig. 8.1.2.2f). The distinctness of the ichthyofauna at habitat O was shown by SIMPER to be due to the fact that it was characterised by only two species, *L. wallacei* and *A. elongata*, the second of which was almost always more abundant at other habitats. In contrast, the fish assemblage at habitat D was also characterised by *A. suppositus* and *P. olorum*, and all four of these species were commonly more abundant at this habitat than any other (Table 8.1.2.4f). Habitat L was characterised by the consistent occurrence of *F. lateralis, A. elongata, P. olorum* and *L. wallacei*, but only the first of these species was in greater abundance at this habitat than any other, whereas the remainder were almost always more prevalent at other habitats (Table 8.1.2.4f).

Moderate to high R-statistic values were detected between several pairs of habitats during winter 2006 and summer 2007, particularly for those comparisons involving habitat O and, in winter 2006, also habitats F and L, *i.e.* 0.522-0.826 (Table 8.1.2.3a and c). The greatest differences were detected for F *vs* D, I and O in winter 2006 (R=0.716-0.826) and for O *vs* D and I in summer 2007 (R=0.747-0.751). Samples from habitat O formed a dispersed group that tended to lie on one side of the MDS plot created from the winter 2006 fish assemblage data, but those from several other habitats formed relatively tight groups that were largely discrete from that for O. These included the samples for F, which lay on the opposite side of the plot from

Table 8.1.2.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each habitat in the Wilson Inlet during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2006

	C	**D**	**F**	**G**	**I**	**J**	**L**	**O**
C	*A. elongata* *P. olorum* *L. wallacei* *A. suppositus*							
D	*A. elongata*^{C} *L. wallacei*^{C} *P. olorum*^{C} *A. suppositus*^{C}	*A. elongata* *L. wallacei* *P. olorum*						
F	*P. olorum*^{F} *A. elongata*^{C} *A. suppositus*^{F} *L. wallacei*^{C} *F. lateralis*^{F}	*P. olorum*^{F} *A. suppositus*^{F} *A. elongata*^{F} *F. lateralis*^{F}	*P. olorum* *A. suppositus* *A. elongata*					
G	*A. elongata*^{C} *L. wallacei*^{C} *A. suppositus*^{C} *P. olorum*^{C}		*P. olorum*^{F} *A. suppositus*^{F} *A. elongata*^{F} *L. wallacei*^{G}	*P. olorum* *A. elongata* *L. wallacei*				
I	*A. elongata*^{C} *L. wallacei*^{I} *A. suppositus*^{C} *P. olorum*^{C}		*P. olorum*^{F} *A. suppositus*^{F} *A. elongata*^{F} *L. wallacei*^{I}		*A. elongata* *P. olorum* *L. wallacei*			
J		*A. elongata*^{J} *P. olorum*^{J} *L. wallacei*^{J} *F. lateralis*^{J}	*P. olorum*^{F} *A. suppositus*^{F} *A. elongata*^{J} *F. lateralis*^{F} *L. wallacei*^{J}	*A. elongata*^{J} *P. olorum*^{J} *L. wallacei*^{J} *F. lateralis*^{J}	*A. elongata*^{J} *L. wallacei*^{I} *P. olorum*^{J} *F. lateralis*^{J}	*A. elongata* *P. olorum* *L. wallacei*		
L	*F. lateralis*^{L} *A. suppositus*^{L} *P. olorum*^{L} *A. elongata*^{C} *L. wallacei*^{C}	*F. lateralis*^{L} *A. suppositus*^{L} *P. olorum*^{L} *A. elongata*^{L} *L. wallacei*^{D}		*F. lateralis*^{L} *A. suppositus*^{L} *P. olorum*^{L} *A. elongata*^{L}	*F. lateralis*^{L} *A. suppositus*^{L} *P. olorum*^{L} *L. wallacei*^{I} *A. elongata*^{L}	*A. suppositus*^{L} *P. olorum*^{L} *F. lateralis*^{L} *L. wallacei*^{J} *A. elongata*^{J}	*A. elongata* *F. lateralis* *A. suppositus* *P. olorum*	
O	*A. elongata*^{C} *L. wallacei*^{C} *P. olorum*^{C} *A. suppositus*^{C}		*P. olorum*^{F} *A. suppositus*^{F} *A. elongata*^{F}		*A. elongata*^{I} *L. wallacei*^{I} *P. olorum*^{I}	*A. elongata*^{J} *P. olorum*^{J} *L. wallacei*^{J} *F. lateralis*^{J}	*F. lateralis*^{L} *A. suppositus*^{L} *P. olorum*^{L} *A. elongata*^{L}	*A. elongata* *L. wallacei*

(b) Spring 2006

	C	D	F	I	L	O
C	*P. olorum* *F. lateralis* *L. wallacei* *A. elongata*					
D	*F. lateralis*^{C} *P. olorum*^{C} *A. suppositus*^{C} *L. wallacei*^{D} *A. elongata*^{C}	*L. wallacei* *A. elongata* *A. suppositus* *P. olorum*				
F	*P. olorum*^{F} *F. lateralis*^{C} *A. elongata*^{F} *A. suppositus*^{C} *L. wallacei*^{F}	*P. olorum*^{F} *A. elongata*^{F} *F. lateralis*^{F} *L. wallacei*^{D} *A. suppositus*^{F}	*P. olorum* *A. elongata* *F. lateralis* *L. wallacei*			
I		*F. lateralis*^{I} *P. olorum*^{I} *L. wallacei*^{I} *A. elongata*^{I} *A. suppositus*^{D}	*P. olorum*^{F} *F. lateralis*^{I} *A. elongata*^{F} *A. suppositus*^{F} *L. wallacei*^{I} *M. cephalus*^{F}	*P. olorum* *A. elongata* *L. wallacei* *F. lateralis*		
L		*F. lateralis*^{L} *L. wallacei*^{D} *P. olorum*^{L} *A. suppositus*^{D} *A. elongata*^{L}	*P. olorum*^{F} *F. lateralis*^{L} *A. elongata*^{F} *A. suppositus*^{F} *L. wallacei*^{F}		*F. lateralis* *P. olorum* *A. elongata* *L. wallacei*	
O	*P. olorum*^{C} *F. lateralis*^{C} *A. suppositus*^{C} *L. wallacei*^{C} *A. elongata*^{C}	*F. lateralis*^{O} *L. wallacei*^{D} *P. olorum*^{D} *A. elongata*^{D} *A. suppositus*^{D}	*P. olorum*^{F} *A. elongata*^{F} *F. lateralis*^{F} *A. suppositus*^{F} *L. wallacei*^{F}	*P. olorum*^{I} *F. lateralis*^{I} *A. elongata*^{I} *L. wallacei*^{I}	*F. lateralis*^{L} *P. olorum*^{L} *L. wallacei*^{O} *A. elongata*^{L}	*L. wallacei* *F. lateralis* *A. elongata*

(c) Summer 2007

	C	**D**	**F**	**I**	**L**	**O**
C	*A. elongata* *L. wallacei* *P. olorum*					
D		*L. wallacei* *A. elongata* *F. lateralis* *L. presbyteroides* *A. suppositus* *P. olorum*				
F			*L. wallacei* *A. elongata* *A. suppositus*			
I		*L. wallacei*^{I} *A. elongata*^{I} *L. presbyteroides*^{D} *P. olorum*^{I} *F. lateralis*^{D} *A. suppositus*^{I}		*L. wallacei* *A. elongata* *P. olorum* *A. suppositus*		
L		*L. presbyteroides*^{D} *A. suppositus*^{L} *L. wallacei*^{D} *F. lateralis*^{D} *P. olorum*^{L} *A. elongata*^{L}	*L. wallacei*^{F} *A. suppositus*^{F} *L. presbyteroides*^{F} *P. olorum*^{L} *A. elongata*^{L} *F. lateralis*^{F} *U. carinirostris*^{F}	*L. wallacei*^{I} *A. elongata*^{I} *P. olorum*^{I} *A. suppositus*^{I} *F. lateralis*^{I}	*A. elongata* *L. wallacei* *P. olorum*	
O	*L. wallacei*^{C} *A. elongata*^{O} *A. suppositus*^{O} *P. olorum*^{C} *U. carinirostris*^{C} *F. lateralis*^{O}	*A. elongata*^{O} *L. presbyteroides*^{D} *L. wallacei*^{D} *F. lateralis*^{D} *A. suppositus*^{D} *P. olorum*^{D}	*L. wallacei*^{F} *A. elongata*^{O} *L. presbyteroides*^{F} *A. suppositus*^{F} *P. olorum*^{F} *F. lateralis*^{F}	*L. wallacei*^{I} *A. elongata*^{I} *P. olorum*^{I} *F. lateralis*^{I} *A. suppositus*^{I}	*A. elongata*^{O} *A. suppositus*^{L} *L. wallacei*^{L} *F. lateralis*^{L} *P. olorum*^{L}	*A. elongata* *A. suppositus* *L. wallacei*

(d) Autumn 2007

	C	D	F	I	L	O
C	*L. wallacei* *A. elongata* *L. presbyteroides*					
D	*L. wallacei*^{C} *A. elongata*^{C} *A. suppositus*^{D} *L. presbyteroides*^{C} *U. carinirostris*^{D} *P. olorum*^{D}	*A. suppositus* *L. wallacei* *P. olorum* *U. carinirostris*				
F	*L. wallacei*^{C} *L. presbyteroides*^{F} *A. elongata*^{C} *A. suppositus*^{F} *P. olorum*^{F}	*L. presbyteroides*^{F} *L. wallacei*^{D} *A. elongata*^{F} *A. suppositus*^{D} *U. carinirostris*^{D} *P. olorum*^{D}	*L. presbyteroides* *A. elongata* *A. suppositus* *P. olorum*			
I	*L. wallacei*^{C} *A. elongata*^{C} *L. presbyteroides*^{C} *A. suppositus*^{I} *F. lateralis*^{I} *P. olorum*^{I}	▨	▨	*A. suppositus* *F. lateralis* *P. olorum* *L. wallacei* *L. presbyteroides* *A. elongata*		
L	*L. wallacei*^{C} *L. presbyteroides*^{C} *A. suppositus*^{L} *A. elongata*^{C}	*L. wallacei*^{D} *A. suppositus*^{D} *A. elongata*^{L} *U. carinirostris*^{D} *P. olorum*^{D} *L. presbyteroides*^{L}	*L. presbyteroides*^{F} *L. wallacei*^{F} *A. suppositus*$^{-}$ *F. lateralis*^{L} *A. elongata*^{F} *P. olorum*^{F}	*A. elongata*^{L} *F. lateralis*^{L} *A. suppositus*^{L} *L. presbyteroides*^{I} *L. wallacei*^{I} *P. olorum*^{I}	*A. elongata* *A. suppositus*	
O	*L. wallacei*^{C} *A. elongata*^{O} *L. presbyteroides*^{C} *A. suppositus*^{C} *P. olorum*^{O}	*A. elongata*^{O} *A. suppositus*^{D} *L. wallacei*^{D} *U. carinirostris*^{D} *P. olorum*^{D}	▨	▨	▨	*A. elongata* *A. suppositus* *L. wallacei*

(e) Winter 2007

	C	D	F	G	I	J	L	O
C	*L. wallacei* *A. elongata* *L. presbyteroides* *F. lateralis* *A. suppositus*							
D		*A. suppositus* *A. elongata* *F. lateralis*						
F		*L. presbyteroides*^{F} *L. wallacei*^{F} *A. elongata*^{F} *A. suppositus*^{F} *P. olorum*^{F} *F. lateralis*^{D}	*L. wallacei* *L. presbyteroides* *A. elongata* *A. suppositus* *P. olorum*					
G		*L. presbyteroides*^{G} *A. suppositus*^{D} *A. elongata*^{G} *F. lateralis*^{D} *L. wallacei*^{G}	*L. presbyteroides*^{F} *A. elongata*^{F} *A. suppositus*^{F} *L. wallacei*^{F} *P. olorum*^{F}	*A. elongata* *L. wallacei* *L. presbyteroides*				
I					*A. elongata* *L. wallacei* *L. presbyteroides*			
J		*L. wallacei*^{J} *A. elongata*^{J} *A. suppositus*^{D} *L. presbyteroides*^{J} *F. lateralis*^{D} *P. olorum*^{J}		*L. wallacei*^{J} *A. elongata*^{J} *L. presbyteroides*^{G} *P. olorum*^{J}		*L. wallacei* *A. elongata* *P. olorum*		
L			*L. presbyteroides*^{F} *A. elongata*^{F} *L. wallacei*^{F} *A. suppositus*^{F} *P. olorum*^{F}	*L. presbyteroides*^{G} *A. elongata*^{L} *A. suppositus*^{L} *F. lateralis*^{L} *L. wallacei*^{L} *P. olorum*^{L}			*L. wallacei* *A. elongata* *F. lateralis* *A. suppositus* *P. olorum*	
O		*A. suppositus*^{D} *A. elongata*^{D} *F. lateralis*^{D} *L. presbyteroides*^{D} *L. wallacei*^{D}	*L. wallacei*^{F} *L. presbyteroides*^{F} *A. elongata*^{F} *A. suppositus*^{F} *P. olorum*^{F}	*L. presbyteroides*^{G} *A. elongata*^{G} *L. wallacei*^{G}	*A. elongata*^{I} *L. wallacei*^{I} *L. presbyteroides*^{I} *A. suppositus*^{I} *F. lateralis*^{I}	*L. wallacei*^{J} *A. elongata*^{J} *P. olorum*^{J} *L. presbyteroides*^{J}	*A. elongata*^{L} *L. wallacei*^{L} *A. suppositus*^{L} *F. lateralis*^{L} *P. olorum*^{L}	*A. elongata* *L. wallacei* *P. olorum*

(f) Summer 2008

	C	D	F	G	I	J	L	O
C	*A. elongata* *P. olorum* *F. lateralis* *L. wallacei* *A. suppositus*							
D	*A. suppositus*^{D} *P. olorum*^{D} *L. wallacei*^{D} *F. lateralis*^{C} *A. elongata*^{D}	*A. suppositus* *P. olorum* *A. elongata* *L. wallacei*						
F	*A. suppositus*^{F} *A. elongata*^{F} *H. melanochir*^{F} *F. lateralis*^{C} *L. presbyteroides*^{F} *P. olorum*^{F} *L. wallacei*^{C}	*P. olorum*^{D} *A. suppositus*^{D} *A. elongata*^{F} *L. wallacei*^{D} *H. melanochir*^{F} *F. lateralis*^{F}	*A. elongata* *A. suppositus* *P. olorum* *L. wallacei*					
G	*A. elongata*^{C} *A. suppositus*^{G} *F. lateralis*^{C} *P. olorum*^{G} *L. wallacei*^{G}		*A. elongata*^{F} *A. suppositus*^{F} *H. melanochir*^{F} *P. olorum*^{G} *F. lateralis*^{F}	*A. suppositus* *P. olorum* *L. wallacei* *A. elongata*				
I	*L. wallacei*^{I} *A. elongata*^{I} *F. lateralis*^{C} *P. olorum*^{I} *A. suppositus*^{I}				*L. wallacei* *A. elongata* *A. suppositus* *P. olorum*			
J	*L. wallacei*^{J} *F. lateralis*^{J} *A. elongata*^{J} *A. suppositus*^{C} *P. olorum*^{J} *L. presbyteroides*^{J}	*A. suppositus*^{D} *L. wallacei*^{J} *F. lateralis*^{J} *P. olorum*^{D} *A. elongata*^{D} *L. presbyteroides*^{J}	*L. wallacei*^{J} *A. suppositus*^{F} *F. lateralis*^{J} *H. melanochir*^{F} *A. elongata*^{F} *P. olorum*^{F}	*L. wallacei*^{J} *F. lateralis*^{J} *A. elongata*^{J} *A. suppositus*^{G} *P. olorum*^{G} *L. presbyteroides*^{J}		*L. wallacei* *A. elongata* *P. olorum* *F. lateralis*		
L	*F. lateralis*^{L} *A. elongata*^{C} *A. suppositus*^{C} *P. olorum*^{C} *L. wallacei*^{C}	*F. lateralis*^{L} *A. suppositus*^{D} *P. olorum*^{D} *L. wallacei*^{D} *A. elongata*^{D}	*F. lateralis*^{L} *A. suppositus*^{F} *A. elongata*^{F} *H. melanochir*^{F} *P. olorum*^{F} *L. wallacei*^{F}	*F. lateralis*^{L} *A. suppositus*^{G} *A. elongata*^{L} *P. olorum*^{G} *L. wallacei*^{G} *L. presbyteroides*^{L}	*F. lateralis*^{L} *L. wallacei*^{I} *A. elongata*^{I} *A. suppositus*^{I} *P. olorum*^{I} *L. presbyteroides*^{I}	*L. wallacei*^{J} *F. lateralis*^{L} *A. elongata*^{J} *A. suppositus*^{J} *L. presbyteroides*^{J} *P. olorum*^{J}	*F. lateralis* *A. elongata* *P. olorum* *L. wallacei*	
O	*L. wallacei*^{O} *F. lateralis*^{C} *P. olorum*^{C} *A. elongata*^{C} *A. suppositus*^{C}	*P. olorum*^{D} *A. suppositus*^{D} *L. wallacei*^{O} *A. elongata*^{D}	*A. suppositus*^{F} *A. elongata*^{F} *L. wallacei*^{O} *H. melanochir*^{F} *P. olorum*^{F} *F. lateralis*^{F}	*A. suppositus*^{G} *L. wallacei*^{O} *P. olorum*^{G} *A. elongata*^{O}	*P. olorum*^{I} *A. suppositus*^{I} *L. wallacei*^{I} *A. elongata*^{I} *H. melanochir*^{I} *L. presbyteroides*^{I}	*F. lateralis*^{J} *L. wallacei*^{J} *A. elongata*^{J} *P. olorum*^{J} *A. suppositus*^{J} *L. presbyteroides*^{J}	*F. lateralis*^{L} *L. wallacei*^{O} *A. elongata*^{L} *P. olorum*^{L} *L. presbyteroides*^{L} *A. suppositus*^{O}	*L. wallacei* *A. elongata*

those for O, and those representing C and J, which each formed groups between those for O and F. Samples from habitat L were also quite dispersed, but generally occupied the opposite side of the ordination plot from those for habitat O (Fig. 8.1.2.2a). SIMPER showed that, as in summer 2008, the fish fauna at habitat O was characterised only by *A. elongata* and *L. wallacei*, and that the abundances of each of these species were always greater at other habitats (Table 8.1.2.4a). On the other hand, habitat F was typified by *P. olorum, A. suppositus* and *A. elongata*, each of which was often more abundant at this habitat than any other. A similar situation applied to most of the species that typified L in this season, *i.e. F. lateralis, A. suppositus* and *P. olorum*, and also to those that typified C and J, which are listed in Table 8.1.2.4a.

In contrast to the situation in winter 2006, samples from habitat O formed a particularly tight group on one side of the MDS ordination plot constructed from the fish assemblage data recorded in summer 2007 (Fig. 8.1.2.2c). Although *A. elongata*, *A. suppositus* and *L. wallacei* characterised the ichthyofaunas at this habitat, only the first of these species was commonly found in greater abundance at O than at any other habitat in this season (Table 8.1.2.4c). Samples from habitats D, F and I also formed relatively distinct groups on the ordination plot, while those for C and particularly L were widely dispersed (Fig. 8.1.2.2c). The species that both characterised the fish faunas at these habitats and best distinguished them from other significantly different habitats are given in Table 8.1.2.4c.

During the autumn and particularly the winter of 2007, the composition of the fish fauna throughout Wilson Inlet did not differ significantly between several pairs of habitats, and no pairwise R-statistic, except one, exceeded 0.400 (Table 8.1.2.3d and e, respectively). The minimal differences in ichthyofaunal composition among habitats in these seasons were well reflected by the high degree of overlap among samples belonging to different habitats and/or pronounced group dispersion on the MDS plots constructed from the fish assemblage data recorded in each of these seasons (Fig. 8.1.2.2d and e, respectively). The species that characterised each habitat in autumn and winter 2007 and distinguished the fish faunas of significantly different pairs of habitats are given in Table 8.1.2.4d and e, respectively.

