Determination of the diets of Snapper and Silver Trevally and construction of a food web for the demersal fish community in south-western Australia

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Project No. 2009/006

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The Fisheries Research and Development Corporation plans, invests in and manages fisheries research and development throughout Australia. It is a statutory authority within the portfolio of the federal Minister for Agriculture, Fisheries and Forestry, jointly funded by the Australian Government and the fishing industry.

ISBN: 978-1-921877-06-3

Fisheries Research and Development Corporation Report
FRDC Project 2009/006

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1. NON-TECHNICAL SUMMARY

2009/006: Determination of the diets of Snapper and Silver Trevally and construction of a food web for the demersal fish community in south-western Australia

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Objectives

1) To determine the diets of Snapper (*Pagrus auratus*) and Silver Trevally (*Pseudocaranx georgianus*) when these species co-occur on the lower west coast of Australia and how they change with body size and season.

2) To determine the extent to which the diets of Snapper and Silver Trevally differ when these species occur in very different environments.

3) To construct a reliable food web derived from quantitative dietary data for a wide range of demersal (bottom-dwelling) fish species off the lower west coast of Australia.

OUTCOMES ACHIEVED TO DATE

The project outputs have led to the following outcomes:

1. Managers now have a food web, which provides them with a thorough understanding of the magnitudes of the trophic (feeding) interactions between the main demersal (bottom-dwelling) fish predators and their prey in the marine waters of the lower west coast of Australia. They are thus now in a sounder position to predict how the trophic structure within these waters is likely to be affected by fishing and to assess the risk to the main commercial and/or recreational fish species and their prey of any other anthropogenic or climatic changes. The outcomes will therefore contribute to the implementation of an ecosystem-based approach to fisheries management and thereby facilitate the sustainability of key fish stocks.

2. Managers are now aware that, although there is some overlap in the prey of Snapper and Silver Trevally, the contributions of the various prey to the diets of these two species differ markedly when they co-occur, as in coastal waters on the lower west coast of Australia. Thus, the potential for these species to compete strongly for food resources is likely to be limited, even when both species are abundant.

3. As the dietary compositions of Snapper and Silver Trevally differ markedly between geographical regions, these species are likely to be relatively resilient to changes in the relative abundances of their potential prey. However, managers need to

recognise that the diets of both species change with body size and that, as the smallest Snapper focus intensively on a particular prey (brittle stars), environmental changes to the habitats of those fish could have detrimental effects on the stock as a whole.

4. The collation of the dietary information for Snapper and Silver Trevally and the other major demersal fish species on the lower west coast of Australia provides an invaluable repository of data that can be used as a resource for future studies aimed at gaining a greater insight into the functioning of this ecosystem.

5. An innovative approach has been developed for describing the magnitudes of interactions between predators and prey in a manner that can readily be visualised.

6. The study of the diets of Snapper and Silver Trevally has been published in Estuarine, Coastal and Shelf Science and the details of the food web for demersal fishes on the lower west coast of Australia have been accepted for publication in that same international journal.

The overall aim of this study was to develop a food web that illustrated the trophic relationships that exist between the most abundant demersal fish species and their prey in waters along the lower west coast of Australia. The need for such a web had become particularly important because it would identify the details of those relationships for the main commercial and/or recreational fish species in an area where the stocks of certain of those species had become depleted. This web would thus enable fisheries managers to predict the likely impact(s) of exploitation of those key species on this ecosystem and thus refine their plans for ensuring ecological sustainability of the coastal waters of the lower western Australian coast. In other words, it would help fisheries managers to fulfill their aim to develop an effective ecosystem based approach to the management of crucial fisheries in the most populated region of Western Australia. As traditional food webs are typically very complex, the present study also aimed to develop a simplified version, but which still retained crucial features and incorporated a measure of the relative magnitudes of the interactions between the fish predators and their prey.

During a previous FRDC project (2002/016), detailed quantitative data on the dietary composition of 18 abundant demersal fish species on the lower west coast of Australia were collated and entered in a database, “Guts”, which enabled these data to be readily accessed for a range of statistical analyses (Platell and Hall, 2006). However, at that time, there were no comparable dietary data for either Snapper, one of the most valued commercial and recreational fish species on that coast, or Silver Trevally, which is among the species most frequently caught by recreational fishers on the same coast. The compositions of the prey ingested by those two fish species on the lower west coast were thus determined during the present study.