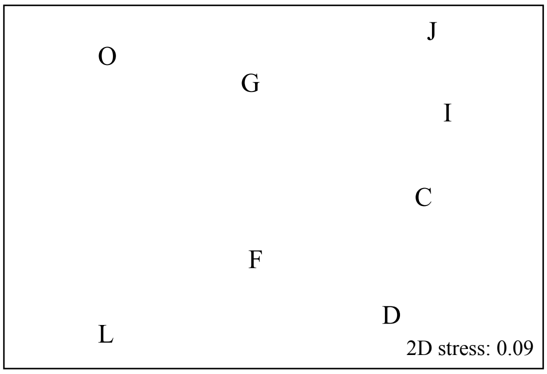
8.1.2.4 Matching spatial patterns between the environmental and fish assemblage characteristics of habitats

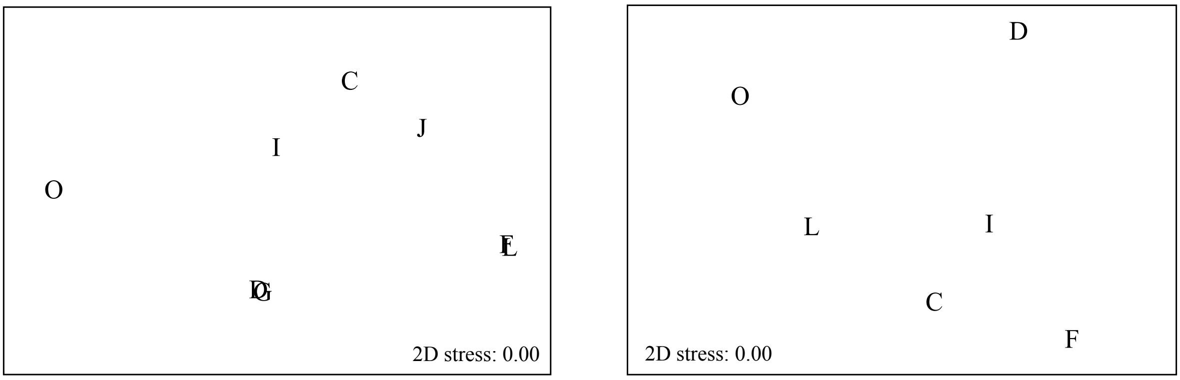
The RELATE procedure was used to test the extent to which the relative differences among habitats, as exhibited by their enduring environmental measurements, matched that displayed by their fish assemblage compositions in each sampling season. Significant results were detected only in winter 2006 and summer 2007 (p=4.7-5%), and the extent of those correlations were, at best, moderate (ρ=0.374-0.532; *cf* Fig. 8.1.2.3a and b, d). Despite the lack of significant matches in spatial pattern between the enduring and fish assemblage matrices in the other sampling seasons, the MDS ordination plots constructed from the latter data demonstrate that, in all seasons, the ichthyofaunal compositions at habitat O were relatively distinct from those at the remaining habitats, which was also reflected by the enduring environmental data (*cf* Fig. 8.1.2.3a and c, e, f and g). However, unlike the enduring characteristics, the average fish assemblage compositions exhibited relatively small differences among several of the remaining habitats in seasons such as autumn and winter 2007 (*cf* Fig. 8.1.2.3a and e, f).

The RELATE procedure was then used to test the extent to which the spatial pattern among habitats exhibited by the fish assemblages in each sampling season was correlated with that of the complementary suite of water quality parameters, *i.e.* salinity, temperature and dissolved oxygen concentration. No significant correlations were detected in any season (p=7.4-74.7%), thus indicating that the spatial differences in fish assemblage composition were even less well explained by differences in water quality than by those in the enduring environmental data. The subsequent use of BIOENV to ascertain whether the above correlations between the complementary fish and water quality matrices could be improved by employing only data for particular subsets of water quality variables, demonstrated that significant results were obtained only for winter 2006 when just salinity data was employed (p=1%, ρ=0.500). It should be noted that the above BIOENV tests were carried out using the averages of data collected at each site rather than habitat type, in order to maximise the number of samples in the reference (fish) matrices and thus minimise the likelihood of the routine finding a subset of water quality variables that provided a good match with those references matrices by chance. For comparability, it should also be recognised that, when the RELATE routine was used to match the complementary fish and water quality matrices constructed from the averages recorded at each site, the correlation values were similar to those obtained above when habitat averages were employed, except for during summer 2007, *i.e.* ρ=-0.147 (site) *vs* 0.461 (habitat).

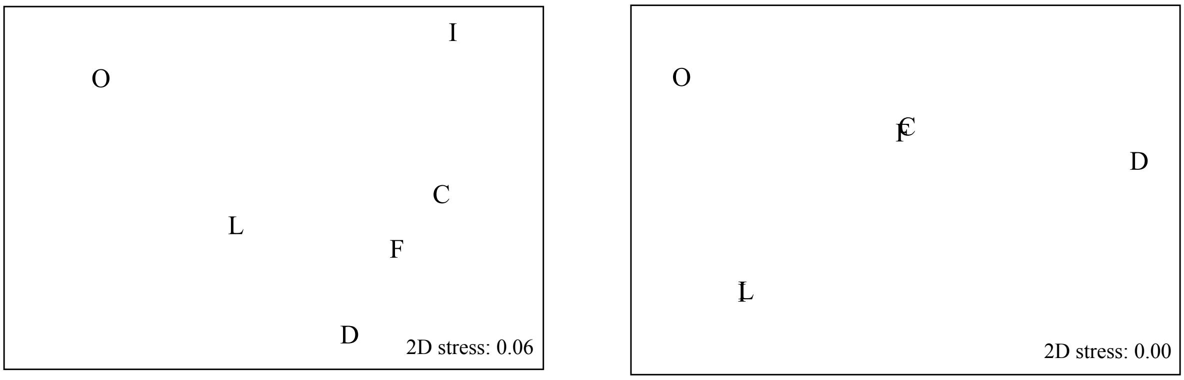
The relationship between the spatial pattern exhibited by the ichthyofaunal composition and that of salinity in winter 2006 was examined by overlaying a bubble plot of the average salinity at each site on an MDS ordination plot constructed from the average fish composition at those same sites (figure not shown). This plot showed that the average salinities at sites representing habitat O (11.5-14‰), which also had a relatively distinct fish faunal composition, were considerably lower than those at sites representing all other habitats (*ca* 18-21‰).

(a) Enduring environmental data

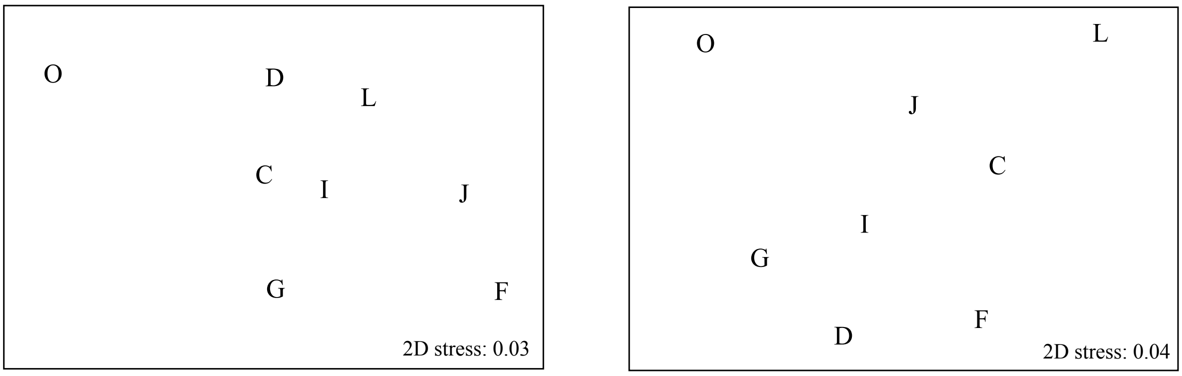



(b) Winter 2006; p=4.7%, ρ=0.374

(c) Spring 2006; p=40.1%, ρ=0.079


(d) Summer 2007; p=5%, ρ=0.532

(e) Autumn 2007; p=77.6%, ρ=-0.236


(f) Winter 2007; p=16.6%, ρ=0.262

(g) Summer 2008; p=7.1%, ρ=0.304

Figure 8.1.2.3: MDS ordination plots constructed from the averages at each habitat type in the Wilson Inlet of their (a) enduring environmental measurements and (b-g) fish faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the above fish faunal data are also provided for each season.

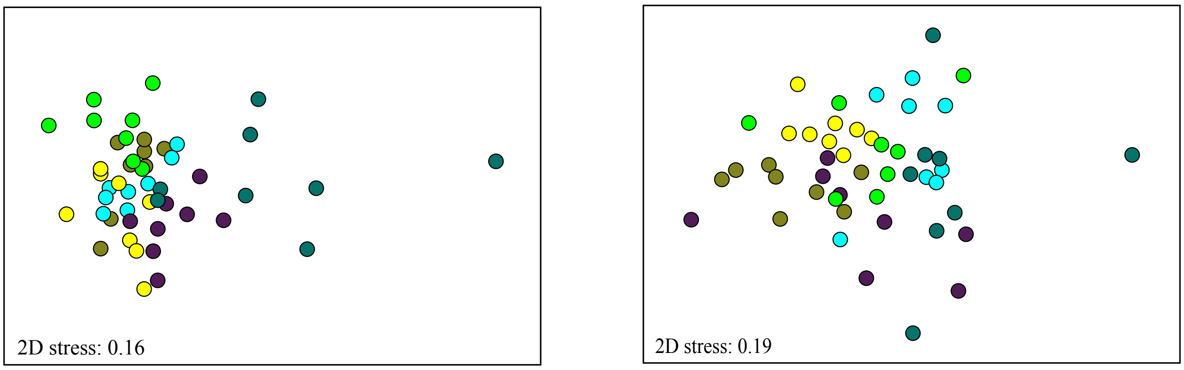
However, several other sites had a relative distinct ichthyofaunal composition in this season, and yet their salinities were not notably different.

8.1.2.5 Composition of fish assemblages among seasons

One-way ANOSIM tests, carried out separately for the fish faunal data recorded at each habitat type, were used to examine the extent and nature of seasonal differences in ichthyofaunal composition in Wilson Inlet between winter 2006 and summer 2008. Significant differences were detected in each case (p=0.1-1.5%), and the overall extents of these temporal differences were generally slightly higher than those for habitat type, *i.e.* Global R=0.161-0.434. The global ANOSIM results obtained for seasonal differences at each habitat type are provided, along with the MDS plots constructed from the same data, in Fig. 8.1.2.4.

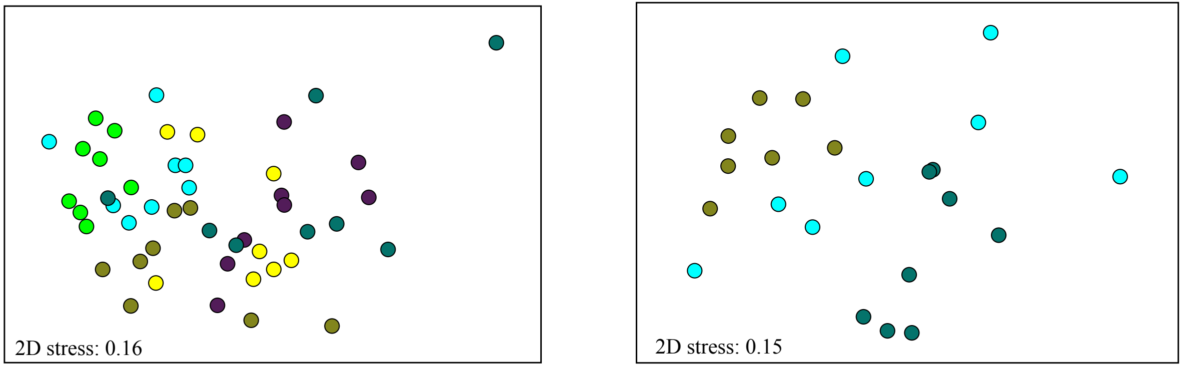
The greatest seasonal differences were detected at habitats O, F, G and D (Global R=0.408-0.434), for which either all or most pairwise comparisons were significant. At the first of these habitats, the greatest seasonal differences, in decreasing order, occurred for summer 2007 *vs* summer 2008 and winter 2007, and for summer 2008 *vs* winter 2007 and winter 2006 (R=0.632-0.936). Such differences were illustrated on the MDS ordination plot shown in Fig. 8.1.2.4h. Thus, samples collected in summer 2007 formed a particularly tight group on one side of the plot that essentially lay above those for summer 2008, which also formed a relatively distinct group. Samples from both winters, and particularly winter 2007, formed dispersed groups that spread to the opposite side of the plot from that occupied by samples representing both summers (Fig. 8.1.2.4h). Samples collected in summer 2007 were characterised and distinguished by highly consistent and abundant catches of particularly *A. elongata* and, compared to winter 2007, also *A. suppositus*, while those collected in summer 2008 were typified and distinguished by highly consistent and abundant catches of primarily *L. wallacei* and, compared to both winters, also *A. elongata*.

The most pronounced seasonal differences at habitat F occurred for autumn 2007 *vs* spring and winter 2006, summer 2007 *vs* spring and winter 2006 and summer 2008 *vs* spring 2006 (R=0.614-0.961). MDS ordination of the ichthyofaunal data recorded at this habitat demonstrated that samples from winter 2006 and particularly spring 2006 formed tight but overlapping groups that lay on one side of the plot, while samples for summer and autumn 2007 formed more dispersed groups, the first of which lay adjacent to those for winter and spring 2006, and the latter of which lay adjacent to those for summer 2007 (Fig. 8.1.2.4c). Samples from summer 2008 also formed a relatively dispersed group, most of which lay beneath those for winter and spring and 2006, and the rest of which intermingled with samples from summer and



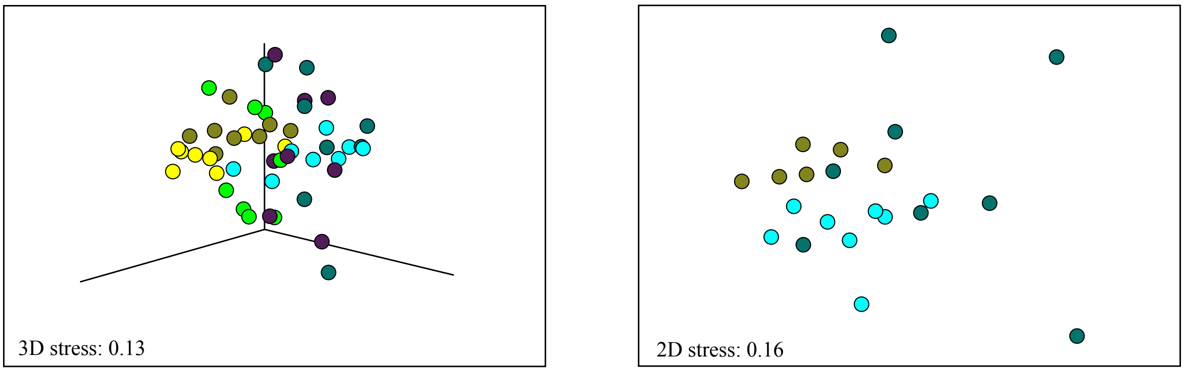
(a) Habitat C; p=0.1%, GR=0.342

(b) Habitat D; p=0.1%, GR=0.408



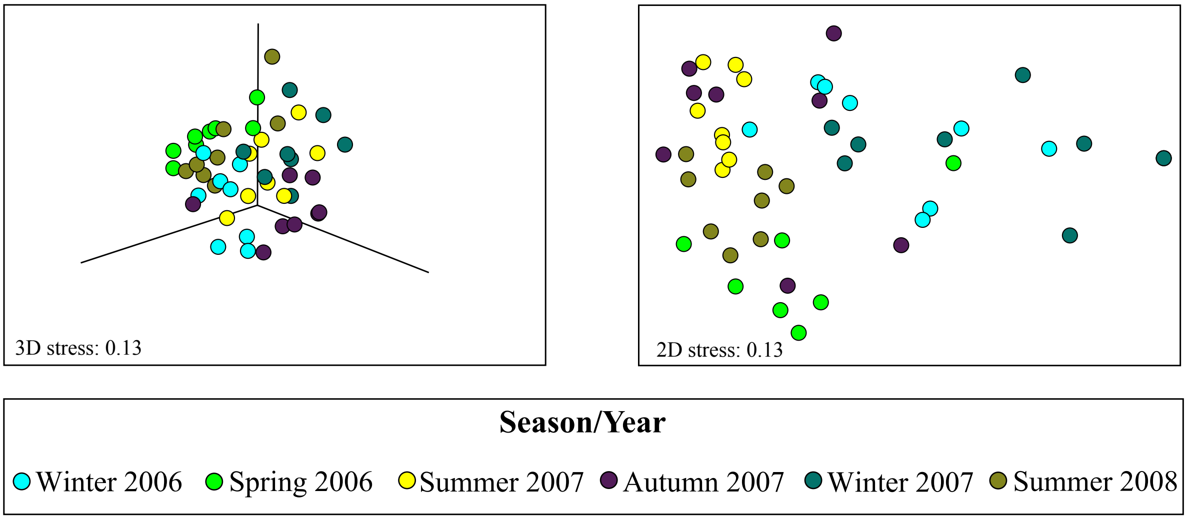
(c) Habitat F; p=0.1%, GR=0.430

(d) Habitat G; p=0.1%, GR=0.417



(e) Habitat I; p=0.1%, GR=0.374

(f) Habitat J; p=1.5%, GR=0.161



(g) Habitat L; p=0.1%, GR=0.326

(h) Habitat O; p=0.1%, GR=0.434

Figure 8.1.2.4: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample in each sampling season at habitat (a) C, (b) D, (c) F, (d) G, (e) I, (f) J, (g) L and (h) O in the Wilson Inlet. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

autumn 2007 (Fig. 8.1.2.4c). The fish assemblages during winter and spring 2006 were both typified by consistent catches of *P. olorum* and *A. elongata*, and also of *A. suppositus* in the case of the former season and of *L. wallacei* in the case of the latter. A greater abundance of *P. olorum* in both of these seasons primarily distinguished their fish faunas from those recorded in summer and autumn 2007, as did a greater prevalence of *L. wallacei* in summer 2007 and *L. presbyteroides* in autumn 2007. The fish faunas recorded in spring 2006 and summer 2008 were best set apart by considerably higher abundances of *P. olorum* in the former season and of *A. suppositus* and *A. elongata* in the latter.

Fish faunal compositions differed significantly between all pairs of seasons at habitat G, but the extent of those differences were markedly higher between summer 2008 and winter 2007 (*i.e.* R=0.837) than between any other pair of seasons (*i.e.* R <0.253). Such results were reflected by the MDS ordination plot of the fish assemblage data recorded in this season. Thus, samples from summer 2008 formed a relatively tight group on one side of the plot that was completely discrete from those representing winter 2007, which formed a slightly more dispersed group in the middle of the plot. Samples from winter 2006 were highly dispersed, however, throughout the entire plot (Fig. 8.1.2.4d). A greater prevalence of *A. suppositus* and *P. olorum* in summer 2008 was most responsible for distinguishing its faunas from those recorded in winter 2007.

The most pronounced seasonal differences at habitat D shared some similarities with those detected at O, *i.e.* summer 2008 *vs* winter 2006 and 2007, and summer 2007 *vs* winter 2006 (R=0.641-0.720). Samples collected in the first of these seasons formed a relatively compact group on one side of the MDS plot constructed from the data recorded at this habitat, just below those from summer 2007, which also formed a tight group. Most of the samples from winter 2006 formed a relatively pronounced group adjacent to those representing each of the summers, while those from winter 2007 were much more dispersed, but entirely discrete from those representing both summers (Fig. 8.1.2.4b). SIMPER demonstrated that greater abundances of *P. olorum, A. suppositus* and *A. elongata* in summer 2008 were most responsible for distinguishing its fish faunas from those recorded in both winters, while greater catches of *L. presbyteroides, L. wallacei* and *F. lateralis* in summer 2007 best separated its faunas from those found in winter 2006.

Relatively prominent differences (*i.e.* R >0.600) were detected by ANOSIM between particular pairs of seasons in each of the remaining habitats, except J. Thus, at habitat C, the composition of the fish assemblages in autumn 2007 was particularly distinct from those in spring 2006 and summer 2008 (R=0.652-0.705), while at habitat I, the fish faunas in summer 2007 differed considerably from those in both winters (R=0.616-0.670) and, at habitat L, the ichthyofaunas in spring 2006 were distinct from those in autumn and winter 2007 (R=0.615-0.786). Such differences were reflected on the MDS plots shown in Fig. 8.1.2.4a, e and g, respectively, by both the greater distances between groups of samples representing each of these seasons and/or the lower level of within-group dispersion. In contrast, the lack of seasonal differences at the channel habitat J are illustrated by the close proximity of groups of samples from different seasons and/or the high degree of within-group dispersion on the MDS plot shown in Fig. 8.1.2.4f. The above seasonal differences at habitat C were primarily due to greater, but not particularly consistent, catches of both *P. olorum* and *F. lateralis* in spring 2006 and summer 2008 than in autumn 2007, and to greater catches of *L. wallacei* in autumn 2007 than in summer 2008. Greater and more consistent numbers of *L. wallacei*, *P. olorum* and *A. suppositus* in summer 2007 than both winters were most responsible for distinguishing the ichthyofaunas of these seasons at habitat I, whereas a greater prevalence of *F. lateralis* in spring 2006 than in both autumn and winter 2007, and of *A. suppositus* in autumn 2007, mainly separated the fish faunas recorded in each of these seasons at habitat L.

8.2 Discussion

8.2.1 Differences in fish assemblages among habitats

The nearshore fish assemblages of Wilson Inlet, like those of the nearby Broke Inlet, which is also seasonally-open and has a basin morphology, were heavily dominated by a small suite of estuarine species, namely the atherinids *Atherinosoma elongata* and *Leptatherina wallacei* and the gobiid *Pseudogobious olorum*. These three species comprised at least 89% of the total number of fish at each of the eight habitats sampled throughout the estuary, and the first two were also particularly abundant in Broke Inlet. Although not especially numerous, several other atherinid or goby species that are able to complete their life cycle within estuaries also occurred consistently and thus regularly characterised the ichthyofaunas of various habitats throughout Wilson Inlet, namely *Afurcagobius suppositus*, *Favonigobius lateralis* and *Leptatherina presbyteroides*. The dominance of the nearshore fish fauna of this system by a small number of euryhaline species that can reproduce within the estuary has been reported by several other workers in seasonally-open systems, and presumably reflects selective pressure for this type of life history strategy when such estuaries are often landlocked for at least several months of the year (Potter *et al.* 1990, 1993). Despite the predominance of the above fish species in Wilson Inlet, significant differences in fish assemblage composition were still detected among the various habitats in each of the six sampling seasons between winter 2006 and summer 2008. However, while the overall extent of these differences was moderate in winter and spring 2006 and summer 2008, it was low in the remaining seasons. The extents of these ichthyofaunal differences were, in several cases, lower than those detected in the comparable Broke Inlet, and often considerably lower than those recorded in the permanently-open Swan Estuary and, to a lesser extent, the Peel-Harvey Estuary (see Chapters 7.1.2, 5.1.2 and 6.1.2, respectively).

The main reasons for the small spatial differences in the nearshore fish assemblage composition throughout Wilson Inlet are likely to include those outlined in Chapter 7.2.1 for the Broke Inlet, and also the following. Firstly, unlike that latter system, Wilson Inlet does not have a conspicuously defined entrance channel and thus lacks any pronounced regional differences in morphology. Secondly, the mouth of this system was only open to the sea for about one month during the 18 month period in which fish were collected for this study, whereas that of Broke Inlet was open for approximately five of the 12 months in which that system was studied. Such limited tidal exchange not only led to very restricted opportunities for marine fish to enter Wilson Inlet, but also contributed to the fact that most water quality characteristics (*e.g.* salinity and temperature) exhibited little spatial variation throughout the estuary in almost all seasons. Thirdly, the small suite of estuarine species that comprised most of the fish fauna in Wilson Inlet did not segregate spatially to the same extent as in other south-western Australian estuaries (*e.g.* Loneragan and Potter 1990, Gill and Potter 1993, Young *et al.* 1997 and Hoeksema *et al.* 2006a). Thus, whereas *L. wallacei, P. olorum* and *A. suppositus* are often found in larger numbers in the upper reaches of estuaries and *F. lateralis* and *L. presbyteroides* are most common in the lower reaches (reflecting, in part, their apparent preferences for lower and higher salinities, respectively), such generalisations did not apply in Wilson Inlet. As discussed below, although some of the above species did occur more consistently and in greater numbers at certain habitats in particular seasons, their relatively homogeneous spatial distribution in Wilson Inlet probably reflects the lack of any marked geomorphological and hydrological differences throughout this basin system.

The most distinct fish faunal compositions in at least two seasons were typically detected at habitats F, L and/or O, which were located on the western, northern and eastern sides of the basin, respectively. Apart from their very different levels of exposure to wave activity from different prevailing winds, they also varied in the composition of their substrate and extent of submerged vegetation. Thus, whereas F and L comprised moderate to large areas of submerged vegetation and, in the case of the latter habitat, also some patches of rock, the substrate at O consisted entirely of bare sand. Moreover, some sites representing habitat F were located close to the mouth of the Denmark River and those from O were relatively close to the mouths of the Sleeman and Hay rivers, while those from L were not close to any riverine water source.

The composition of the fish fauna at habitat F was notably distinct from that of most other habitats in winter and spring 2006, which was attributable largely to the prevalence of *P. olorum* in both of these seasons and of *A. suppositus* and *A. elongata* in winter and spring, respectively. Thus, during these occasions, these species always occurred in greater numbers at F than at any other habitat. Each of these species was also recorded in the highest overall mean densities at F, particularly in the case of *P. olorum*. Given the affinities of the first two of these species for submerged vegetation and highly sheltered waters (Gill and Potter 1993, Humphries and Potter 1993), it is highly relevant that habitat F contains moderately large areas of the seagrass *Ruppia megacarpa* and, due to its location along the western shore of Wilson Inlet, is among the most protected from prevailing westerly and south-westerly winds. *Atherinosoma elongata* has also been found by Humphries and Potter (1993) to be most abundant in those areas of Wilson Inlet that contain dense *R. megacarpa*. However, this widely distributed and schooling atherinid species ranked first in terms of abundance at all habitats throughout this system, comprising at least 45% of the catch, and differences in its overall abundance or proportional contribution did not seem to be particularly tightly linked to the prevalence of *R. megacarpa*.

Aside from the distinctiveness of the ichthyofaunal composition at F in particular seasons, this habitat also contained the greatest overall number of fish species and mean densities. Each of the species that occurred exclusively at this habitat were either estuarine and marine, *i.e. Platycephalus speculator* and *Arenigobius bifrenatus*, or marine estuarine-opportunists*, i.e. Pelates octolineatus* and *Pseudorhombus jenynsii,* and several other species that occurred at F and just one other habitat also belonged either to the latter life history category or were marine stragglers. The occurrence of these marine species at F probably reflects its proximity to the channel and, unlike habitats J and I that were located closest to the estuary mouth yet contained relatively few marine species, the considerable beds of submerged vegetation and thus levels of food and shelter it contained. The latter, in conjunction with the shelter provided by its location within the estuary, most likely also contributed to the higher overall fish densities recorded at habitat F. However, unlike the situation at particular habitats in Broke Inlet, very few of the marine species at F or any other habitat in the Wilson Inlet were represented by their 0+ juveniles. Such findings reflect, in part, the highly limited period over which the mouth of Wilson Inlet was open during the current study, compared with the situation in Broke Inlet. Moreover, the entrance channel to that latter system is considerably deeper and often wider than that of Wilson Inlet, and thus the volume of tidal exchange when the bar is open is far greater. Consequently, there is far less opportunity for the 0+ recruits of those marine species that migrate inshore to enter Wilson Inlet, as was also reported by Potter *et al.* (1993) in their study of the nearshore fish faunas of this system.

The ichthyofaunal composition of habitat L was distinct from that of several other habitats in winter 2006 and summer 2008, which reflected mainly the predominance of the gobiid *F. lateralis* in both of these seasons and of *P. olorum* and *A. suppositus* in the former season. The overall mean density of the first of these species was also far greater at L than at any other habitat in Wilson Inlet, which was also reflected by the fact that it was the third most abundant species at this habitat, but was not abundant elsewhere throughout the system. The greatest densities of this small benthic species have previously been shown to occur over sandy substrates in both Wilson Inlet (Humphries and Potter 1993) and the Swan Estuary (Gill and Potter 1993). Indeed, silty substrates have been shown by the latter workers to clog the gills of this gobiid and thus lead to its death. Thus, even though habitat L contained appreciable areas of dense *R. megacarpa*, it also comprised patches of coarser sand which would provide a suitable substrate for *F. lateralis*. Moreover, like *P. olorum* and *A. suppositus*, *F. lateralis* is also far more abundant in areas with minimal water disturbance (Gill and Potter 1993). Thus, while habitat L was moderately exposed to both westerly and southerly winds, the considerable and particularly dense submerged vegetation beds at this habitat would provide an effective buffer from wave activity. The presence of these nearby seagrass beds would also lead to greater abundances of the preferred food sources of *F. lateralis*, namely polychaetes, crustaceans and/or detritus (Gill and Potter 1993, Humphries and Potter 1993). Lastly, although euryhaline*,* *F. lateralis* is better suited to higher salinities and, as mentioned above, is thus often most abundant in the more saline lower reaches of several estuaries in south-western Australia (*e.g.* Loneragan and Potter 1990, Gill and Potter 1993, Young *et al.* 1997, Hoeksema *et al.* 2006a). Although the mean densities of this gobiid were considerably higher at habitats I and J in the lowermost reaches of Wilson Inlet than in most other habitats in this system, probably reflecting their predominantly coarse sandy substrates and comparative shelter from most winds, they were far lower than that recorded at L in the middle reaches of the basin. Such findings most likely reflect both the minimal spatial variability in salinity throughout Wilson Inlet in all sampling seasons, and also the comparatively greater sediment and water disturbance at I and J, the latter of which is attributable to the lack of submerged vegetation and highly dynamic nature of the shallow sandy delta in this region of the estuary.

The nearshore fish faunas at the small habitat O were distinct during winter 2006 and both summers, which was due largely to their depauperate composition. Thus, the two commonly occurring atherinid species that characterised this habitat in the first of these seasons, *i.e. A. elongata* and *L. wallacei*, always occurred in greater densities at other habitats. This was frequently the case for the species that characterised O in both summers, with the exception of the first of the above species in summer 2007 and the latter species in summer 2008. Moreover, the mean number of species, density and taxonomic distinctness of the fish assemblage at O was often lower than those at most other habitats in several seasons. Such findings presumably reflect the fact that this shallow sandy habitat lacked any benthic structural heterogeneity and thus shelter, and that it was one of the most exposed throughout Wilson Inlet to waves generated from prevailing westerly and south-westerly winds. Moreover, it was the only habitat in this system to experience markedly different mean salinities to that at any other habitat in at least one of the seasons in which fish were sampled. Thus, during winter 2006, mean salinities at O fell to 11.5‰, presumably reflecting the proximity of this habitat to the mouths of the Hay and Sleeman rivers, whereas those of all other habitats ranged between 19 and 21‰. Such reductions in salinity may help account for the particularly depauperate fish fauna at O during this season. However, given the particularly good osmoregulatory abilities of the fish species that dominated the fish assemblages in Wilson Inlet (Prince *et al.* 1982, Gill and Potter 1993), the latter may be less likely.

8.2.2 Spatial relationships between the environmental and faunal characteristics of habitats

The spatial pattern of the average enduring environmental differences among habitats in the Wilson Inlet was significantly and moderately well correlated with that exhibited by the composition of the fish fauna during winter 2006 and summer 2007. However, no such significant match was detected in the remaining four seasons, indicating that the relative differences in the enduring environmental measurements among habitats did not provide a good surrogate for those exhibited by the composition of the fish fauna. These latter findings were often attributable to a lack of pronounced spatial differences in ichthyofaunal composition among many of the habitats throughout the estuary (see preceding subsection), despite considerable differences in their enduring characteristics. The only habitat that had a relatively distinct average ichthyofaunal composition in most seasons was O, which was also reflected by the distinctiveness of its enduring environmental characteristics. Given the above results, there is reduced value in using the habitat prediction tool developed for Wilson Inlet in Chapter 3.3.2 and the associated list of typifying species for each habitat and season to ascertain those fish species likely to be most prevalent at any nearshore site in this system throughout the year. Thus, the nearshore fish fauna at any location in Wilson Inlet is likely to be typified by several of the six atherinid and goby species that occur commonly throughout this system for much of the year, namely *A. elongata, L. wallacei, P. olorum, F. lateralis, A. suppositus* and/or *L. presbyteroides*. However, the extent of ichthyofaunal differences among habitats and the correlation between spatial patterns exhibited by the fish fauna and those of the enduring environmental characteristics may be greater when the mouth of this system has been open to the sea for a considerable period.

In addition to the above findings, the pattern of differences among habitats displayed by the fish fauna was not significantly matched with that exhibited by the suite of water quality parameters (*i.e.* salinity, temperature and dissolved oxygen) in any season, thus indicating that they exerted little influence on the spatial distribution of fish throughout the estuary. This was further reinforced by the fact that, even after BIOENV was used to identify that particular combination of the above water quality variables that maximised the spatial correlation with the fish assemblage data, the only season in which a significant match was obtained was winter 2006, which was achieved when data for just salinity was employed. These findings reflect not only the relatively small differences in fish assemblage composition among the majority of habitats in most seasons, but also that the magnitude of salinity and water temperature varied little throughout the estuary in each season. Moreover, although dissolved oxygen concentration varied conspicuously among habitats in seasons such as winter 2007, it did not result in a similar pattern of differences in the composition of the ichthyofauna in that season. The significant BIOENV results obtained during winter 2006 reflected the fact that this was the only season in which one habitat (O) had a notably different mean salinity to those recorded throughout the rest of the estuary, and that the fish fauna at that habitat in that season was also particularly distinct, due largely to its depauperate composition (see preceding subsection).

8.2.3 Seasonal differences in fish assemblage composition among habitats

The extents of the differences in ichthyofaunal composition among seasons at each habitat were typically larger than those detected among habitats in each of the various seasons. At many habitats, some of the most pronounced seasonal differences in fish assemblage composition often occurred between summer 2007 and/or 2008 and one or more of the remaining seasons. Moreover, it was also largely the case that the greatest mean number of fish species and densities were recorded during one or both of these summers at most habitats.

The distinctiveness of the fish assemblages during summer 2007/2008 at several habitats was often due to the more consistent and abundant catches of *A. suppositus*, *P. olorum* and/or *L. wallacei*. Given the affinities of each of these species for areas containing submerged vegetation (Gill and Potter 1993, Humphries and Potter 1993), such findings may be related to the pronounced seasonal fluctuations in the biomass of the seagrass *R. megacarpa* that grows extensively throughout Wilson Inlet, and which typically reaches its maxima in summer (Department of Environment 2003). However, given that each of the above estuarine species typically spawn between late winter and late spring (Gill and Potter 1993, Prince and Potter 1983), and that their mean lengths were often lowest during one or both summers (data not shown), it seems likely that their prevalence at this time of year reflects the recruitment of their 0+ juveniles. This recruitment period also coincides with that time of year in which water temperatures in Wilson Inlet were at or approaching their maxima, and thus most likely to promote the rapid growth of these juvenile fish.

Conversely, the lowest mean number of fish species and densities were often recorded during winter 2006 and/or 2007 at most habitats, and the composition of the fish assemblages during these seasons often differed the most from that recorded in one or both summers. Such findings may reflect the pronounced decline in biomass of *R. megacarpa* at this time of year, which is estimated to be approximately half of that in summer (Department of Environment

2003), and thus the reduction in food and shelter for several of the small estuarine species that dominate the fish fauna of Wilson Inlet. Furthermore, the densities of *P. olorum* and *A. suppositus* have been shown to be positively correlated with water temperature in other estuaries in south-western Australia (Gill and Potter 1993), and it may thus be relevant that the temperatures during both winters in Wilson Inlet were far lower than those in both summers, *i.e.* 13.3-14.7 *vs* 22-24.8°C.

Variability in the overall extent of seasonal differences in ichthyofaunal composition among habitats may be related, in part, to differences in the areas of submerged vegetation they contained, and thus the subsequent influence of seasonal changes in the biomass of that plant material. Thus, two of the four habitats at which the overall seasonal differences in fish composition were greatest contained moderate to large areas of submerged vegetation, *i.e.* F and D, whereas that at which by far the smallest seasonal differences in ichthyofaunal composition occurred contained very little vegetation, *i.e.* J. In the case of habitat O, however, which did not contain any submerged vegetation beds and yet had the largest overall seasonal differences in fish composition, such findings are likely to reflect the marked differences in water depth between summer and winter at this particularly shallow habitat and, during winter 2006, the markedly lower mean salinities that were recorded at this habitat compared to all others throughout the estuary in that season.

9. Relationships between habitat types and faunal assemblages in the Wellstead Estuary

9.1 Results

9.1.1 Water quality parameters

Replicate data for salinity, water temperature and dissolved oxygen, which were recorded at each site representing the five habitat types sampled in the small and normally-closed Wellstead Estuary during six seasons between winter 2006 and summer 2008, were each subjected to a preliminary three-way PERMANOVA test to ascertain whether their spatial differences were most appropriately analysed at the habitat or site level. These tests demonstrated that, in the case of salinity, there were significant differences between sites assigned to the same habitat, and there was a significant site x season interaction. The relative importance of each of these significant terms, however, was approximately half that of the habitat term. No significant differences were detected between sites or for the site x season interaction in the case of water temperature and dissolved oxygen. In view of the above results, the replicate data for salinity were subsequently subjected to a site x season PERMANOVA, while that for both temperature and dissolved oxygen were subjected to a habitat x season PERMANOVA to more thoroughly investigate their spatial and temporal differences.

The magnitude of salinity differed significantly among sites and seasons and the interaction between these main effects was also significant ($p=0.001$). However, the relative importance of seasonal changes on salinity differences was far greater than that of either site or the interaction term (Table 9.1.1.1). This was evident from the plot shown in Fig. 9.1.1.1a, in which salinities throughout the estuary during winter 2006, spring 2006 and winter 2007 (24.9-36.2‰) were almost always lower than those recorded in summer and autumn 2007 (34.6-45.8‰), which, with one exception, were always lower than those recorded in summer 2008 (36.45-63.2‰). In each season, salinities were lower at sites representing habitat F in the upper reaches, particularly during summer 2008 and, to a lesser extent, summer 2007. However, these declines in salinity were only relatively slight in the remaining seasons. Variability in the extent of spatial differences in salinity among seasons, combined with some slight differences in the rank order of seasons among particular sites, contributed to the relatively weak site x season interaction detected by PERMANOVA (Fig. 9.1.1.1a).

Table 9.1.1.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for a site x season PERMANOVA on the data for salinity and habitat x season PERMANOVAs on the data for water temperature and dissolved oxygen concentration recorded throughout the Wellstead Estuary during winter and spring 2006, summer, autumn and winter 2007 and summer 2008. df = degrees of freedom. Significant results are highlighted in bold.