The dietary data for a further 15 demersal fish species that were studied after the construction of the original database, together with those for Snapper and Silver Trevally, were added to that initial database and thus provide dietary data for 35 species that are abundant on the lower west coast of Australia and which include the main commercial and recreational demersal fish species on that coast.

With Snapper and Silver Trevally, emphasis was focused on determining statistically the extents to which the diets of these two fish species differ on the lower west coast of

Australia, where they are abundant and co-occur. The diets of Snapper were also determined for stocks in the Kalbarri region, much further to the north on the mid-west coast, and for those of Silver Trevally on the south coast and much further to the east, to ascertain the extent to which the diets of these two species vary with region and thus presumably the compositions of potential prey.

The diets of Snapper on the lower west coast of Australia change with body size, reflecting a progressive increase in the size, type and robustness of their prey. During growth, the diet of this species shift increasingly from the consumption of brittle stars to scalefish and crabs, with starfish becoming a major contributor to the diet of the largest individuals. The diet also changed seasonally, and more particularly during the early part of growth, presumably reflecting seasonal variations in the availability of brittle stars. and other prey. The food of Silver Trevally on the same coast shifted with increasing body size from the consumption of smaller bottom-dwelling invertebrates, including shrimps and small snails, to the ingestion of scalefish and larger crabs, and did not change conspicuously with season.

The overall prey of Snapper comprises, to a greater extent, taxa that possess either hard and/or protective shells/exoskeletons, e.g. sea urchins and large crabs, or are structurally robust, e.g. starfish, than that of Silver Trevally, which tend to be smaller and generally less robust, i.e. small shrimps and small snails. These dietary differences mean that these two species are unlikely to be competing strongly for food resources on the lower west coast of Australia.

The overall composition of the diets of Snapper on the mid west coast differed from that on the lower west coast mainly through the consumption of greater volumes of the heart urchin and smaller volumes of scalefish and crabs. In contrast, most of the main prey taxa of Silver Trevally on the south coast, e.g. certain small crustaceans (shrimps), differed from those on the lower west coast, where they comprised other crustacean groups, scalefish, and small snails. These comparisons strongly indicate that Snapper and more particularly Silver Trevally are able to compensate for variations in the availability of the taxa that comprise their main potential prey.

The dietary data for each length class of each of the 35 demersal fish species were separated statistically into groups within which the diets were similar, termed predator guilds. The prey types were then subjected to the same procedure, but in a novel manner, to identify which groups of prey (prey guilds) were ingested in similar proportions by one or more groups of identifiable predator guilds. The relationships between the predator and prey guilds were then plotted in a form similar to a traditional food web, which produced a complex pattern. A novel method (a shade plot) was thus developed whereby the magnitudes of the relationships between the predator and prey guilds were illustrated in a form that would be far more easily interpretable by both scientists and managers.

KEYWORDS: Snapper, Silver Trevally, Gut contents, Food resources, Body size, Region, Season, Predator and prey guilds, SIMPROF.

2. ACKNOWLEDGEMENTS

Our gratitude is expressed to many friends and colleagues, who helped collect samples and particularly to Peter Coulson, Emily Fisher, Elaine Lek and Michael Taylor from the Centre for Fish and Fisheries Research at Murdoch University and to Dr David Fairclough, Brett Crisafulli and Paul Keay from the Department of Fisheries Western Australia. Special thanks are due to many recreational and commercial fishers who supplied fish and to the ever helpful assistance provided by the Marmion Angling and Aquatic Club, Ocean Reef Sea Sports Club and Esperance Deep Sea Angling Club. Norm Hall, Fiona Valesini, James Tweedley and Kris Parker all provided useful advice on statistical issues and Access databases.

Financial support was provided by the West Australian Marine Science Institution and the Fisheries Research and Development Corporation. Ben French was a recipient of an International Postgraduate Student Scholarship from Murdoch University. Bob Clarke acknowledges his Adjunct Professorship at Murdoch University and Honorary Research Fellowship at the Plymouth Marine Laboratory. The authors are grateful to the anonymous FRDC and journal referees for their thorough reviews and suggestions for improvements.