	Salinity					**Temperature**					**Dissolved Oxygen**			
	df	MS	Pseudo F	COV	p	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects														
Habitat						4	**12.765**	**8.611**	**0.686**	**0.001**	**8.048**	**3.233**	**0.481**	**0.024**
Season	5	**1563.400**	**4198.000**	**8.840**	**0.001**	5	**383.120**	**258.460**	**4.368**	**0.001**	**41.017**	**16.475**	**1.388**	**0.001**
Site	9	**129.940**	**348.900**	**3.286**	**0.001**									
Two-way Interactions														
Habitat * Season						20	0.739	0.499	-0.431	0.958	1.199	0.482	-0.568	0.971
Season * Site	45	**9.109**	**24.460**	**2.090**	**0.001**									
Residual	60	0.372		0.610		90	1.482		1.218		2.490		1.578	

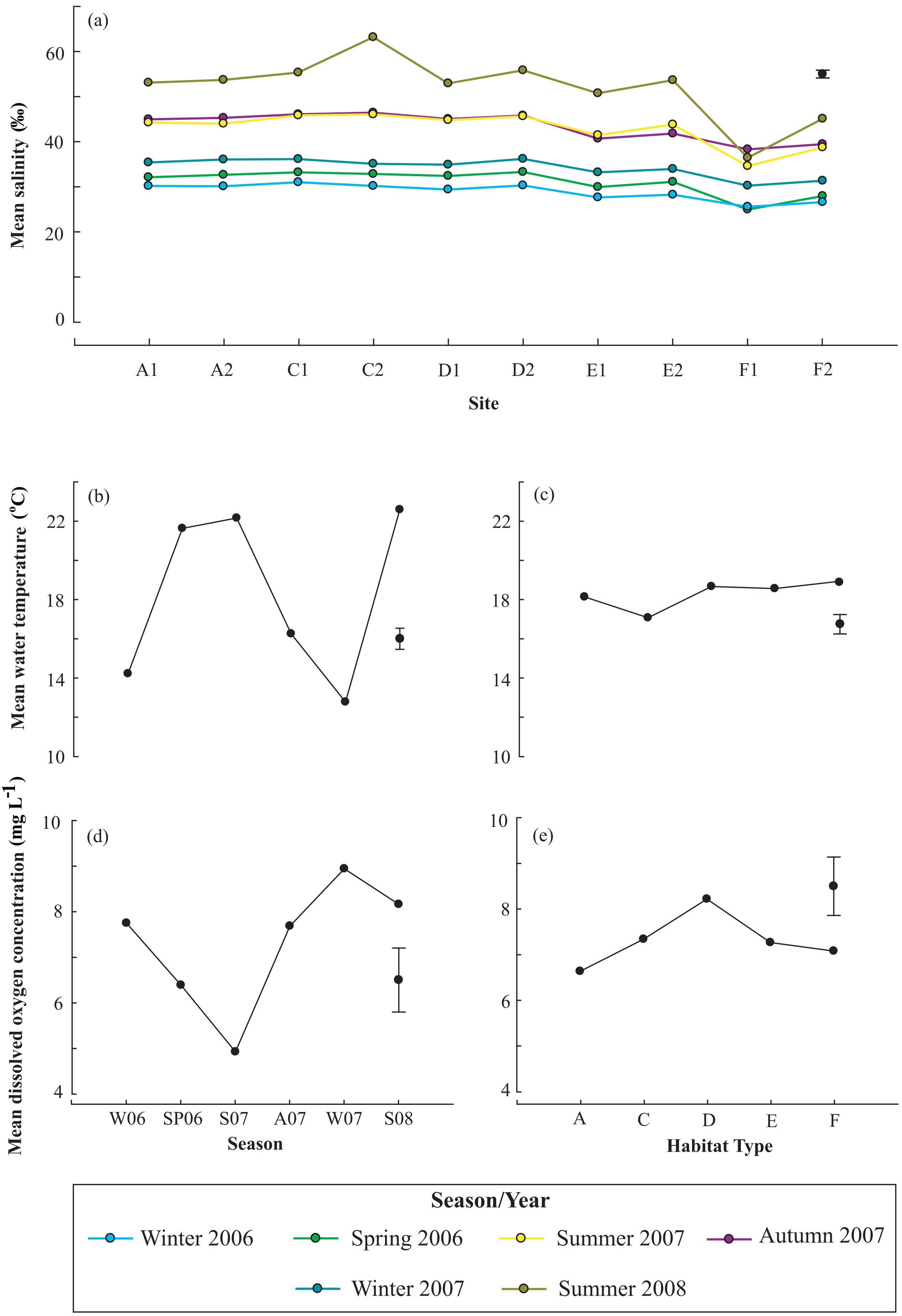


Figure 9.1.1.1: Mean (a) salinity, (b-c) water temperature and (d-e) dissolved oxygen concentration at each habitat type/site in the Wellstead Estuary between winter 2006 and summer 2008. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

Water temperature and dissolved oxygen both differed significantly among habitats and seasons (p=0.001-0.024), but there was no significant interaction between these main effects for either dependent variable. Furthermore, in both cases, the influence of season was markedly greater than that of habitat, *i.e. ca* six and three times stronger for water temperature and dissolved oxygen, respectively (Table 9.1.1.1). Water temperature was significantly lower in both winters (12.8-14.2°C) than in all other seasons, and significantly lower in autumn 2007 (16.3°C) than spring 2006 and both summers (21.6-22.6°C; Fig. 9.1.1.1b). Temperatures were also slightly but significantly lower at habitat C, which is located closest to the bar of the estuary, than at all other habitats except A (*i.e.* 17.1 *vs* 18.5-18.9°C; Fig. 9.1.1.1c). The concentration of dissolved oxygen was significantly lower in summer 2007 than in all other seasons except spring 2006 (*i.e.* 4.9 *vs* 7.6-8.9 mg L^{-1}; Fig. 9.1.1.1d) and was significantly higher at habitat D than A (8.2 *vs* 6.6 mg L^{-1}; Fig. 9.1.1.1e).

9.1.2 Fish assemblages

9.1.2.1 Species mean density and length characteristics at each habitat type

Eighteen fish species and 286 182 individuals (*i.e.* after the number of fish in each sample was adjusted to that in 100 m^2 and summed) were recorded throughout the Wellstead Estuary during the six sampling seasons between winter 2006 and summer 2008 (Table 9.1.2.1). The overall mean density of fish recorded in this small system, *i.e.* 1192 fish 100 m^{-2}, was far greater than that in the permanently-open and far larger Swan and Peel-Harvey estuaries on the lower west coast (*i.e.*183 and 363 fish 100 m^{-2}, respectively) and the seasonally-closed and large Broke and Wilson inlets on the south coast, *i.e.* 139 and 334 fish 100 m^{-2}, respectively (see Chapters 5.1.2.1, 6.1.2.1, 7.1.2.1 and 8.1.2.1, respectively). Similar numbers of species were recorded at each habitat type in the Wellstead, with the lowest being found at C and D in the lower reaches of the system (9 species) and the greatest at E in the upper reaches (12 species). However, there were considerable differences in the mean density of fish among habitats, which showed the opposite trend to that of number of species. Thus, by far the greatest mean fish density was recorded at C followed by D (2004 and 1535 fish 100 m^{-2}, respectively), and the least was found at E (570 fish 100 m^{-2}; Table 9.1.2.1).

The estuarine species *Atherinosoma elongata, Leptatherina wallacei* and *Pseudogobius olorum* ranked first, second and third in abundance, respectively, at all habitats except C, where the latter species ranked fourth. Furthermore, *Favonigobius lateralis,* an estuarine and marine species, also ranked in the top five most abundant species at each habitat (Table 9.1.2.1). *Atherinosoma elongata* comprised the large majority of the overall catch at every habitat,

Table 9.1.2.1: Mean density (M), standard deviation (^{SD}), rank by density (R), percentage contribution to the overall catch (%) and length range and median length (L^{Med}) of each fish species recorded at each habitat type in the Wellstead Estuary between winter 2006 and summer 2008. Abundant species (*i.e.* those that contribute >5% to the catch) are highlighted in grey. The life-history category of each species is also provided (^{E}=estuarine, ^{EM}=estuarine and marine, ^{O}=marine estuarine-opportunist, ^{S}=marine straggler). The total number of species, number of samples collected and the total number of individuals (*i.e.* after the number of fish in each sample had been adjusted to that in 100 m^2 and summed) are given for each habitat type.

	Habitat type A				Habitat type C				Habitat type D			
Species name	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$709.20^{700.17}$	79.33	1	$16\text{-}80^{40}$	$1838.31^{2093.61}$	91.72	1	$12\text{-}79^{35}$	$1186.48^{1846.95}$	77.29	1	$14\text{-}90^{40}$
Leptatherina wallacei ^{E}	$137.66^{153.64}$	15.40	2	$17\text{-}78^{39}$	$92.42^{167.19}$	4.61	2	$14\text{-}61^{33}$	$329.71^{767.39}$	21.48	2	$15\text{-}75^{38}$
Pseudogobius olorum ^{E}	$44.04^{58.70}$	4.93	3	$14\text{-}62^{29}$	$15.91^{15.86}$	0.79	4	$12\text{-}58^{32}$	$16.13^{35.66}$	1.05	3	$17\text{-}59^{31}$
Favonigobious lateralis ^{EM}	$2.33^{4.32}$	0.26	4	$18\text{-}59^{40}$	$57.29^{114.18}$	2.86	3	$18\text{-}84^{33}$	$1.29^{3.25}$	0.08	4	$18\text{-}66^{41}$
Engraulis australis ^{EM}	$0.36^{1.11}$	0.04	5	$52\text{-}74^{72}$					$0.11^{0.55}$	0.01	7	$67\text{-}78^{70}$
Acanthopagrus butcheri ^{E}	$0.20^{0.67}$	0.02	6	$43\text{-}155^{127}$	$0.07^{0.30}$	<0.01	7	$67\text{-}125^{100}$	$0.81^{2.66}$	0.05	5	$42\text{-}174^{100}$
Leptatherina presbyteroides ^{EM}	$0.16^{1.00}$	0.02	7	$32\text{-}66^{45}$								
Gambusia affinis ^{F}	$0.05^{0.28}$	0.01	8	$21\text{-}28^{25}$								
Gymnapistes marmoratus ^{O}	$0.02^{0.12}$	<0.01	9	55	$0.11^{0.34}$	0.01	5	$70\text{-}128^{108}$	$0.02^{0.12}$	<0.01	8	90
Afurcagobius suppositus ^{E}	$0.02^{0.12}$	<0.01	9	30								
Cristiceps australis ^{S}					$0.07^{0.50}$	<0.01	6	52				
Haletta semifasciata ^{S}					$0.04^{0.17}$	<0.01	8	$236\text{-}259^{259}$				
Aldrichetta forsteri ^{O}					$0.02^{0.12}$	<0.01	9	190	$0.02^{0.12}$	<0.01	8	112
Atherinid sp. (juvenile) $^{-}$									$0.52^{3.61}$	0.03	6	$12\text{-}24^{18}$
Number of species		**10**				**9**				**9**		
Total mean density		**894**				**2 004**				**1 535**		
Number of samples		**48**				**48**				**48**		
Total number of fish		**42 914**				**96 203**				**73 684**		

Species name	Habitat type E				Habitat type F			
	M^{SD}	%	R	L^{Med}	M^{SD}	%	R	L^{Med}
Atherinosoma elongata ^{E}	$427.41^{597.37}$	74.96	1	$15\text{-}79^{40}$	$486.17^{679.98}$	50.72	1	$16\text{-}79^{42}$
Leptatherina wallacei ^{E}	$98.33^{179.73}$	17.25	2	$16\text{-}61^{37}$	$379.53^{584.03}$	39.59	2	$16\text{-}69^{38}$
Pseudogobius olorum ^{E}	$42.26^{50.76}$	7.41	3	$13\text{-}64^{35}$	$84.68^{144.48}$	8.83	3	$17\text{-}59^{27}$
Favonigobious lateralis ^{EM}	$1.65^{3.19}$	0.29	4	$16\text{-}70^{42}$	$0.59^{1.95}$	0.06	5	$23\text{-}70^{44}$
Engraulis australis ^{EM}	$0.11^{0.75}$	0.02	6	$60\text{-}67^{65}$	$0.11^{0.55}$	0.01	7	$53\text{-}57^{55}$
Acanthopagrus butcheri ^{E}	$0.22^{0.68}$	0.04	5	$24\text{-}242^{122}$	$7.13^{19.60}$	0.74	4	$55\text{-}187^{81}$
Leptatherina presbyteroides ^{EM}	$0.04^{0.25}$	0.01	8	53	$0.22^{1.49}$	0.02	6	$55\text{-}59^{56}$
Gambusia affinis ^{F}								
Gymnapistes marmoratus ^{O}	$0.04^{0.17}$	0.01	8	$49\text{-}85^{49}$	$0.02^{0.12}$	<0.01	9	96
Afurcagobius suppositus ^{E}								
Cristiceps australis ^{S}								
Haletta semifasciata ^{S}								
Aldrichetta forsteri ^{O}					$0.02^{0.12}$	<0.01	9	263
Atherinid sp. (juvenile) $^{-}$								
Urocampus carinirostris ^{EM}	$0.07^{0.50}$	0.01	7	57				
Amoya bifrenatus ^{EM}	$0.04^{0.17}$	0.01	10	$125\text{-}163^{144}$	$0.11^{0.55}$	0.01	7	$57\text{-}70^{64}$
Ammotretis rostratus ^{O}	$0.02^{0.12}$	<0.01	11	140	$0.02^{0.12}$	<0.01	9	121
Cnidoglanis macrocephalus ^{EM}	$0.02^{0.12}$	<0.01	12	119				
Number of species		**12**				**11**		
Total mean density		**570**				**959**		
Number of samples		**48**				**48**		
Total number of fish		**27 369**				**46 012**		

representing between *ca* 51% (habitat F) and 92% (habitat C) of the total number of individuals. The mean density and percentage contribution of *L. wallacei* was substantially greater at habitat F, followed by D, than at the remaining habitats and particularly C, *i.e. ca* 330-380 fish 100 m^{-2} representing 21-40% of the catch *vs ca* 92-138 fish 100 m^{-2} representing *ca* 5-17% of the catch. *Pseudogobius olorum* represented less than 10% of the catch at every habitat, with the contributions being least at the two lower estuary habitats D and C (0.79 - 1.05%) and the greatest at the uppermost habitat F (8.83%).

Some species were found only at one or two habitats, albeit in small numbers. For instance, the estuarine and marine species *Urocampus carinirostris* and *Cnidoglanis macrocephalus* were recorded only at the upper estuary habitat E, and *Amoya bifrenatus*, also an estuarine and marine species, and *Ammotretis rostratus*, a marine estuarine-opportunist, were found only at this habitat and the uppermost habitat F. Likewise, the lowermost habitat C was the only one to contain the marine stragglers *Cristiceps australis* and *Haletta semifasciata* (Table 9.1.2.1).

9.1.2.2 Spatial and temporal differences in mean species richness, density and taxonomic distinctness

Initial PERMANOVA tests were used to ascertain whether spatial differences in the mean number of species, density and taxonomic distinctness of the fish fauna recorded seasonally throughout the Wellstead Estuary between winter 2006 and summer 2008 were most appropriately analysed at the site or habitat level. Such tests indicated that the former was most appropriate for each dependent variable, given the significant site and/or site x season effects that were detected in each case. Replicate data for the number of fish species, density and taxonomic distinctness were thus each subjected to a site x season PERMANOVA to better elucidate the extent and nature of their spatio-temporal differences, which showed that there were significant site, season and site x season effects in each case (p=0.001-0.028; Table 9.1.2.2).

The relative influence of the interaction term on the mean number of species was greater than that for season and particularly that for site (Table 9.1.2.2). This was evident from the plot shown in Fig. 9.1.2.1a, which illustrated that there were marked differences in the seasonal rank order of this dependent variable among sites. For instance, the highest and lowest mean number of species at site A2 were recorded during spring 2006 and winter 2006/2007, respectively, whereas those at site C2 were recorded in winter 2007 and summer 2008, respectively. Furthermore, the seasonal range in mean number of species differed considerably among sites, *e.g.* 2.75-3.75 at D2 *vs* 2.75-5 at F1. Clear seasonal and particularly site trends were thus difficult

Table 9.1.2.2: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (p) for site x season PERMANOVAs on the number of species, density and quantitative taxonomic distinctness of the fish assemblages recorded throughout the Wellstead Estuary during winter and spring 2006, summer, autumn and winter 2007 and summer 2008. df = degrees of freedom. Significant results are highlighted in bold.

		Number of Species				**Density**				**Quantitative Taxonomic Distinctness**			
	df	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p	MS	Pseudo F	COV	p
Main Effects													
Site	9	**1.250**	**2.174**	**0.168**	**0.028**	**6.729**	**10.122**	**0.503**	**0.001**	**280.320**	**3.622**	**2.908**	**0.001**
Season	5	**3.897**	**6.777**	**0.288**	**0.001**	**33.007**	**49.653**	**0.899**	**0.001**	**1301.000**	**16.812**	**5.531**	**0.001**
Two-way Interaction													
Site * Season	45	**1.247**	**2.168**	**0.410**	**0.002**	**2.358**	**3.547**	**0.651**	**0.001**	**246.370**	**3.184**	**6.500**	**0.001**
Residual	180	0.575		0.758		0.665		0.815		77.385		8.797	

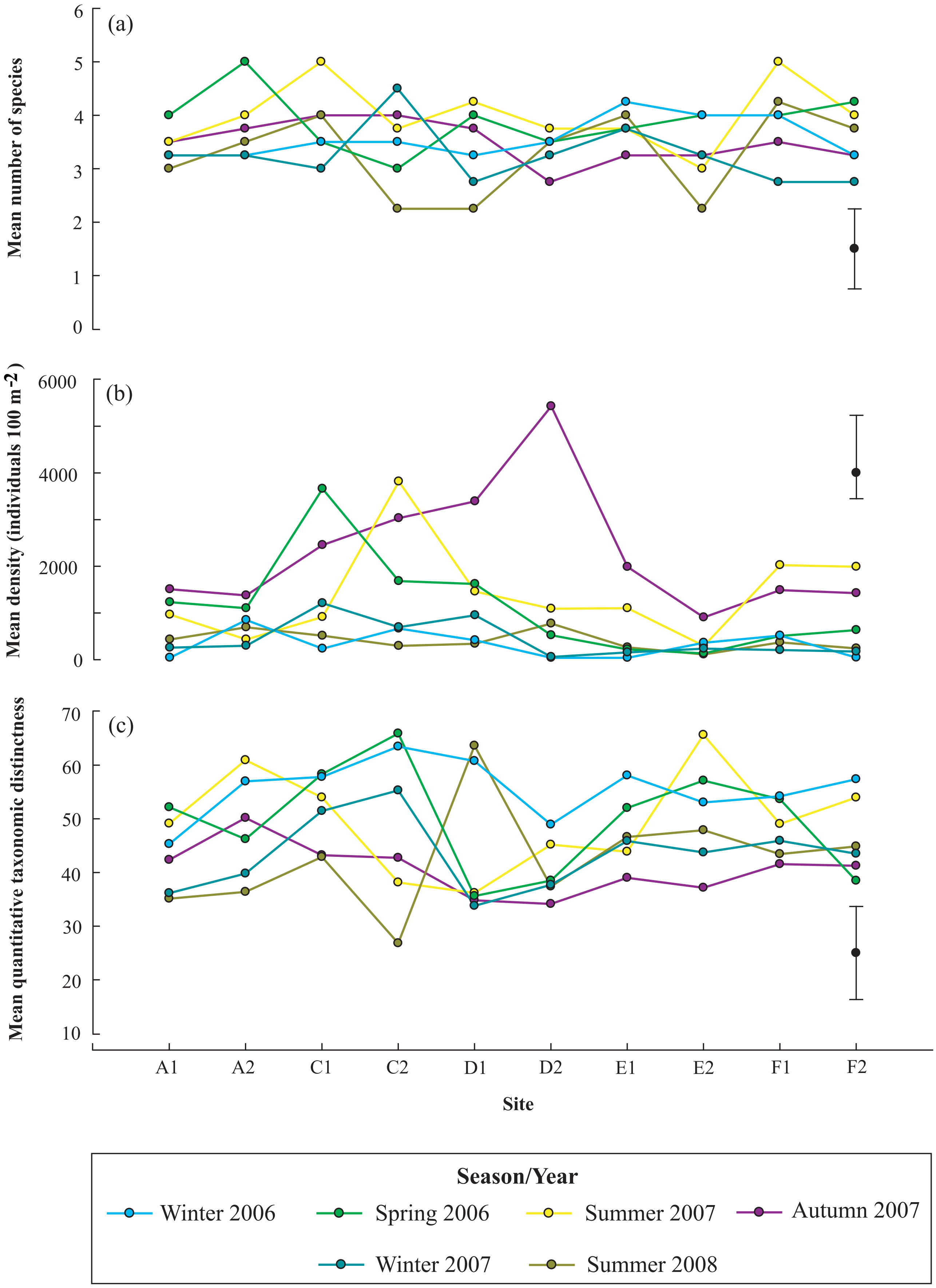


Figure 9.1.2.1: Mean (a) number of species, (b) density and (c) quantitative taxonomic distinctness of the fish assemblages recorded at each site in the Wellstead Estuary between winter 2006 and summer 2008. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

to discern for this dependent variable, but it was often true that the greatest or second greatest mean number of species was recorded in summer 2007, whereas the least was often recorded in winter 2007 or summer 2008 (Fig. 9.1.2.1a).

With respect to mean fish density, the influence of season was the most important, followed by that for the interaction term (Table 9.1.2.2). Thus, although the extent and rank order of seasonal differences in this dependent variable varied among sites, thereby contributing to the significant site x season interaction, mean values were almost always greatest during summer and/or autumn 2007, while the lowest were typically recorded during winter 2006 or 2007 or summer 2008 (Fig. 9.1.2.1b). These seasonal differences were particularly pronounced at sites representing the lower estuary habitats C and D. For example, at D2, a mean density of only *ca* 40 fish 100 m^{-2} was recorded during winter 2006, while *ca* 5500 fish 100 m^{-2} were recorded during autumn 2007, which was markedly higher than the second greatest density recorded at this site, *i.e. ca* 1090 fish 100 m^{-2} in summer 2007. The least seasonal differences were found at E2, where mean densities ranged from 100-300 fish 100 m^{-2} in all seasons except autumn 2007 (*ca* 900 fish 100 m^{-2}), and at both sites representing habitat A (*ca* 40-1500 fish 100 m^{-2}). During most seasons, the greatest densities of fish were often found at sites representing habitats C and/or D (Fig. 9.1.2.1b).