3. BACKGROUND

The focus of the fishery studies in Node 4 of the Western Australian Marine Science Institute was to develop an ecosystem-based fishery management for the State's fisheries. This led to an exploration of the methods by which the ecosystem effects of fishing may be monitored and assessed, and an evaluation of the extent to which the data that are available are adequate to understand the implications of changes in stock structure or climate.

In 2007, the Department of Fisheries identified that the stocks of several key species in the demersal fisheries of south-western Australia were severely depleted. This led to management changes that included the total closure of the commercial fishery and seasonal closures of the recreational fishery for selected demersal fish stocks. The ecosystem impacts of the decline were unable to be fully assessed, however, as no dietary data had been published for two key species, namely Snapper and Silver Trevally. Because of their concern for this demersal ecosystem, the Department of Fisheries Western Australia requested the Centre for Fish and Fisheries Research at Murdoch University to apply for residual research funds from the West Australian Marine Science Institute to collect dietary data for the missing species and to produce a food web for this ecosystem.

Although Margaret Platell had collected and collated the dietary data that were then available when undertaking FRDC 2002/016, no studies of the diets of Western Australian Dhufish, Breaksea Cod, Snapper and Silver Trevally had yet been undertaken. Since that time, however, the diets of several of the missing species, i.e. Western Australian Dhufish and Breaksea Cod, have been studied at Murdoch University (recently published in Platell et al., 2010). However, the diets of Snapper and Silver Trevally remained unstudied.

The focus of FRDC 2002/016 was to collect and collate all of the available dietary data for the main demersal fish species on the lower west coast of Australia and to identify the gaps in knowledge. Although the available data were inputted to a database, “Guts”, no attempt was made to convert the prey taxa to a common format using common categories, as this would have modified the data from the format in which they had been collected and reported. When constructing a food web, however, there is a requirement that the matrix of the dietary compositions of the different species contains common categories of prey taxa. This requires that the data reported in the different dietary studies are converted to a common form, using common dietary categories. Diets of individuals of species may change with body size and season, however, and, when such dietary data exist, it is important that the influence of these variables is considered when constructing the food web for a suite of fish species. In developing the application, future use of the resulting data in ecosystem modeling was a key focus and guided the identification of the outputs that the study should produce. Another key consideration was the need to minimise costs while maintaining the quality of the project output. Accordingly, we planned that the project would be undertaken as a component of a proposed PhD study.

Because of its concern that demersal fish stocks in south-western Australia had become seriously depleted, the Department of Fisheries Western Australia requested us to apply for research funds from the Western Australian Marine Science Institute (WAMSI) to produce a food web for this ecosystem. Accordingly, we submitted an application for a dietary study for Snapper (*Pagrus auratus*) and Silver Trevally (*Pseudocaranx georgianus*), for which there are no such data for West Australian stocks, and for incorporating these data into our dietary database to produce a food web for the demersal fish community on the lower west coast of Australia. Although our application was supported by the relevant WAMSI Research Steering Committee and there was still an urgent need for the data, prior commitments to previouslyarranged WAMSI projects and limited residual funds reduced the funding available to WAMSI for a number of projects including the proposed dietary study. We were thus advised to approach the FRDC to provide the additional funds that were essential for obtaining (1) sufficiently sound data on size-related and seasonal changes in the dietary compositions of Snapper and Silver Trevally and for undertaking (2) the very time-consuming task of converting all of the available dietary data for demersal fishes into a common form that would then be used to construct a sound food web.

3.1 RANKING OF LENGTH-CLASS, SEASONAL AND REGIONAL EFFECTS ON DIETARY COMPOSITIONS OF THE CO-OCCURRING PAGRUS AURATUS *(SPARIDAE) AND* PSEUDOCARANX GEORGIANUS *(CARANGIDAE)*

The successful co-occurrence of abundant fish species is regarded as depending, at least to some extent, on the partitioning of resources among those fish species and thus to a beneficial reduction in the potential for interspecific competition for those resources (Connell, 1980; Ross, 1986; Platell and Potter, 2001). Ross (1986) considered resources to be partitioned along three axes, i.e. habitat, food and time, of which food is the most important. The partitioning of food resources among fish species of similar size in the same habitat should not be taken, however, as implying that the prey species ingested by each of those species need to be completely discrete. Rather, it is far more likely to involve differences in the compositions of the prey (i.e. variations in the relative abundances of the prey) at a level which allows the effects of predation to be spread among those species (Platell et al*.,* 2010; Lek et al., 2011). Furthermore, any comparison between the dietary compositions of co-occurring medium to large-sized fish species should take into account the fact that the food ingested by such species typically changes with body size (Werner and Gilliam, 1984; Platell et al., 1998a, 2010; Cocheret de la Morinière et al., 2003; Sommerville et al., 2011) and generally with season and often with region/habitat (Packer et al., 1994; Platell et al., 1998a, 2010; Mariani et al., 2002; Chuwen et al., 2007; Fanelli et al., 2011; Schückel et al., 2011). There have, however, been no attempts to quantify in rank order the effects of body size (length class), season and region on the dietary composition of any species.

An understanding of the role played by a fish species within an ecosystem and how prey might be partitioned between that and other potentially competing species requires sound volumetric or gravimetric data on the dietary compositions of those species to elucidate whether those compositions change with body size and time of year and, if so, how. From studies in a gulf and estuary in New Zealand, the diet of *P. auratus* in those waters, which did not include the larger individuals of this species, changes with increasing body size from smaller prey, such as small crustaceans, to larger prey, such as crabs and teleosts (Colman, 1972; Usmar, 2011). Any exploration of the dietary composition of *P. auratus* should bear in mind, however, that this species belongs to the Sparidae and that the dietary composition of at least some of the species within this family varies greatly among habitats, presumably reflecting the ability of such species to feed opportunistically on the main and most accessible prey in the environment (Sarre et al., 2000; Mariani et al., 2002; Tancioni et al., 2003; Chuwen et al., 2007; Platell et al., 2007). The limited dietary data for *Pseudocaranx* species demonstrate that these species feed extensively on small benthic invertebrates, zooplankton and, when larger, on small bentho-pelagic fish (Rainer and Unsworth, 1991; Platell et al., 1997; Sazima, 1998; Hindell et al., 2000; Bulman et al., 2001; Hindell, 2006).

The possession by sparids, such as *P. auratus*, of medium-sized strong canines and rounded molars and oral jaws capable of exerting a strong crushing force enable this species to capture and masticate their prey (Stoner and Livingston, 1984; Wainwright and Richard, 1995; Hernandez and Motta, 1997; Gomon et al., 2008). In contrast, carangids, including those of *Pseudocaranx* species, have far weaker oral jaws and irregular rows of small teeth, and possess pharyngeal jaws (Grubich, 2003; Gomon et al., 2008).

Furthermore, *Pseudocaranx* species can use ram feeding to obtain their prey (Sanderson et al., 1996; Sazima, 1998). The above differences would presumably be accompanied by marked differences in the composition of the prey of *P. auratus* and *P. georgianus*, even when these species co-occur.

For the first component of this FRDC project, volumetric dietary compositions have been determined for a wide size range of both *P. auratus* and *P. georgianus* collected seasonally from over reef environments on the lower west coast of Australia, where they are both abundant and co-occur. Dietary data have also been collected for *P. auratus* from waters much further north and for *P. georgianus* from the western south coast of Australia where, respectively, those species are also both numerous. Employing contemporary multivariate statistical analyses, the resultant data were used to explore the relative extents to which the dietary composition of each species is related to body size (length class) and season, and whether the same trends are exhibited by such variables for each species in both of the regions in which it was sampled. They were also employed to confirm that the compositions of the diets of *P. auratus* and *P. georgianus* differ when these species co-occur and to test whether such interspecific differences are stronger than those related to length class and season and how they reflect interspecific differences in feeding morphology and behaviour. Finally, the results of the present and other relevant studies are discussed to ascertain whether *P. auratus* and *P. georgianus* are likely to be at least moderately opportunistic in their feeding behaviour and thus be able to adapt to any modifications in prey composition that might result from anthropogenic effects, including climate change.