Mean taxonomic distinctness of the fish assemblage in the Wellstead Estuary exhibited considerable variability in the extent and order of seasonal differences among sites (Fig. 9.1.2.1c), and it is thus not surprising that the greatest proportion of the variation in this dependent variable was accounted for by the site x season interaction (Table 9.1.2.2). For example, mean taxonomic distinctness ranged between *ca* 27 (summer 2008) and 66 (spring 2006) at the lowermost site C2, whereas it ranged only between *ca* 38 (spring 2006/autumn 2007) and 57 (winter 2006) at both sites representing the uppermost habitat F. Differences in season exerted a considerably greater influence on this dependent variable than those among sites, and thus clear spatial trends were difficult to detect (Table 9.1.2.2, Fig. 9.1.2.1c). The greatest or second greatest mean taxonomic distinctness was recorded in winter 2006 at all but two sites, while the lowest or second lowest mean value was recorded in either autumn 2007 or summer 2008 (Fig. 9.1.2.1c).

9.1.2.3 Composition of fish assemblages among habitats

The abundances of the various fish species in replicate samples collected at each site representing each habitat in the Wellstead Estuary during each of the six sampling seasons were initially subjected to a three-way PERMANOVA to determine, firstly, whether spatial differences in these data were most appropriately analysed at the site or broader habitat level and, secondly, whether these spatial differences were required to be examined separately for each season. This test detected significant differences among all main effects and interactions, but demonstrated that the relative influence of differences among habitats was considerably greater than that for site. Furthermore, one-way ANOSIM tests, carried out separately on the data collected in each sampling season in view of the above results, demonstrated that there were few significant differences in fish composition between sites assigned to the same habitat (and particularly significant differences with an R-statistic greater than 0.400) in all seasons except winter and spring 2006. During the latter two seasons, significant intra-habitat differences were detected in four and three cases, respectively (*i.e.* out of five), and the R-statistic associated with those differences exceeded 0.400 in almost all cases. However, given the relatively small ichthyofaunal differences between sites assigned to the same habitat, especially when compared to those between sites in different habitats, the following analyses were carried out at the broader habitat level. They were also performed separately for the data recorded in each season, in view of the significant seasonal main effect and interaction detected by the above PERMANOVA test.

One-way ANOSIM tests for habitat type demonstrated that there were significant differences in fish assemblage composition among habitats in each of the six sampling seasons (p=0.1%; Table 9.1.2.3). Relatively large overall differences were detected in spring 2006 (Global R=0.675; Table 9.1.2.3b), whereas the extent of those during the remaining seasons were moderate to low (Global R=0.203-0.343; Table 9.1.2.3a, c-f).

The ichthyofaunal composition differed significantly between all pairs of habitats during spring 2006, with the differences between the lowermost habitat C and all other habitats being particularly high (R=0.813-0.998; Table 9.1.2.3b). The distinctness of the fish fauna at habitat C was clearly evident on the MDS plot constructed from the replicate data collected in spring 2006, with all samples representing this habitat forming a pronounced, discrete group that lay on the opposite side of the plot from samples collected from the two upper estuary habitats, F and E (Fig. 9.1.2.2b). Samples representing the latter two habitats intermingled to some extent, but showed a definite tendency to separate into groups, as reflected by their moderately high pairwise R (*i.e.* 0.586; Table 9.1.2.3b). Samples from the middle estuary habitats D and A also tended to form groups that lay adjacent to those from upper estuary habitats, with some degree of intermingling. All but one of the samples from A formed a particularly tight group whose composition was the most similar to that of D, but notably different from those of both E and F (R=0.542-0.623; Table 9.1.2.3b, Fig. 9.1.2.2b). SIMPER showed that the fauna at C was both characterised and distinguished by particularly consistent and abundant catches of *F. lateralis*

Table 9.1.2.3: R-statistic and/or significance level (p) values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal composition among habitat types in the Wellstead Estuary during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2006; p=0.1%, Global R=0.203

	A	C	D	E
C	0.283			
D	0.078	0.400		
E	0.012	0.331	-0.050	
F	0.097	0.590	0.113	0.110

(b) Spring 2006; p=0.1%, Global R=0.675

	A	C	D	E
C	0.853			
D	0.363	0.813		
E	0.623	0.998	0.626	
F	0.542	0.996	0.439	0.586

(c) Summer 2007; p=0.1%, Global R=0.343

	A	C	D	E
C	0.420			
D	0.423	0.142		
E	0.008	0.267	0.176	
F	0.613	0.695	0.440	0.362

(d) Autumn 2007; p=0.1%, Global R=0.304

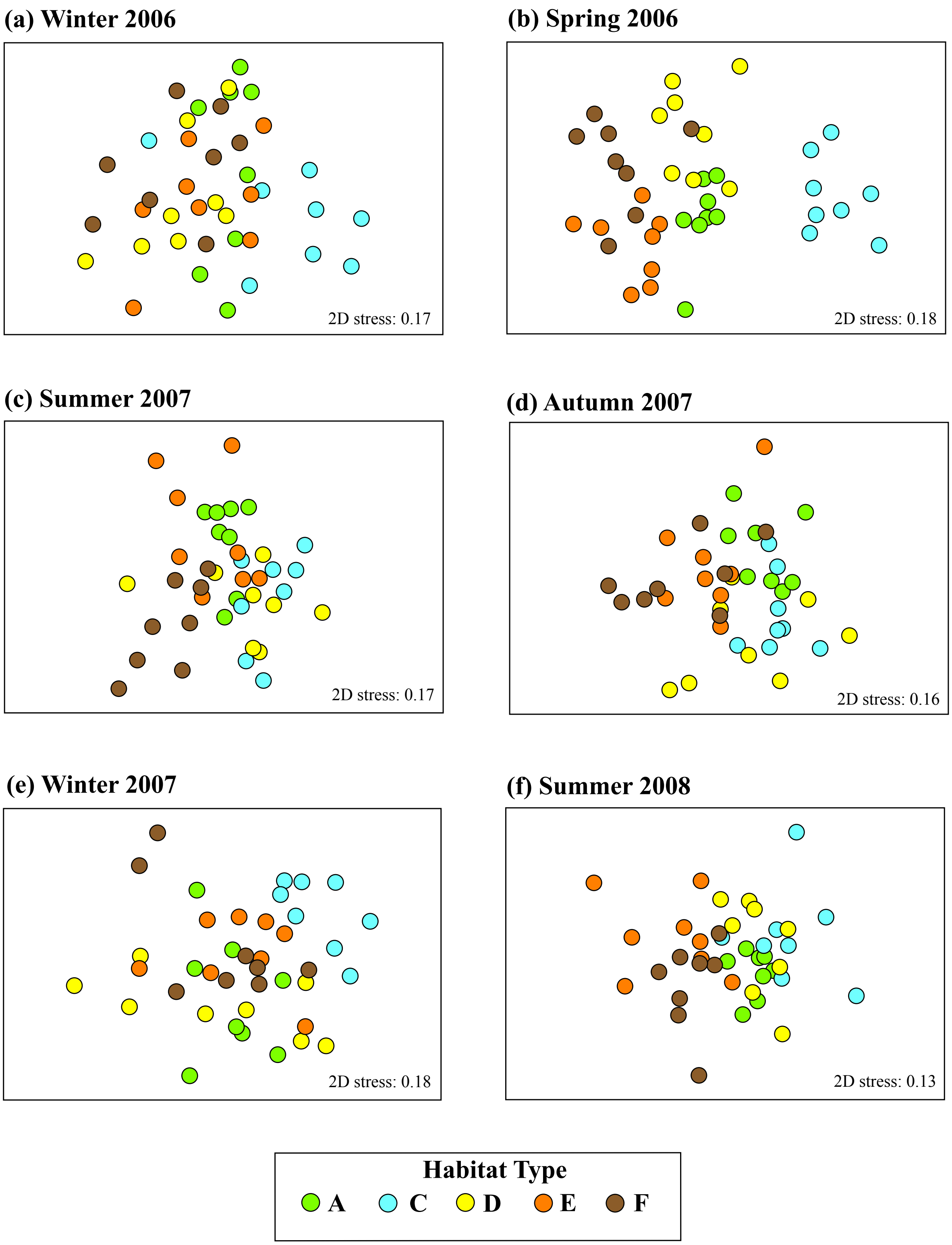
	A	C	D	E
C	0.193			
D	0.335	0.228		
E	0.243	0.436	0.232	
F	0.412	0.571	0.397	0.068

(e) Winter 2007; p=0.1%, Global R=0.241

	A	C	D	E
C	0.633			
D	0.089	0.571		
E	0.076	0.397	0.212	
F	-0.048	0.405	0.143	-0.030

(f) Summer 2008; p=0.1%, Global R=0.337

	A	C	D	E
C	0.235			
D	0.264	0.078		
E	0.516	0.391	0.360	
F	0.559	0.532	0.556	0.110


(a) Winter 2006

(b) Spring 2006

(c) Summer 2007

(d) Autumn 2007

(e) Winter 2007

(f) Summer 2008

Figure 9.1.2.2: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample at each habitat type in the Wellstead Estuary during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008.

and *A. elongata* (Table 9.1.2.4b). Habitats E and F were both characterised by *P. olorum, L. wallacei* and *A. elongata*, and also by *F. lateralis* in the case of the former habitat and *A. butcheri* in the latter. *Pseudogobius olorum* was more abundant at E than at all other habitats except A, while *L. wallacei* and *A. butcheri* were always most abundant at F (Table 9.1.2.4b).

The next most pronounced differences in ichthyofaunal composition among habitats were found during the summers of 2007 and 2008 (Global R=0.343-0.337). While a few pairs of adjacent habitats did not differ significantly during these seasons (*e.g.* E *vs* F in summer 2008), the majority of the pairwise comparisons were significant (Table 9.1.2.3c and f). During both summers, the most distinct habitat was F, as reflected by the fact that pairwise R-statistics involving this habitat were often greater than 0.500. However, it is interesting that, particularly during summer 2008, the ichthyofaunal composition at F was similarly distinct from those at all other habitats except E, and was not conspicuously the most divergent from that at C. The composition of the fish assemblage at habitat A was also considerably different from those at C and D in summer 2007 and E in summer 2008 (*i.e.* R >0.400; Table 9.1.2.3c and f). Such trends were also illustrated on the MDS plots constructed from the fish faunal data collected in each summer by the relative location and degree of dispersion of groups of samples representing each habitat (Fig. 9.1.2.2c and f). Thus, samples from habitat F formed a group that intermingled to the greatest extent with those from E, particularly in summer 2008, but generally lay similar distances from groups of samples representing the other habitats. As in spring 2006, samples representing habitat A formed the tightest group on the MDS plots constructed from the summer 2007 and 2008 data, while those from habitats D and C were comparatively dispersed in summer 2007 and 2008, respectively. The majority of samples from A lay adjacent to, but largely separate from, those for C and D in summer 2007 and those for E in summer 2008 (Fig. 9.1.2.2c and f). SIMPER demonstrated that, in summer 2007, the fish fauna at habitat F was characterised by the same suite of species listed above for spring 2006, and was distinguished by the fact that it almost always contained higher abundances of each of these species than any other habitat. Habitat A, which was also characterised by *P. olorum, A. elongata* and *L. wallacei*, was best distinguished by the fact that it contained greater abundances of the first of these species than all other significantly different habitats, except F (Table 9.1.2.4c). During summer 2008, the fish assemblages at habitats F and A were typified by the same suite of species as in summer 2007, except that *A. butcheri* was not characteristic of the former habitat. However, this latter species was still shown by SIMPER to be relatively important in distinguishing the faunas at F from those of all other habitats in this season. *Pseudogobius olorum* and *L. wallacei* were also always

Table 9.1.2.4: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each habitat in the Wellstead Estuary during (a) winter 2006, (b) spring 2006, (c) summer 2007, (d) autumn 2007, (e) winter 2007 and (f) summer 2008, as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey.

(a) Winter 2006

	A	**C**	**D**	**E**	**F**
A	*P. olorum* *F. lateralis* *L. wallacei* *A. elongata*				
C	*F. lateralis*^{C} *P. olorum*^{A} *A. elongata*^{C} *L. wallacei*^{A}	*F. lateralis* *A. elongata* *P. olorum*			
D		*F. lateralis*^{C} *P. olorum*^{D} *A. elongata*^{C} *L. wallacei*^{C}	*P. olorum* *A. elongata* *F. lateralis*		
E		*F. lateralis*^{C} *P. olorum*^{E} *A. elongata*^{C}		*P. olorum* *F. lateralis* *A. elongata*	
F		*F. lateralis*^{C} *P. olorum*^{F} *L. wallacei*^{F} *A. elongata*^{C}			*P. olorum* *L. wallacei* *A. elongata*

(b) Spring 2006

	A	**C**	**D**	**E**	**F**
A	*P. olorum* *A. elongata* *L. wallacei* *F. lateralis*				
C	*F. lateralis*^{C} *P. olorum*^{A} *A. elongata*^{C} *L. wallacei*^{A}	*F. lateralis* *A. elongata*			
D	*P. olorum*^{A} *A. elongata*^{A} *L. wallacei*^{D} *F. lateralis*^{A} *E. australis*^{A}	*F. lateralis*^{C} *A. elongata*^{C} *L. wallacei*^{D} *P. olorum*^{D}	*A. elongata* *L. wallacei* *P. olorum*		
E	*A. elongata*^{A} *P. olorum*^{A} *L. wallacei*^{A} *E. australis*^{A}	*F. lateralis*^{C} *A. elongata*^{C} *P. olorum*^{E}	*A. elongata*^{D} *P. olorum*^{E} *L. wallacei*^{D} *F. lateralis*^{E}	*P. olorum* *A. elongata* *L. wallacei* *F. lateralis*	
F	*A. butcheri*^{F} *A. elongata*^{A} *P. olorum*^{A} *F. lateralis*^{A} *L. wallacei*^{F}	*F. lateralis*^{C} *A. elongata*^{C} *A. butcheri*^{F} *L. wallacei*^{F} *P. olorum*^{F}	*A. butcheri*^{F} *P. olorum*^{F} *L. wallacei*^{F} *A. elongata*^{D}	*A. butcheri*^{F} *L. wallacei*^{F} *P. olorum*^{E} *F. lateralis*^{E} *A. elongata*^{F}	*L. wallacei* *P. olorum* *A. elongata* *A. butcheri*

(c) Summer 2007

	A	C	D	E	F
A	*P. olorum* *A. elongata* *L. wallacei*				
C	*A. elongata*^{C} *P. olorum*^{A} *F. lateralis*^{C} *L. wallacei*^{C}	*A. elongata* *P. olorum* *F. lateralis* *L. wallacei*			
D	*L. wallacei*^{D} *A. elongata*^{D} *P. olorum*^{A} *A. butcheri*^{D}	*A. elongata*^{C} *L. wallacei*^{D} *F. lateralis*^{C} *A. butcheri*^{D} *P. olorum*^{C}	*A. elongata* *L. wallacei* *P. olorum*		
E		*A. elongata*^{C} *P. olorum*^{E} *F. lateralis*^{C} *L. wallacei*^{C}	*A. elongata*^{D} *P. olorum*^{E} *L. wallacei*^{D} *A. butcheri*^{D}	*P. olorum* *A. elongata*	
F	*P. olorum*^{F} *A. butcheri*^{F} *L. wallacei*^{F} *A. elongata*^{F}	*P. olorum*^{F} *A. butcheri*^{F} *L. wallacei*^{F} *A. elongata*^{C} *F. lateralis*^{C}	*P. olorum*^{F} *A. butcheri*^{F} *L. wallacei*^{F} *A. elongata*^{F}	*P. olorum*^{F} *A. butcheri*^{F} *L. wallacei*^{F} *A. elongata*^{F}	*P. olorum* *A. elongata* *L. wallacei* *A. butcheri*

(d) Autumn 2007

	A	C	D	E	F
A	*A. elongata* *P. olorum* *L. wallacei*				
C	*A. elongata*^{C} *F. lateralis*^{C} *L. wallacei*^{C} *P. olorum*^{C}	*A. elongata* *P. olorum* *L. wallacei* *F. lateralis*			
D	*A. elongata*^{D} *L. wallacei*^{D} *P. olorum*^{A}	*L. wallacei*^{D} *A. elongata*^{D} *F. lateralis*^{C} *P. olorum*^{C}	*A. elongata* *L. wallacei*		
E	*L. wallacei*^{E} *A. elongata*^{A} *P. olorum*^{E}	*A. elongata*^{C} *F. lateralis*^{C} *L. wallacei*^{E} *P. olorum*^{E}	*A. elongata*^{D} *L. wallacei*^{D} *P. olorum*^{E}	*A. elongata* *L. wallacei* *P. olorum*	
F	*L. wallacei*^{F} *P. olorum*^{F} *A. elongata*^{A}	*A. elongata*^{C} *L. wallacei*^{F} *P. olorum*^{F} *F. lateralis*^{C}	*A. elongata*^{D} *L. wallacei*^{D} *P. olorum*^{F}		*A. elongata* *P. olorum* *L. wallacei*

(e) Winter 2007

	A	C	D	E	F
A	*A. elongata* *L. wallacei* *P. olorum*				
C	*A. elongata*^{C} *P. olorum*^{C} *L. wallacei*^{A} *F. lateralis*^{C}	*A. elongata* *P. olorum*			
D	▨	*A. elongata*^{C} *P. olorum*^{C} *L. wallacei*^{D} *F. lateralis*^{C}	*L. wallacei* *A. elongata*		
E	*L. wallacei*^{A} *P. olorum*^{E} *A. elongata*^{A}	*A. elongata*^{C} *P. olorum*^{C} *L. wallacei*^{E} *F. lateralis*^{C}	*P. olorum*^{E} *A. elongata*^{D} *L. wallacei*^{D} *E. australis*^{D}	*L. wallacei* *P. olorum* *A. elongata*	
F	▨	*A. elongata*^{C} *P. olorum*^{C} *L. wallacei*^{F} *F. lateralis*^{C}	*L. wallacei*^{D} *A. elongata*^{D} *P. olorum*^{F}	▨	*A. elongata* *P. olorum* *L. wallacei*

(f) Summer 2008

	A	C	D	E	F
A	*A. elongata* *L. wallacei* *P. olorum*				
C	*L. wallacei*^{A} *A. elongata*^{A} *P. olorum*^{A} *F. lateralis*^{C}	*A. elongata* *L. wallacei* *P. olorum*			
D	*L. wallacei*^{A} *A. elongata*^{D} *P. olorum*^{D}	▨	*A. elongata* *P. olorum*		
E	*P. olorum*^{E} *A. elongata*^{A} *L. wallacei*^{A}	*P. olorum*^{E} *A. elongata*^{C} *L. wallacei*^{E} *F. lateralis*^{C}	*A. elongata*^{D} *P. olorum*^{E} *L. wallacei*^{E}	*P. olorum* *A. elongata* *L. wallacei*	
F	*A. elongata*^{A} *P. olorum*^{F} *L. wallacei*^{F} *A. butcheri*^{F}	*P. olorum*^{F} *L. wallacei*^{F} *A. elongata*^{C} *A. butcheri*^{F}	*L. wallacei*^{F} *A. elongata*^{D} *A. butcheri*^{F} *P. olorum*^{F}	▨	*P. olorum* *L. wallacei* *A. elongata*

more abundant at F than at any other habitat, while this was also often true of *A. elongata* and *L. wallacei* at habitat A. (Table 9.1.2.4f).

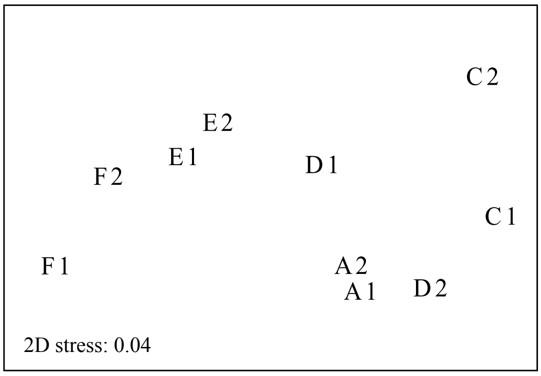
During the remaining seasons, there was relatively little distinction in ichthyofaunal composition among habitats, with the exception of habitat C. During both winters, samples from C formed a group that lay mainly to one side of those from all other habitats (Fig. 9.1.2.2a and e), which was also reflected by the fact that only those pairwise comparisons involving this habitat were significant in winter 2006, and were higher than all other pairwise comparisons in winter 2007 (Table 9.1.2.3a and e). The greatest ichthyofaunal differences were for habitat C *vs* F in winter 2006 and C *vs* A and D in winter 2007, and the species most responsible for such differences are listed in Table 9.1.2.4a and d, respectively. The MDS plot constructed from the data collected during autumn 2007 showed that, while the samples from habitat C intermingled with those for D and A, they largely formed a separate group adjacent to those from habitats E and F (Fig. 9.1.2.2d). Such trends were also mirrored by the extent of the pairwise R-statistics provided in Table 9.1.2.3d. Habitat C was mainly distinguished from the faunas of both habitats E and F by the fact that it contained higher densities of *F. lateralis* and *A. elongata* (Table 9.1.2.4d).

9.1.2.4 Matching spatial patterns between the environmental and fish assemblage characteristics of habitats

The RELATE routine was used to test the extent to which the relative spatial differences among sites, as defined by their enduring environmental characteristics, matched that exhibited by their fish assemblage compositions in each of the six sampling seasons. Note that, due to the small number of habitats present within this small system, this matching procedure was carried out using the averages of data recorded at each site rather than habitat, in order to increase the number of samples in the complementary environmental and fish resemblance matrices and thus maximise the reliability of the results.

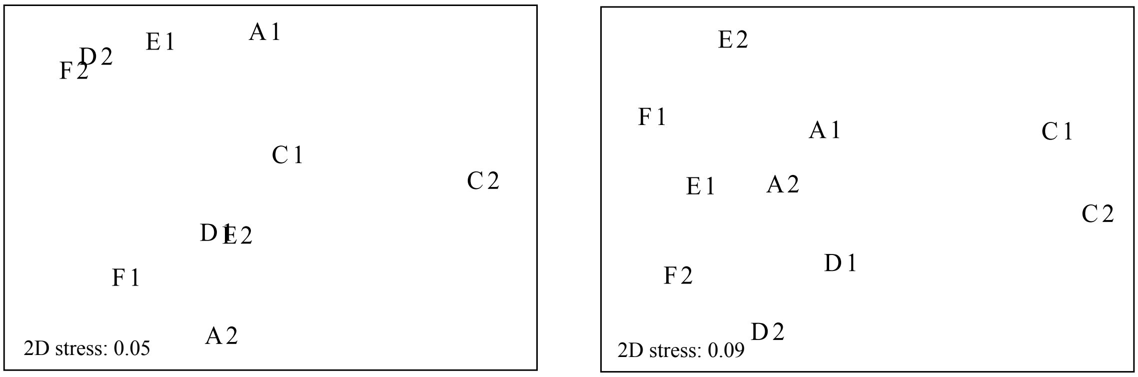
A significant correlation in spatial pattern between the enduring environmental and fish faunal matrices was detected in three of the six sampling seasons, namely spring 2006, summer 2007 and summer 2008 (p=0.3-0.7%), which were also those seasons during which the greatest overall differences in fish assemblage composition were detected among habitats (see subsection 9.1.2.3). The extents of those significant matches, which were moderate at best, were greatest during spring 2006 and summer 2008 (ρ=0.534 and 0.547, respectively) and least in summer 2007 (ρ=0.399). These results are illustrated by the reasonably similar distribution of points on the MDS plots shown in Fig. 9.1.2.3a of the enduring environmental composition at each site *vs*

(a) Enduring environmental data



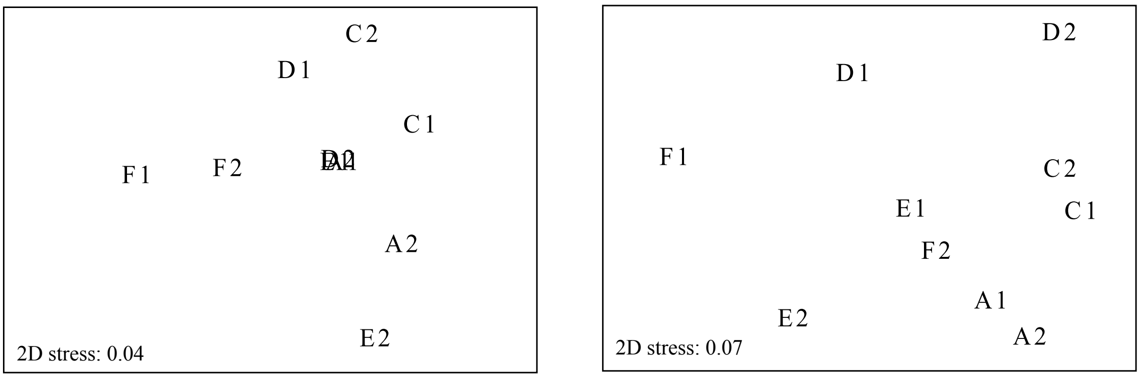
(b) Winter 2006; p=16.3%, ρ=0.135

(c) Spring 2006; p=0.3%, ρ=0.534



(d) Summer 2007; p=0.7%, ρ=0.399

(e) Autumn 2007; p=5.3%, ρ=0.254



(f) Winter 2007; p=16.5%, ρ=0.158

(g) Summer 2008; p=0.3%, ρ=0.547

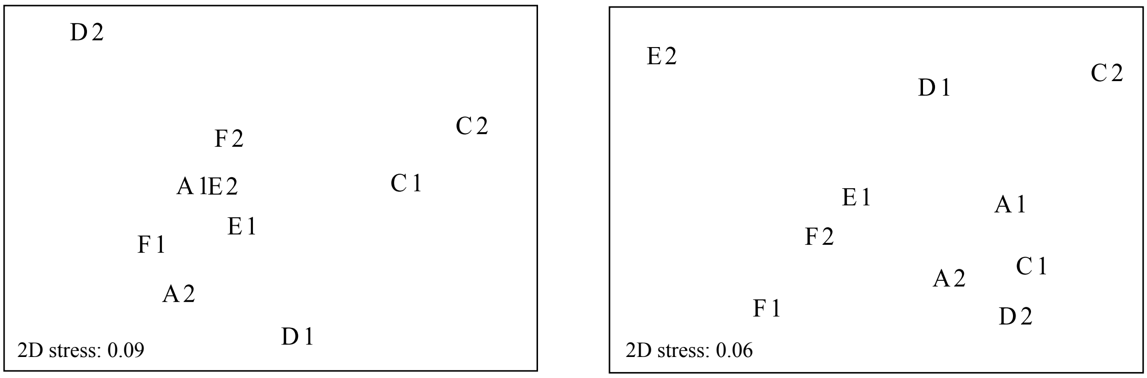


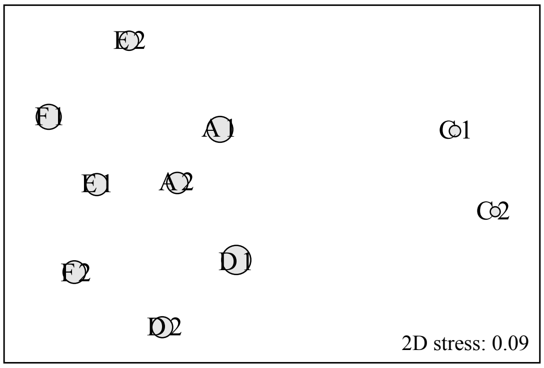
Figure 9.1.2.3: MDS ordination plots constructed from the averages at each site in the Wellstead Estuary of their (a) enduring environmental measurements and (b-g) fish faunal composition in a particular sampling season. The significance levels (p) and rho values (ρ) obtained from RELATE tests in which the matrix constructed from the above environmental data was correlated with that derived from the fish faunal data are also provided for each season.

Fig. 9.1.2.3c, d and g of the average fish faunal composition recorded at each site in spring 2006, summer 2007 and summer 2008, respectively. The correlation between the enduring environmental data and the fish faunal data collected in autumn 2007 verged on significance (*i.e.* p=5.3%), which reflected, in particular, their similarities in the spatial relationships between sites representing habitats A and C (*cf* Fig. 9.1.2.3a and e). The MDS plots constructed from the fish faunal data recorded during each winter, however, illustrated that there was either little separation of the points representing the various sites, with the exception of those representing habitat C, and/or relatively large differences between sites assigned to the same habitat type (*cf* Fig. 9.1.2.3a and b, f).

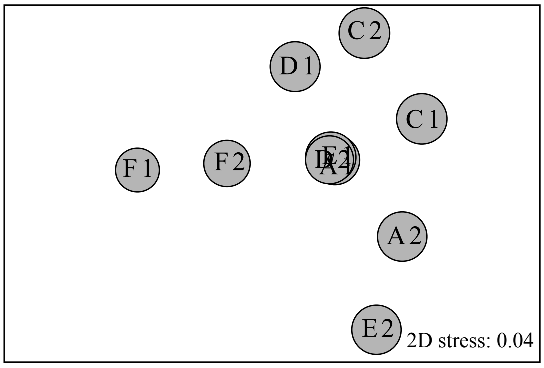
RELATE was then used to ascertain the extent to which the spatial pattern exhibited by the fish assemblages throughout the Wellstead Estuary in each season matched that displayed by the suite of water quality parameters (*i.e.* salinity, temperature and dissolved oxygen) that were recorded at the same sites on the same sampling occasions. These tests demonstrated a significant match for only two of the six sampling seasons, namely spring 2006 and summer 2007 (p=0.6-2%), and that the extents of the correlations were slightly lower those obtained above for the same seasons when the enduring environmental and fish matrices were matched, *i.e.* ρ=0.447 and 0.482, respectively. Highly insignificant p values were recorded for the remaining seasons (*i.e.* p=12.8-58.4%).

BIOENV was subsequently used to determine whether the above correlations between the complementary fish and water quality matrices could be improved by employing only data for particular subsets of water quality variables, rather than the full suite. Significant results were obtained only for the same two seasons in which RELATE detected significant correlations, and the improvements in the associated ρ values were only slight, *i.e.* 0.532 for spring 2006 when data for only water temperature were employed and 0.486 for summer 2007 when data for both salinity and water temperature were employed. The relationships between the spatial patterns exhibited by the average composition of the fish assemblages and the average magnitude of the water quality parameter(s) selected by the BIOENV procedure are illustrated, for spring 2006 and summer 2007, by the MDS and associated bubble plots shown in Fig. 9.1.2.4. During the first of these seasons, sites representing the lower estuary habitat C, which clearly had a distinct fish composition from that at the remaining sites, also had the lowest water temperatures, *i.e. ca* 20.4°C *vs* 21.3-23°C (Fig. 9.1.2.4a). This was also true, but to a lesser extent, in summer 2007 (Fig. 9.1.2.4c). Furthermore, sites representing habitat F, which contained a relatively distinct fish fauna in this latter season, also had the lowest salinities, *i.e. ca* 35-39‰ *vs* 41-46‰ (Fig. 9.1.2.4b).

(a) Spring 2006; p=5%, ρ=0.532



(b) Summer 2007; p=4%, ρ=0.486



(c) Summer 2007; p=4%, ρ=0.486

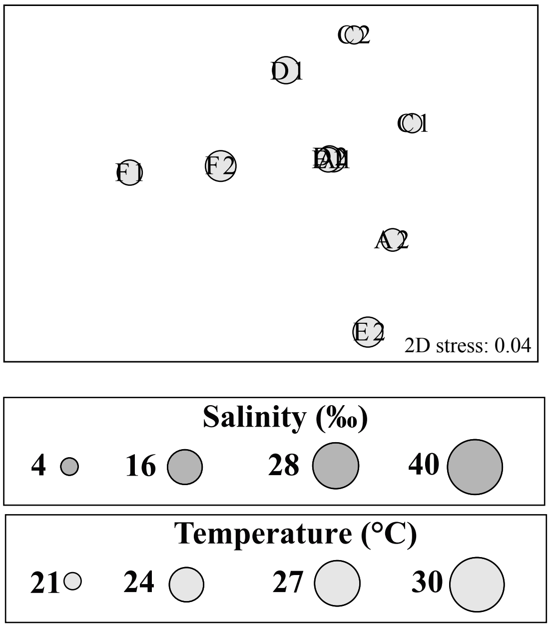


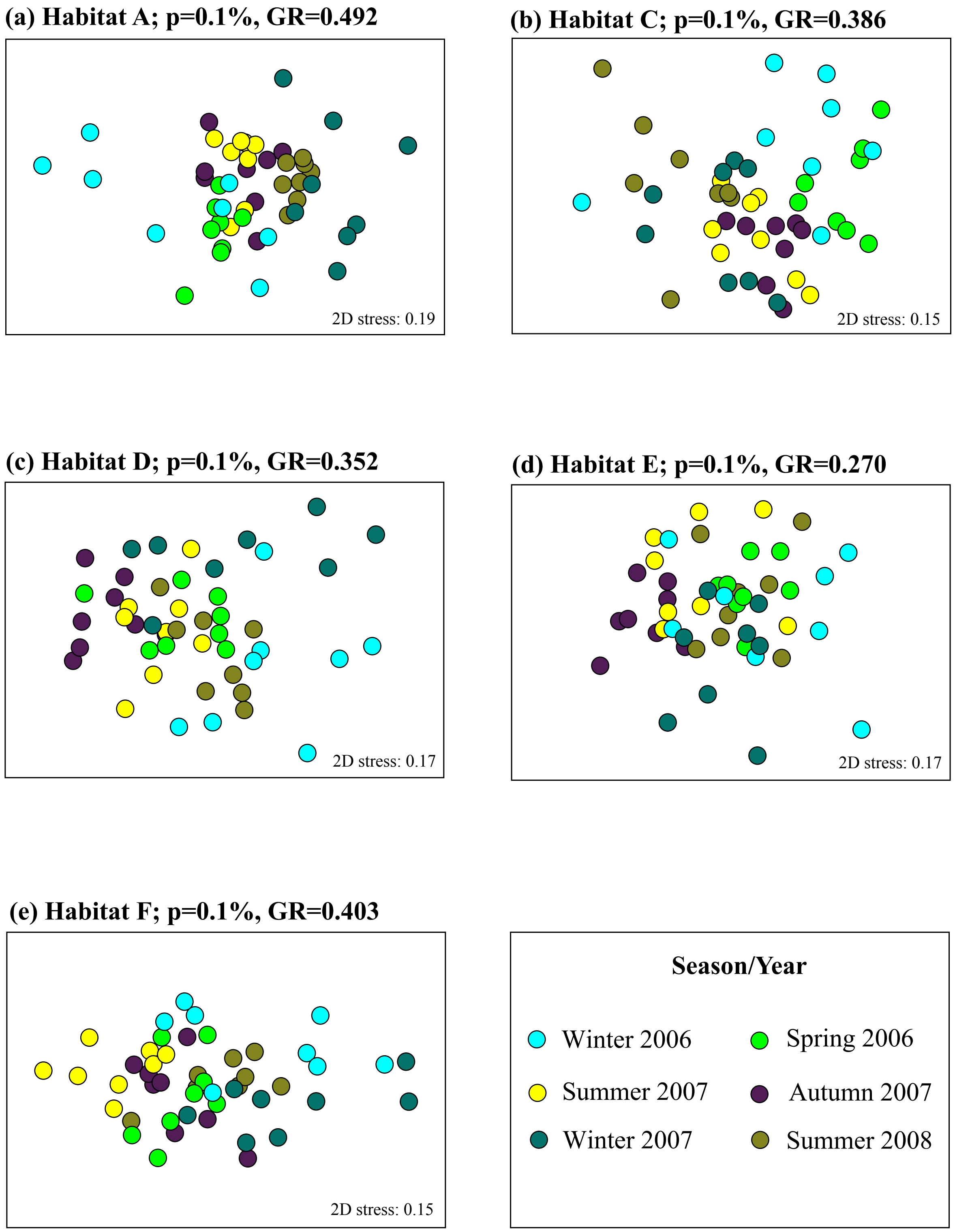
Figure 9.1.2.4: MDS ordination plots derived from the average fish faunal composition recorded at each site in the Wellstead Estuary in a particular sampling season. The magnitude of those water quality variables selected by the BIOENV routine when one of the matrices constructed from the above faunal data was matched with that constructed from the complementary water quality data, are displayed for each site as circles of proportionate sizes. The significance levels (p) and rho values (ρ) obtained from the above BIOENV tests are also provided.

9.1.2.5 Composition of fish assemblages among seasons

One-way ANOSIM tests, performed separately for the fish assemblage data recorded at each habitat type, demonstrated that ichthyofaunal composition differed significantly among sampling seasons in each case (p=0.1%), and that the overall extents of those temporal differences were moderate to low, *i.e.* Global R=0.270-0.492 (Fig. 9.1.2.5). The extents of these temporal differences mostly lay within a similar range to those detected previously for habitat type, *i.e.* Global R=0.203-0.675.

The greatest overall seasonal differences in fish faunal composition were detected at habitat A in the middle reaches of the estuary, followed by those at the uppermost habitat, F, *i.e.* Global R=0.492 and 0.403, respectively. Fish compositions differed significantly between all pairs of seasons at habitat A, but the most pronounced, in decreasing order, were for summer 2008 *vs* spring 2006, summer 2007 and autumn 2007, and for winter 2007 *vs* spring 2006, summer 2007 and autumn 2007 (p=0.1-0.2%; R=0.614-0.859). The samples representing summer 2008 on the MDS plot constructed from the data recorded at this habitat formed a particularly tight group that lay adjacent to, but discrete from, those for summer 2007 and spring 2006, most of which also formed relatively tight groups (Fig. 9.1.2.5a). Samples from autumn 2007 were also positioned alongside those from summer 2008, but were more dispersed and intermingled to a considerable degree with those from the above two seasons. However, samples collected during each winter clearly exhibited the greatest degree of dispersion, which was also true for most other habitat types (Fig. 9.1.2.5). Thus, samples from winter 2006 extended from one side of the plot to the middle, where they intermingled with those from spring 2006, summer 2007 and autumn 2007, while winter 2007 samples extended from the opposite side of the plot towards the middle, where they intermingled with those from summer 2008 (Fig. 9.1.2.5a). The fish fauna in summer 2008 was characterised by consistently high catches of *A. elongata, P. olorum* and *L.wallacei*, but the abundances of each of these species were consistently higher in spring 2006, as was that of *F. lateralis*, which was not recorded during summer 2008. The abundances of the first two of these species were also consistently higher during summer and autumn 2007 than summer 2008, while the opposite was true for *L. wallacei*. Compared to the ichthyofaunas in spring 2006, summer 2007 and autumn 2007, those in winter 2007 contained consistently lower abundances of *P. olorum*, *A. elongata* and, in the case of spring 2006, also *F. lateralis*. However, the abundances of *L. wallacei* were higher during winter 2007 than in both summer and autumn 2007.

Relatively large differences in ichthyofaunal composition were also detected for summer 2008 *vs* summer and autumn 2007 and for summer 2007 *vs* winter 2006 and 2007 at habitat F



(a) Habitat A; p=0.1%, GR=0.492

(b) Habitat C; p=0.1%, GR=0.386

(c) Habitat D; p=0.1%, GR=0.352

(d) Habitat E; p=0.1%, GR=0.270

(e) Habitat F; p=0.1%, GR=0.403

Figure 9.1.2.5: MDS ordination plots constructed from the fish assemblage data recorded in each replicate sample in each sampling season at habitat (a) A, (b) C, (c) D, (d) E and (e) F in the Wellstead Estuary. Significance level (p) and Global R-statistic (GR) values from ANOSIM tests for differences in faunal composition among seasons are also provided for each habitat type.

(p=0.1-0.2%; R=0.642-0.738). MDS ordination of the data recorded at this habitat type showed that samples from summer 2007 formed a relatively tight group on one side of the plot, but that those representing both winters formed highly dispersed groups that extended from the opposite side of the plot to the margin of the summer 2007 samples (Fig. 9.1.2.5e). Samples from summer 2008 formed a comparatively tight group that lay mainly in the middle of the plot, with most of those from spring 2006 and autumn 2007 being located between the groups representing the two summers (Fig. 9.1.2.5e). Consistently lower catches of *P. olorum* and *A. elongata* in summer 2008 than both summer and autumn 2007 mainly distinguished the ichthyofaunas of these seasons, in addition to the greater prevalence of *L. wallacei* and *A. butcheri* in autumn 2007 and summer 2008, respectively. Considerably higher catches of *P. olorum, A. elongata, A. butcheri* and *L. wallacei* in summer 2007 distinguished the fish assemblages in this season from those in both winters.