3.2 AN INNOVATIVE STATISTICAL APPROACH TO CONSTRUCTING A READILY COMPREHENSIBLE FOOD WEB FOR A DEMERSAL FISH COMMUNITY

There has been an increasing and worldwide recognition of the need to adopt an ecosystem-based approach to fisheries management (EBFM) in order that ecosystems, and thus the fisheries they support, are sustained in a healthy state (Ecosystems Principles Advisory Panel, 1996; Bergen Declaration, 2002; Essington and Punt, 2011; Espinoza-Tenorio et al., 2012). Such an approach involves considering the ecosystem as a whole, rather than just the target species, and thus represents a holistic approach that emphasises the importance of understanding the reciprocal interactions of humans and marine resources (Pikitch et al., 2004; Curtin and Prellezo, 2010; Dickey-Collas et al., 2010; Espinoza-Tenorio et al., 2012). In its report to the United States Congress, the Ecosystem Principles Advisory Panel (1996) recommended that a Fisheries Ecosystem Plan (FEP) should be developed and that this should involve a series of actions. One of the eight suggested actions included the proposal that a conceptual model of the food web in an ecosystem should be constructed, based on data for the predator and prey of each targeted species over time. This would then permit the anticipated effects of the allowed harvest on predator-prey dynamics to be addressed.

The production of a sound food web requires a thorough understanding of the trophic interrelationships of the main fished and unfished species in that ecosystem. Such webs are traditionally constructed using the trophic interactions between the various predators and their prey and is typically based on analyses of gut contents and/or stable isotope ratios (Ecosystems Principles Advisory Panel, 1996; de Ruiter et al., 2005; Field and Francis, 2006; Moloney et al., 2011). When developed from gut content data, they are often represented by complex spider-web or birds-nest diagrams (e.g. Hori et al., 1993; Link, 2002). Consequently, they are often so complex that they “conceal more than they reveal” and, as a result, fundamental patterns may be obscured by the high level of detail (Raffaelli, 2000). The need to reduce the complexity of the representation of the interactions between predators and their prey led many workers to combine predator species into either functional groups (Raffaelli, 2000) or trophic guilds that comprise species with similar prey (Root, 1967; Bulman et al., 2001; Reum and Essington, 2008) and thereby reduce the number of entities within the food web. This thereby facilitates a clearer understanding of the main aspects of the structure and function of ecosystems (Fulton et al., 2007) and the potential for interspecific competition (Pianka, 1980). Scientists have also attempted to reduce the complexity of food webs by decreasing the number of prey entities through, for example, combining them into functional categories (e.g. Reum and Essington, 2008). The above efforts to reduce complexity involve a degree of subjectivity regarding the level and extent to which the predator and/or prey species are grouped, which has often varied among studies and thus hindered comparisons between studies.

The dietary compositions of many fish species change as those species increase in body size (Werner and Gilliam, 1984; Blaber and Bulman, 1987; Platell et al., 1998a, 2010; Shepherd and Clarkson, 2001; Cocheret de la Morinière et al., 2003; French et al., 2012) and also sometimes change with time of year (Jaworski and Ragnarsson, 2006; Lek et al., 2011; Schückel et al., 2011). It is thus necessary to consider whether the details of the food web are influenced by the body sizes of the various species and/or are related to season, recognising that, although a number of species may undergo size-related and/or seasonal changes, they may not all follow the same trends and body size may thereby not exert an overall significant influence on the structure of the food web. In a study of the guild structure of fishes in Puget Sound (USA), based on the diets of 21 species, the individuals were separated into large and small fish, when data were available for both size groups, and according to the season of sampling, i.e. autumn, summer and winter (Reum and Essington, 2008). That dietary study had the great advantage of identifying statistically the various groups of predators that consume similar prey, through using the permutation-based SIMPROF test (Clarke et al., 2008), which does not assume any a priori hypotheses as to which predators form a guild. In the context of time of year, that study found no evidence that the structure of the overall food web changed with season, which is consistent with the conclusions drawn from comparable detailed studies of fish communities on the upper shelf of south-eastern Australia and the mid-slope of southern Tasmania (Bulman et al., 2001; 2002).

The initial aim of this second component of the FRDC project was to produce a food web that illustrates the relationships between the abundant demersal fish species and their prey on the lower west coast of Australia, through employing the detailed quantitative dietary data that were derived from analyses of the gut contents of those species in samples covering a wide size range of each species and each season (Table 6.1). It soon became apparent that, as in numerous other studies, traditional approaches would yield a complex food web that was not readily comprehensible and thus of immediate value to managers and ecologists. We thus used an innovative multivariate approach, which involved the use of SIMPROF, to identify statistically the various predator and prey guilds and thereby reduce, to a manageable level, the number of groups required for constructing the food web. This approach, which is still based on sound quantitative data and a series of objective statistical hypothesis tests, enabled us to produce a food web in the form of a readily interpretable ‘shade plot’ that reveals the magnitude of the trophic relationships between the fish predators and their prey.

4. NEED

Implementation of ecosystem-based fishery management requires a sound knowledge of food webs if the indirect effects of fishing on trophic structure are to be understood. There was thus an urgent need to construct a quantitative food web so that we can understand the ways in which the marked declines in the abundances of important fish species off the lower west coast of Australia, which led to the recent closure of the metropolitan commercial fishery, are likely to have impacted on the ecosystem. While there are sound dietary data for most of the more abundant and important species in this region, no such data are available for Snapper and Silver Trevally. Snapper was a primary target species for commercial fishers, and they both continue to be of great importance to recreational fishers. Sound dietary data for Snapper and Silver Trevally, which take into account the ways in which their diets change with body size and season, are essential for the construction of a reliable food web. There was a need to combine the new dietary data for these species with those that were collated in the database developed in FRDC 2002/016 and with the results obtained during more recent studies, converting them into common dietary categories, size categories and a common format before they can be used to construct a reliable food web. The opportunity existed, while Ian Potter remained actively involved in research, to apply the experience and knowledge that he and Margaret Platell possess (noting that these two biologists have been involved in collecting much of the available dietary data for the demersal fish species of south-western Australia) to bring together the results of approximately 15 years of research to create a food web for this region that will be invaluable for future research and management.

5. OBJECTIVES

1) To determine the diets of Snapper and Silver Trevally when these species co-occur on the lower west coast of Australia and how they change with body size and season.

2) To determine the extent to which the diets of Snapper and Silver Trevally differ when these species occur in very different environments.

3) To construct a reliable food web derived from quantitative dietary data for a wide range of demersal fish species off the lower west coast of Australia.

This report contains an account of two studies. (I) “Ranking of length-class, seasonal and regional effects on dietary compositions of the co-occurring *Pagrus auratus* (Sparidae) and *Pseudocaranx georgianus* (Carangidae)” and (II) “An innovative statistical approach to constructing a readily comprehensible food web for a demersal fish community”. Note that, as the second study incorporated the data from the first study, the materials and methods of both studies are presented together in sequence (6.1 and 6.2) and the same follows for the results (7.1 and 7.2) and discussion (8.1 and 8.2) sections.

Objectives 1 and 2 are addressed in Part I of the Report. Objective 3 is addressed in Part II of the report.

6. METHODS

6.1 RANKING OF LENGTH-CLASS, SEASONAL AND REGIONAL EFFECTS ON DIETARY COMPOSITIONS OF THE CO-OCCURRING PAGRUS AURATUS *(SPARIDAE) AND* PSEUDOCARANX GEORGIANUS *(CARANGIDAE)*

6.1.1 Sampling localities and regimes

Pagrus auratus and *Pseudocaranx georgianus* were collected from around reefs in marine waters on the lower west coast of Australia between ca 31°00'S and 32°30'S (Fig. 6.1). The former and latter species were also obtained respectively from around reef environments in marine waters further north between ca 27°30'S and 28°15'S on the mid west coast and from between ca 34°30'S, 119°E and 34°S, 123°E on the south coast (Fig. 6.1).