The extent of the seasonal differences at the lowermost habitats C and D was similar, *i.e.* Global R=0.352-0.386, but the patterns of those seasonal differences were considerably different. Thus, whereas the greatest differences were evident for spring 2006 *vs* summer 2008 and winter 2007 at habitat C (p=0.1-0.2%; R=0.661-0.814), such differences were minimal at habitat D (p=2.5-4.2%; R=0.176-0.208). Furthermore, the most pronounced seasonal differences at habitat D, *i.e.* autumn 2007 *vs* winter 2006 and summer 2008 (p=0.1%; R=0.686-0.769), were only moderate at habitat C (p=0.1%; R=0.498-0.517). Such differences were illustrated by the MDS plots derived from the data recorded at each of these habitats. Thus, at habitat C, samples from spring 2006 (and most of those from winter 2006) lay on the opposite side of the plot from the dispersed group of samples collected in summer 2008, and adjacent to, but entirely discrete from, the samples collected in winter 2007. However, samples from each of these seasons intermingled considerably on the plot constructed from the data collected at habitat D (*cf* Fig. 9.1.2.5b and c). At this latter habitat, samples from autumn 2007 formed a relatively tight group on the opposite side of the plot from the highly dispersed group of samples collected in winter 2006, and which lay alongside the group of samples taken in summer 2008.
SIMPER showed that, at habitat C, the faunas collected in spring 2006 were primarily distinguished from those in summer 2008 and winter 2007 by notably greater abundances of *F. lateralis* and *A. elongata.* At habitat D, autumn 2007 ichthyofaunas contained markedly greater abundances of *A. elongata* and *L. wallacei* than those recorded in winter 2006 or summer 2008.

Seasonal differences at habitat E in the upper reaches of the Wellstead Estuary were relatively minor overall (Global R=0.270), which reflected the high degree of intermingling of groups of samples from different seasons and/or dispersion on the MDS plot of the fish assemblage data recorded at this habitat (Fig. 9.1.2.5d). However, samples from autumn 2007 and spring 2006 formed relatively tight and entirely discrete groups, which was reflected by their high pairwise R-statistic (p=0.1%; R=0.817). This was due mainly to the greater prevalence of *A. elongata* and *L. wallacei* in the former season and *P. olorum* and *F. lateralis* in the latter.

9.2 Discussion

9.2.1 Differences in fish assemblages among habitats

The composition of the nearshore fish assemblages differed significantly among the various habitats throughout the small, normally-closed Wellstead Estuary during each of the six seasons in which they were sampled between winter 2006 and summer 2008. However, while the overall extent of those differences was large in spring 2006, it was moderately low to low in the other seasons. With the exception of the former season, the extents of the differences in ichthyofaunal composition among habitats throughout the Wellstead Estuary were comparable to the majority of those in the seasonally-open Broke and Wilson Inlets, which are located further west along the south coast, but considerably less than most of those detected in the permanently-open Swan and Peel-Harvey estuaries on the lower west coast. Such findings mainly reflect the fact that, like those other two south coast systems, the nearshore fish fauna throughout Wellstead Estuary was heavily dominated by a small suite of estuarine atherinid and/or goby species, namely *Atherinosoma elongata, Leptatherina wallacei* and/or *Pseudogobius olorum*, which almost always ranked first, second and third, respectively, at all habitats and comprised 97.1-99.8% of the total catch. As discussed in Chapters 7.2 and 8.2 for the Broke and Wilson inlets, respectively, and which is even more pertinent to the Wellstead Estuary, the dominance of their nearshore fish fauna by species that can complete their life cycle within estuaries presumably reflects selective pressure for such a life history strategy when such systems become closed off from the sea for extended periods (Potter *et al.* 1990). The first of the above species was particularly numerous at all habitats, which paralleled the findings of Young and Potter (2002) in their study of the nearshore fish fauna throughout Wellstead Estuary, and was primarily responsible for the exceptionally high overall mean density of fish recorded in this system during the current study. Thus, this normally-closed estuary, which remained closed for the duration of the project, contained an average of three to eight times more fish per unit area than each of the other four study estuaries. It is also interesting that its surface area is *ca* 19-52 times less than those of the other four systems.

The most distinct fish assemblages in the Wellstead Estuary during several seasons were detected at the uppermost habitat F and lowermost habitat C, while those of A in the middle reaches and E in the upper reaches were also notably distinct in one or two seasons. This spatial pattern of relative ichthyofaunal differences is similar in some respects to that recorded in the Swan Estuary (Chapter 5.1.2) which, despite pronounced differences in bar state (*i.e.* normally-closed *vs* permanently-open) and overall size, is like the Wellstead in that it is also a drowned river valley system (Hodgkin and Hesp 1998). Habitat C also contained by far the largest overall mean density of fish, which was nearly four times greater than that at E, at which the least was recorded. Similar findings were also obtained in the Swan Estuary, in which the lowermost habitat contained a much greater mean density of fish than any other, while among the lowest was found at one of the habitats in the upper estuary.

The fish faunas at F were relatively distinct in all seasons except both winters, and were commonly typified by *L. wallacei, Acanthopagrus butcheri* and *P. olorum*. In each of the above seasons, the first two of these species were almost always more abundant at this habitat than at any other, and this was also frequently true for the latter. Moreover, while *A. butcheri* helped distinguish the faunas at habitat D in the middle to lower reaches during summer 2007, it never characterised or distinguished the faunas of any other habitat in any other season. The prevalence of the above three species at the uppermost habitat F was also reinforced by the fact that their overall mean densities were greater, and often markedly so, than those recorded elsewhere in the system. These species were also particularly abundant in the upper reaches of the Swan Estuary, where their mean densities were notably higher than at any other habitat in that system. In contrast, while *L. wallacei* and *P. olorum* also occurred regularly and/or in relatively large numbers in the nearshore waters of the Broke and Wilson inlets, they exhibited far less affiliation for habitats located within the vicinity of the rivers of those systems, and were typically widely distributed throughout their large basins and/or entrance channels. The affinities of these two euryhaline species for estuarine waters with reduced salinities and, in the case of the latter, also for areas that are highly sheltered, have silty substrates and contain appreciable areas of submerged or fringing vegetation, have been discussed widely in Chapters 5.2.1-8.2.1 and demonstrated by numerous other workers in south-western Australian estuaries (*e.g.* Prince *et al.* 1982, Gill and Potter 1993, Potter and Hyndes 1994, Young *et al.* 1997, Hoeksema and Potter 2006, Hoeksema *et al.* 2006a). It is thus relevant that, due to the narrowness of the banks in the uppermost reaches of the Wellstead Estuary, habitat F had small fetches in all directions and was thus the most sheltered from wave activity, comprised a silty substrate and had moderate areas of fringing samphire in its shallowest waters. Moreover, although salinities at F ranged between *ca* 25 and 45‰ throughout the study, they were always slightly lower than those at all other habitats in the system, which ranged between *ca* 28 and 63‰. Habitat E, located just downstream from F, shared several of the above environmental characteristics and also contained relatively high mean densities of *P. olorum*. This gobiid species was also found in comparable mean densities at A, which also comprised a silty substrate and particularly large quantities of fringing reeds along its shallow banks, and was mainly responsible for distinguishing the ichthyofauna of this habitat in spring 2006 and summer 2007, during which it was relatively distinct.

Acanthopagrus butcheri has also been shown by numerous other workers in south-western Australian estuaries to occur predominantly in the upper reaches of those systems (*e.g.* Loneragan and Potter 1990, Potter and Hyndes 1994, Hoeksema *et al.* 2006a), despite its particularly impressive ability to survive and reproduce in a wide range of salinities, temperatures and dissolved oxygen concentrations (Sarre and Potter 1999, Partridge and Jenkins 2002, Hoeksema *et al.* 2006b, Hassel *et al.* 2008) and consume a variety of food sources (Sarre *et al.* 2000). The affinity of this larger estuarine species for habitats in the upper reaches of estuaries must thus also be related to other environmental attributes that are commonly found in those regions, such as the presence of submerged snags and dark tannin-stained waters, both of which provide protection from predation, and deeper waters, which would facilitate the movement of this highly mobile and larger species. Although the first two of these environmental attributes were present at F, they also characterised various other habitats in the Wellstead Estuary, *e.g.* A, D and E. Thus, the far greater frequency of occurrence and mean density of *A. butcheri* at the former habitat is presumably related to its notably deeper waters, as reflected by its very short wave shoaling margin and particularly steeply sloping substrate.

In contrast to habitat F, the fish faunas of the lowermost habitat C, which were particularly distinct in both winters and spring 2006, were typified mainly by highly abundant and consistent numbers of *A. elongata* and a prevalence of the estuarine and marine goby *Favonigobius lateralis*. Thus, in each of the above seasons and various others, these two species were always caught in the greatest numbers at C, which was also reflected by their far greater overall mean densities at this habitat compared to all others. The spatial distribution of the latter species in the Wellstead Estuary closely parallels that recorded in various other estuaries in south-western Australia (*e.g.* Gill and Potter 1993, Young *et al.* 1997, Hoeksema *et al.* 2006a), including the findings in the current study of the Swan and Peel-Harvey estuaries and Broke Inlet (see Chapters 5.1.2, 6.1.2 and 7.1.2, respectively). Thus, *F. lateralis* has an affinity for more marine salinities, highly protected waters and substrates that comprise coarser sands as opposed to silts, the latter of which is known to clog the gills of this small benthic species and lead to its mortality (Gill and Potter 1993, Humphries and Potter 1993). Given that the salinities at all habitats throughout Wellstead Estuary approached or far exceeded those of marine waters on all sampling occasions and, while only moderate, the levels of exposure to wave activity were among the greatest at C, the far greater numbers of *F. lateralis* at this lowermost habitat are apparently due mainly to its substrate comprising coarse marine sands, compared with mainly fine silt and mud throughout the remainder of the system. Moreover, the substantial beds of the seagrass *Ruppia megacarpa* present at C, which were the largest of any habitat in the system, would provide extra buffering of water disturbance and thus suitable shelter for this gobiid. The particularly large numbers of *A. elongata* at C may also reflect the extensive *R. megacarpa* beds at this habitat, as this atherinid species in Wilson Inlet has been shown by Humphries and Potter (1993) to be most abundant in those areas that contain dense beds of this seagrass. *Palemonetes australis*, a decapod also typically associated with vegetation and which comprised a large proportion of the diet of *A. elongata* in Wilson Inlet, was also particularly abundant in the submerged vegetation beds at habitat C.

Aside from the highly abundant fish species that can complete their life cycles within estuarine waters, small numbers of marine estuarine-opportunists or marine stragglers were also found at various habitats throughout Wellstead Estuary. These species presumably entered this system during the 10 month period just prior to the commencement of sampling when the estuary mouth was open. Moreover, the essentially marine salinities at most habitats throughout the estuary in the first two sampling seasons, *i.e.* winter and spring 2006, would be highly suitable for stenohaline marine stragglers recorded in this system, namely *Cristiceps australis* and *Haletta semifasciata.* These latter two species, which are also typically associated with submerged vegetation, were recorded only at habitat C, presumably reflecting its vicinity to the mouth of the system and/or the particularly extensive beds of *R. megacarpa* it contained. However, the various other marine species, which were marine estuarine-opportunists, were recorded at several or all habitats throughout the system.

9.2.2 Spatial relationships between the environmental and faunal characteristics of habitats

The pattern of spatial differences in the average enduring environmental characteristics among sites representing the various habitats in the Wellstead Estuary was significantly and moderately well correlated with that exhibited by the composition of the fish fauna during spring 2006 and both summers. It is relevant that these were the same seasons in which the greatest overall differences in ichthyofaunal composition were detected among the various habitats throughout this system (see subsection 9.2.1). Such findings indicate that, at this time of year, the relative spatial differences in the enduring environmental measurements of habitats can be used statistically as a surrogate for predicting those in the composition of the nearshore fish fauna. However, the spatial pattern exhibited by the enduring environmental data was not significantly matched with that of the ichthyofaunal data in the remaining three seasons. One of the main reasons for these latter findings was a lack of differentiation in the average fish assemblage composition among many sites throughout the system, despite relatively pronounced differences in their enduring environmental characteristics. Such results reflect the overwhelming dominance of the fish fauna of the Wellstead Estuary by a very small suite of species, some of which are common throughout the system. They also reflect the pronounced schooling behaviour of the two most abundant species, *A. elongata* and *L. wallacei*, which accounted for the large majority of the total catch at all habitats. Thus, unanticipated ichthyofaunal differences between sites from habitats with relatively similar environmental characteristics were often attributable to differences in the abundance of one or both of these species, which probably reflects more the chance of intercepting large schools of these ubiquitous atherinids, rather than any particular affinity they may have for the environmental attributes of those sites.

Given the above, it is still likely that the habitat prediction tool developed for Wellstead Estuary in Chapter 3.3.2 and the list of species that characterise each habitat in any given season, can be used to reasonably predict those species likely to typify the fish fauna at any nearshore site in this system throughout the year. Thus, as (i) significant and moderate correlations were obtained between the enduring environmental and ichthyofaunal data during those seasons in which the spatial differences in ichthyofaunal composition were greatest and (ii) the insignificant correlations obtained in the remaining seasons were due mainly to a lack of spatial differences in the fish assemblage and/or the chance of encountering schools of the two most common and typically widespread species, it is unlikely that the results of above predictive scheme will be misleading.

The significant and moderate correlations between the spatial patterns exhibited by the average fish assemblage composition and those of the suite of water quality parameters during spring 2006 and summer 2007 mainly reflected the relative distinctness of the fish faunas at the lowermost habitat C and uppermost habitat F, and the slightly lower mean water temperature and salinity, respectively, recorded at those habitats relative to all others. The insignificant results obtained in the remaining seasons reflected not only the small spatial differences in the composition of the fish fauna, but also those in water quality variables such as salinity and temperature, which varied little throughout the estuary on most sampling occasions. Moreover, although some of the abundant and/or consistently occurring fish species in Wellstead Estuary are known to have an affinity for lower or higher salinities, all are extremely euryhaline, and particularly the highly abundant *A. elongata* (Prince *et al.* 1982, Young and Potter 2002, Hoeksema *et al.* 2006a). Such findings indicate that spatial differences in the magnitude of salinity, temperature and/or dissolved oxygen are unlikely to be useful in predicting spatial differences in the composition of the fish assemblages throughout the Wellstead Estuary at any finer level of spatial resolution.

9.2.3 Seasonal differences in fish assemblage composition among habitats

Moderate to low differences in ichthyofaunal composition were detected among seasons at the various habitats in Wellstead Estuary, with the greatest being recorded at habitats A and F in the middle and uppermost reaches, respectively, and the least at habitat E in the upper reaches. At most habitats however, the greatest seasonal differences occurred between winter 2006, winter 2007 and/or summer 2008 *vs* one or more of the remaining seasons, and often reflected the lower number and abundance of typifying species in at least one of the former three seasons. Such trends were also reflected by the fact that the mean number of fish species and density was typically the lowest, or close to the lowest, in winter 2007, summer 2008 and, in the case of density, also winter 2006. It is interesting to note however, that while the mean taxonomic distinctness (*i.e.* diversity) of the fish assemblage was often among the lowest in summer 2008, it was commonly the greatest or second greatest in winter 2006 (see below).

The above seasonal differences in the characteristics of the ichthyofauna at the various habitats in the Wellstead Estuary are likely to reflect both the reproductive and recruitment patterns of the various estuarine species that dominated its fish assemblage, and also the seasonal changes in water quality characteristics such as salinity and temperature. Thus, the four most abundant and consistently occurring species throughout the estuary, namely *A. elongata, L. wallacei, P. olorum* and *F. lateralis*, all spawn between late winter and late spring, and their 0+ recruits are thus commonly found during late spring and summer (Gill and Potter 1993, Prince and Potter 1983). The relatively high abundances of these four species at various habitats in the Wellstead Estuary during spring 2006, summer 2007 and/or autumn 2007, combined with the fact that their mean lengths were often at their lowest during one of the first two seasons (data not shown), thus indicate that their prevalence at this time of year was primarily due to an influx of their 0+ juveniles. Moreover, other workers have found a positive relationship between water temperature and the abundance of gobiid species such as *P. olorum* and *F. lateralis,* and suggest that such findings most likely reflect their migration to shallow nearshore waters during warmer months of the year (Gill and Potter 1993). It is thus relevant that close to the highest mean water temperatures were recorded during spring 2006 and summer 2007.

In contrast to the situation in summer 2007, the relatively low number of fish species and densities recorded in summer 2008 throughout the Wellstead Estuary, despite the recruitment patterns of the above estuarine species and the warm water temperatures at that time of year, most likely reflect the particularly high mean salinities recorded during that sampling season. Thus, with the exception of the uppermost habitat F, at which salinities ranged between *ca* 36 and 45‰, those throughout the rest of the estuary ranged between *ca* 51 and 63‰. Although *L. wallacei* has been recorded in salinities of *ca* 55‰ (Prince *et al.* 1982), other workers in various estuaries along the south coast of Australia have found few individuals of this species in salinities that exceed 30‰ (Hoeksema *et al.* 2006a). The latter workers also recorded few *F. lateralis* in salinities greater than 50‰, but found that the exceptionally euryhaline *P. olorum* and *A. elongata* could withstand salinities of *ca* 75 and 135‰, respectively. The particularly low density of *L. wallacei* and *F. lateralis* at all habitats in the Wellstead Estuary during summer 2008, except for at F in the case of the former species, thus presumably reflects the inability of these species to osmoregulate in such elevated salinities.

Lastly, in contrast to the trends in the mean number of fish species and density during winter 2006, the comparatively high mean taxonomic distinctness of the fish assemblage in this season reflected, in part, the presence of marine species such as *C. australis*, *Gymnapistes marmoratus* and *Ammotretis rostratus*. Thus, these species had presumably entered the system in the preceding months before the mouth of the estuary closed in late April 2006, and were either caught exclusively or at the greatest number of habitats in winter 2006. The subsequent reduction in this diversity index coincided with the reduced or lack of capture of such marine species in the following seasons, which presumably reflected their mortality.

10. General Discussion

This study has produced fully quantitative methods for, firstly, classifying the various local-scale nearshore habitats within a range of estuaries in south-western Australia and, secondly, predicting the habitat type to which any new site in these systems belongs. Both approaches have employed measurements for a suite of enduring environmental criteria, all of which are likely to either directly influence the distribution of estuarine fish and benthic invertebrate fauna, or provide good surrogates for influential variables, and can be easily derived from readily available mapped data. This study has also examined the biological validity of the habitat classification produced for each estuary by testing, in each season, whether (i) the compositions of particular faunal assemblages differ significantly among habitats and (ii) the pattern of spatial differences among habitats, as exhibited by their faunal composition, is significantly correlated with that of the enduring environmental characteristics used to classify those habitats. Statistical demonstration that the latter is true then enables reliable prediction of the faunal species that are likely to typify the assemblages at any nearshore site in an estuary at any time of year. This is achieved simply by using the habitat prediction tool to assign that site to its most appropriate habitat type on the basis of its enduring environmental characteristics, and then consulting the lists of characteristic species provided. Such outcomes have a multitude of applications for estuarine resource planning, monitoring and ecology.

The habitat classification and prediction approaches developed in this study are fully quantitative, in that they employ accurate measurements of a range of enduring environmental criteria and that the decision rules for assigning sites to habitat types are derived from rigorous statistical tests, *i.e.* Similarity Profiles (SIMPROF) and Linkage Tree (LINKTREE; Clarke *et al.* 2008). These multivariate tests, which are both relatively new and the latter of which has been applied in a novel way in the current study, have led to (i) the separation of sites within each estuary into an optimal series of habitats, each of which differ significantly in their enduring environmental characteristics and thus do not contain redundant classes and (ii) a series of reliable and easily interpretable environmental thresholds for predicting the habitat of any new site. The results from these schemes are thus unambiguous and repeatable among users. Moreover, while the habitat classification and prediction approaches were developed for the Swan, Peel-Harvey and Wellstead estuaries and Broke and Wilson inlets in south-western Australia, they can readily be applied to any estuary, adding, if appropriate, data for further enduring characteristics, accepting that any new criteria must be able to be easily measured from available mapped sources.

These approaches represent considerable advances on several other published methods for classifying and/or predicting local-scale habitats in coastal waters that (i) contain, even in part, subjective decision rules and are thus dependent on the interpretation of those criteria by users, and also cannot be used as a basis for statistically predicting the type of fauna likely to occupy particular habitats and (ii) have not demonstrated statistically that the environmental attributes of derived classes differ significantly from each other and thus represent distinct habitats. The approaches to estuarine habitat classification and prediction developed in this study represent the first of their kind in Australia and, with respect to some of their characteristics, anywhere in the world. They also have an advantage over schemes that initially require the collection of a large suite of environmental and/or biotic data in the field at various spatio-temporal scales, and over those that are designed specifically for just one faunal group. Furthermore, some other schemes, and particularly those that are hierarchical and have been designed to encompass all marine and estuarine waters from a local to a national scale, are exceedingly complex at their finer levels and require not only the above field data, but also lead to different habitat classifications depending on the objectives of the study, the species of biota being investigated and various time scales.

The compositions of the faunal assemblages differed significantly among habitats in all estuaries and seasons. In the permanently-open Swan Estuary on the lower west coast of Australia, the overall extents of the differences among habitats in the composition of their fish, benthic macroinvertebrate, nematode and hyperbenthic faunal assemblages were moderate to large. The differences were typically greatest among the fish and nematode faunas and least among the hyperbenthic fauna, the last of which contained a large proportion of ubiquitous planktonic taxa with poor swimming ability and thus limited capacity to actively select habitats. The pattern of spatial relationships among habitats, as defined by the composition of each of the above faunal assemblages were, in each season, also significantly and moderately to exceptionally well correlated with that displayed by the enduring environmental data. This demonstrates that the spatial pattern in the enduring environmental measurements among habitats provides a good to excellent surrogate for identifying spatial differences in the compositions of each of the above faunal assemblages in each season. Thus, the fish and/or benthic invertebrate species likely to typify any nearshore site in the Swan Estuary at any time of the year can be confidently predicted by simply assigning that site to its most appropriate habitat using its enduring environmental measurements and the habitat prediction tool developed for this system, and then consulting the lists provided to ascertain which species characterise that habitat in any given season.

The composition of the fish fauna in the nearby and permanently-open Peel-Harvey Estuary also exhibited moderate to large overall differences among habitats in each season, whereas small spatial differences were detected in the composition of the hyperbenthic fauna. The spatial pattern among habitats in the compositions of the above assemblages was moderately to well correlated with that exhibited by the enduring environmental data in most seasons. Such findings indicate that the enduring environmental data and the relevant habitat prediction tool can be used to reliably predict the faunal species likely to occur at any nearshore site in this system. However, these correlations were generally not as high as those recorded in the Swan Estuary. Furthermore, low and/or insignificant results were obtained for both of the above faunal assemblages in one or both summers. These findings partly reflect the highly unusual and, in some respects, artificial geomorphology of the Peel-Harvey Estuary, which has multiple sources of both riverine and tidal waters that, unlike those of the Swan Estuary, are not located at opposite ends of a longitudinal axis. Indeed, the two major tributaries entering this system lie near the natural entrance channel. Moreover, the relatively deep artificial entrance channel, which is located at the junction of the two large basins of this system and a considerable distance from the natural channel, results in substantial exchange of marine and estuarine waters throughout most of this system. The above features account both for the less pronounced differences in fish assemblage composition between the tidal portions of the rivers and those of the basins and entrance channel compared to a drowned river valley system such as the Swan Estuary, and for the greater homogeneity of ichthyofaunal composition among several of the basin habitats. However, in some cases, the reduced spatial correlations between the faunal and enduring environmental data were attributable to the highly distinctive nature of the assemblages at some especially shallow basin habitats, which largely reflected their particularly depauperate compositions when the water depths at those habitats fell to very low levels in the warmer seasons of the year.

The conclusion that the predictive schemes developed for the Swan and Peel-Harvey estuaries were reliable was enhanced by the fact that the faunal species that typified the assemblages at each test site throughout both of these estuaries were generally the same as those that were predicted to occur there by using the habitat and faunal predictive tools developed for those systems.

The overall extents of the differences in ichthyofaunal composition among habitats in the seasonally-open Broke and Wilson inlets and the normally-closed Wellstead Estuary on the south coast, and the correlations in spatial pattern between their complementary faunal and enduring environmental data, were moderate to low. Moreover, of the six seasons in which the fish assemblages were sampled in the latter two systems, the above correlations were insignificant on four and three of those occasions, respectively. This was often attributable to a lack of ichthyofaunal differences among many habitats in each of these three systems, despite relatively pronounced differences in their enduring environmental characteristics. Thus, the extents of the spatial differences in fish assemblage composition in the Broke and Wilson inlets and Wellstead Estuary were often considerably lower than those detected in the permanently-open Swan and Peel-Harvey estuaries. Such findings largely reflected the fact that the nearshore fish fauna at every habitat in the three south coast estuaries was heavily dominated (*i.e. ca* 89-100%) by a very small suite of euryhaline atherinid and/or gobiid species that can complete their life cycle within estuarine waters, *i.e. Atherinosoma elongata, Leptatherina wallacei, L. presbyteroides, Pseudogobius olorum* and/or *Afurcagobius suppositus*. Moreover, some species such as *A. elongata*, which comprised 38-92% of the total catch at each habitat in all three of these systems, were particularly widespread. The overwhelming prevalence of these estuarine species presumably reflects (i) selective pressure for such a life history strategy when these systems can be closed to the sea for extended periods, (ii) limited opportunities for marine species to enter these systems, (iii) the greater nearshore wave energy along the south coast compared to that along the lower west coast, and thus a less favourable environment for the 0+ juveniles of marine species that migrate inshore and (iv) limitations in the geographical range of particular fish species that are relatively common in estuaries along the lower west coast, but do not extend to the south coast. The lack of spatial differentiation in fish assemblage composition was among the most pronounced in Wilson Inlet and Wellstead Estuary, which either remained closed to the sea for the entire 18 month period in which fish were sampled in the current study, or opened only for a very short time. Moreover, Wilson Inlet also lacked any distinctive differences in regional geomorphology and, like Broke Inlet, contained a less diverse benthic environment than the other study estuaries, while salinities in the exceptionally small Wellstead Estuary reached values in the last sampling season that are beyond the tolerance levels of many fish species.

In addition to the influence of the smaller spatial differences in ichthyofaunal composition throughout the Broke and Wilson inlets and Wellstead Estuary, the low and/or insignificant spatial correlations between the fish assemblage and enduring environmental data in these systems also reflected the pronounced schooling behaviour of the atherinid species that dominated their fish faunas. Thus, unanticipated ichthyofaunal differences between habitats with relatively similar enduring environmental characteristics were often attributable to differences in the abundance of one or more of the above-mentioned atherinid species, which probably more reflects the chance of intercepting large schools of these ubiquitous species, rather than any particular affinity that they might have for the environmental attributes of those habitats.

Despite the relatively low and sometimes insignificant correlations in spatial pattern between the fish assemblage and enduring environmental data in the three south coast estuaries, it is still likely that the predictive tools developed for these systems can be used to reasonably determine those species likely to typify the fish assemblage at any nearshore site in these estuaries throughout the year. Thus, as (i) those habitats that contained relatively distinctive fish assemblages in these systems typically also had distinctive enduring environmental characteristics and (ii) a main cause of the low spatial correlations between the fish assemblage and enduring environmental data was typically a lack of ichthyofaunal differences among many habitats, it is unlikely that the results of the habitat and fish prediction procedures will produce misleading results. However, particularly in the case of Wilson Inlet and Wellstead Estuary, it is recommended that further sampling of the fish assemblages is undertaken during periods when the mouths of these systems have been open for appreciable periods, followed by a re-examination of the spatial correlations between the fish assemblage and enduring environmental data.

It is important to recognise that, in most of the cases in which significant spatial correlations were detected between the complementary faunal assemblage and enduring environmental data in each of the five study estuaries, the suite of enduring criteria better explained the spatial distribution of the faunal assemblages in each season than the complementary suite of water quality variables (*i.e.* salinity, temperature and dissolved oxygen concentration) and, in the case of the benthic invertebrate assemblages, the suite of sediment parameters (*i.e.* mean grain size, transition zone depth, organic matter content and chlorophyll concentration). This was also often the case even after the BIOENV routine (Clarke and Ainsworth 1993) was used to select the particular combination of water/sediment quality variables that best mirrored the spatial distribution patterns of the faunal assemblages. Moreover, in those cases in which the spatial correlations between faunal assemblage and enduring environmental data were not significantly matched, neither were those between the faunal and water/sediment quality data. These findings imply, firstly, that the other elements of the estuarine environment that are captured by the suite of enduring criteria but not by the water or sediment parameters measured in the field, *e.g.* exposure to wave activity and extent of cover by submerged vegetation, are also important in discriminating among the spatial patterns exhibited by the fish and/or invertebrate fauna in the various study estuaries. They also imply that the enduring variables chosen as surrogates to reflect particular environmental attributes (*e.g.* distance from estuary mouth as a surrogate for spatial differences in a wide range of water and/or sediment parameters) are likely to be capturing the influence of those attributes on the spatial distribution of fish and/or benthic invertebrates throughout these systems. Such results have important consequences for future studies of faunal assemblage/habitat relationships in south-western Australian estuaries, as they highlight the value of considering a varied range of environmental attributes in combination, rather than just one or a few that reflect only a limited component of the environment. Furthermore, they also demonstrate the value of using enduring variables as surrogates for capturing spatial differences in particular non-enduring environmental characteristics, which may minimise the need to collect the latter type of data in the field in future studies. The substantial variability in replicate field measurements of particular non-enduring environmental characteristics, such as dissolved oxygen concentration and sediment grain size, also contribute to the difficulties in using such data to establish reliable relationships between spatial differences in their magnitude and the composition of faunal assemblages.

11. Benefits

The sectors of industry and community that will benefit from adopting the outputs of this study include the following.

- Fisheries and environmental managers of south-western Australian estuaries, who now have (i) quantitative inventories of the local-scale nearshore habitats throughout the Swan and Peel-Harvey estuaries, Broke and Wilson inlets and Wellstead Estuary, and the fish and, in selected systems, benthic invertebrate assemblages that occupy each of those habitats throughout the year, (ii) the ability to reliably predict the fish and, in selected estuaries, benthic invertebrate species that are likely to characterise the fauna at any nearshore site in the above systems at any time of year and (iii) the ability to apply the habitat classification and habitat/faunal prediction approaches to other estuaries in south-western Australia. The approaches developed in this study will also benefit estuarine resource managers in other areas of Australia and the rest of the world.
- Estuarine ecologists, who can employ the above approaches as a framework for investigating a range of ecological interactions between (i) habitats and their faunas and (ii) different groups of biota at selected habitats.
- Recreational and commercial fishers, who, through the further development of management practices to better conserve those estuarine habitats that are essential to key species, will benefit from more sustainable fish resources.
- The general community, who can gain a better understanding of the environmental and faunal characteristics of the various habitats present within estuaries.

12. Further Developments

The outputs of this study on quantitative approaches for classifying nearshore habitats within selected estuaries in south-western Australia and predicting the habitat and characteristic fish and benthic invertebrate species at any nearshore site in those systems, could be developed further in the following ways.

- To make the current habitat and faunal prediction schemes as simple as possible for end users, a spatially-continuous habitat map of each study estuary could be produced in a Geographic Information System (GIS), in which all nearshore waters are classified according to their most appropriate habitat and the various characteristics of the fish and benthic invertebrate assemblages that typify each habitat in each season are incorporated as underlying metadata. Thus, users of the scheme would simply need the geographic coordinates of their site of interest to ascertain its habitat type and characteristic fauna, without the need to measure any of its enduring environmental characteristics or to consult species lists.
- Assemblages of faunal taxa other than those investigated during the present study (*e.g.* benthic macroinvertebrates in the Broke and Wilson inlets) could be examined seasonally to determine the extent to which their characteristics differ among habitats of the selected systems. Furthermore, additional seasonal sampling of the faunal assemblages that have been studied could be undertaken to determine whether the relationships between faunal composition and habitats differ among years. This would be particularly valuable in those systems in which there are marked interannual variations in the length of time that their mouths are open to the sea.
- The enduring environmental measurements of the nearshore sites initially selected for classification in all study estuaries could be combined in a single database and then subjected to the classification procedure (Chapter 3.2.3.1-3.2.3.2) to elucidate the extent of the differences between sites from separate systems. This would produce a habitat classification for all estuaries studied in south-western Australia, and thus provide a quantitative framework for investigating spatial differences in the characteristics of the faunal assemblages across all systems. The combined habitat classification could also incorporate additional enduring environmental criteria to reflect other important attributes

of those systems, such as whether an estuary was permanently-open, seasonally-open or normally closed.

- The classification and prediction approaches developed in this study could be applied to other estuaries throughout Australia and the rest of the world.
- The above approaches could complement the finer levels of a nested habitat classification scheme developed for Australian marine and estuarine waters, such as that of Mount *et al.* 2007.

13. Project Outputs and Planned Outcomes

13.1 Project Outputs

1. Readily usable and quantitative methods by which managers and ecologists can identify the local-scale habitat type to which any nearshore site in selected south-western Australian estuaries belongs and, subsequently, the likely composition of the fish and benthic invertebrate faunas at that site at any time of year.
2. An inventory of the different local-scale habitat types and their fish and benthic invertebrate faunas within the selected estuaries, including succinct and quantitative details of their environmental and assemblage characteristics, respectively.
3. An understanding of the ways in which the fish and invertebrate faunas are related to different habitats.
4. Details of the ways in which the composition of the faunas at each habitat change among seasons.

13.2 Planned Outcomes

1. To provide reliable tools for improving management strategies to conserve the fish faunas and their key habitats in selected estuaries in south-western Australia.

The above project outputs have been achieved for each of the selected estuaries in south-western Australia and thus contribute directly to the above planned outcome by providing, at a spatial scale comparable to that at which estuarine managers most often work, the ability to quantitatively identify the following. (i) Reliable habitat and faunal benchmarks, against which the effects of future environmental change can be determined, (ii) those habitats that are most important to key fish and benthic invertebrate species and/or are most biodiverse, and thus are priority candidates for inclusion within conservation areas, and (iii) those fish and benthic invertebrate species that are most likely to occur at any nearshore site in an estuary, and thus, for example, those that are most likely to be impacted by proposed anthropogenic modifications to particular estuarine locations.

These tools represent considerable advances on other methods for classifying habitats and predicting faunal composition that are available to environmental and fisheries managers of south-western Australian estuaries. Such methods have either been devised at inappropriate spatio-temporal scales and/or have not demonstrated statistically that (i) the suite of environmental characteristics of each of the derived habitats differ significantly, and thus that habitat inventories are free from redundant classes, (ii) the compositions of relevant faunal assemblages differ among habitats and that the pattern of their spatial differences is correlated with that exhibited by the environmental criteria used to define those habitats and/or (iii) the fish and/or benthic invertebrate fauna at any site and time of year can be readily and reliably predicted from easily obtainable criteria, without the need for further sampling in the field.

2. *To provide a framework for ecologists to investigate the extent to which ecological inter-relationships differ among habitat types in estuaries.*

The project outputs and data collected provide a sound basis for ecologists working at local scales in south-western Australian estuaries to determine which underlying factors in particular nearshore habitats have produced the observed relationships between (i) the biota and the environment and (ii) different groups of biota. Examples of such fundamental ecological questions may include (i) which particular environmental attributes of selected habitats are most closely related to the prevalence of their characteristic fish and benthic invertebrate species and (ii) whether the trophic characteristics (*i.e.* predator/prey relationships) or level of competition of selected faunal species vary among habitats.

The outputs of this study also provide a sound ecological framework for investigating in detail the extent to which the fish and benthic invertebrate faunas vary between comparable habitats in different south-western Australian estuaries, and for forecasting the ways in which faunal assemblages and ecological interactions are likely to differ in response to projected environmental change. Furthermore, the habitat framework developed for each of the selected estuaries in this study can be used as a basis for ecologists to investigate the extent to which other types of faunal assemblages differ among habitats.

14. Conclusions

Each of the objectives and planned outcomes of this study have been achieved.

- Fully quantitative approaches for, firstly, classifying local-scale nearshore habitats in estuaries and, secondly, predicting the habitat of any nearshore site in those systems, have been developed. The approaches have been applied to selected estuaries in south-western Australia, namely the permanently-open Swan and Peel-Harvey estuaries, the seasonally-open Broke and Wilson inlets and the normally-closed Wellstead Estuary. Both of these methods have employed measurements of enduring, biologically-relevant environmental criteria that can be easily obtained from digitally-mapped data sources. Furthermore, the classification approach has also satisfied each of the other criteria specified in the first objective of this study, namely that it demonstrates statistically that the enduring environmental characteristics of the derived habitats differ significantly, and that it easily accommodates the inclusion of new environmental criteria. These approaches represent advances on other published methods for classifying and predicting habitats at local scales in estuarine and coastal waters.
- Statistical analysis of the data collected seasonally for the fish assemblages at the various habitats throughout each estuary has demonstrated the following. (i) The composition of the ichthyofaunas differed significantly among habitats in each estuary in every season and (ii) the pattern of differences among habitats, as defined by the composition of the fish assemblages, is significantly correlated with that of the enduring environmental measurements during each season in the Swan and Peel-Harvey estuaries and Broke Inlet, and in two and three of the six seasons in the Wilson Inlet and Wellstead Estuary, respectively. The compositions of the benthic macroinvertebrate, nematode and/or hyperbenthic faunal assemblages also differed significantly among habitats in the Swan and Peel-Harvey estuaries, and the spatial pattern of their differences among habitats in each season was almost always significantly related to that of the enduring environmental data. These findings thus demonstrate that measurements for the enduring environmental characteristics employed in this study typically provide a sound basis for predicting the fish and benthic invertebrate species likely to occur at any nearshore site in the selected estuaries. Furthermore, these enduring criteria typically fulfil this function better than water or sediment parameters measured in the field.

- A quantitative method has been developed for readily predicting the habitat type and subsequently the species likely to characterise the fish and benthic invertebrate assemblages at any nearshore site in an estuary in any season. This predictive method has been validated for both the fish and hyperbenthic faunas at various test sites in the Swan and Peel-Harvey estuaries in each season.

We consider that the approaches developed in this study have the potential to be widely applicable and of considerable value to resource managers and ecologists working in estuaries.

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16. Appendices

16.1 Project Staff

The following staff were employed, either full-time or part-time, to undertake work on this project for some or all of its duration.

- **Fiona Valesini;** Research Fellow
- **Natasha Coen;** Research Assistant
- **Michelle Wildsmith;** Research Assistant.
- **Mathew Hourston;** Research Assistant.
- **Claire Bartron;** Research Assistant
- **Emma Sommerville;** Research Assistant
- **Jessica Poole;** Research Assistant
- **Timothy Carter;** Research Assistant
- **Steven Cossington;** Research Assistant

Salaries for the following staff were provided as in-kind contribution to the project by Murdoch University.

- **Professor Ian Potter;** Centre for Fish and Fisheries Research, Murdoch University.
- **Professor Bob Clarke;** Director of PRIMER-E Ltd, Plymouth Marine Laboratory, United Kingdom.
- **Professor Richard Warwick;** Plymouth Marine Laboratory, United Kingdom.

16.2 Publications

The following journal manuscripts have been submitted or published, to date, from work undertaken as part of this project.

- Valesini, F.J., Hourston, M., Wildsmith, M.D., Coen, N.J. and Potter, I.C. (submitted). New quantitative approaches for classifying and predicting local-scale habitats in estuaries. *Estuarine, Coastal and Shelf Science.*
- Hourston, M. and Warwick, R.M. (in press). New species of free-living aquatic Nematoda from south-western Australia. *Records of the Western Australian Museum.*
- Wildsmith, M.D., Rose, T.H., Potter, I.C., Warwick, R.M., Clarke, K.R. and Valesini, F.J. (in press). Changes in the benthic macroinvertebrate fauna of a large microtidal

estuary following extreme modifications aimed at reducing eutrophication. *Marine Pollution Bulletin.*

- Hourston, M., Potter, I.C., Warwick, R.M., Valesini, F.J. and Clarke, K.R. (2009). Spatial and seasonal variations in the ecological characteristics of the freeliving nematode assemblages in a large microtidal estuary. *Estuarine, Coastal and Shelf Science,* **82**: 309-322.