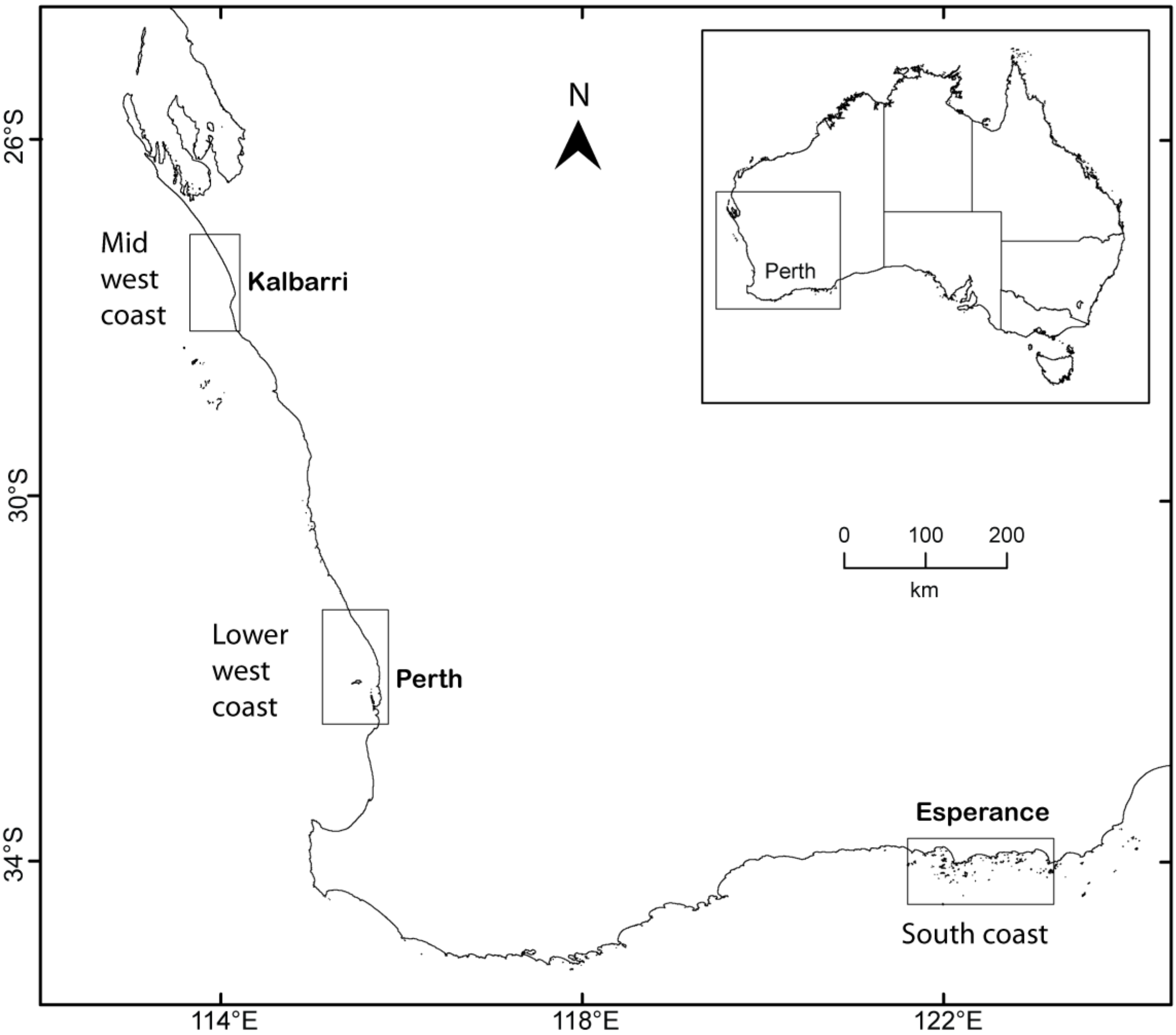


Figure 6.1 Map showing the sampling regions in western Australia for *Pagrus auratus* on its mid west and lower west coasts and for *Pseudocaranx georgianus* on its lower west and south coasts. Inset shows the location of the sampling regions in Australia.

The reef environments on the west coast comprise limestone outcrops that are encrusted with the macroalga *Ecklonia radiata* and surrounded by areas of sand, which are sometimes colonised by seagrass, consisting mainly of *Amphibolis antarctica, Amphibolis griffithii, Posidonia australis* and *Posidonia sinuosa*, whereas the reef environments on the south coast consist predominantly of granite boulders that are sparsely covered by macroalgae, represented by *Sargassum* spp. (Kendrick, 1999; Sanderson et al., 2000; Wernberg et al., 2003; Tuya et al., 2009). The samples of both species on the lower west coast were collected monthly between January 2009 and February 2011, while those of *P. auratus* from the mid west coast were obtained at least seasonally during the same period and those of *P. georgianus* from the south coast at least bimonthly between July 2009 and February 2011.

The small individuals of both species, i.e. with a total length (TL) <200 mm, were sampled exclusively by otter trawling using a net with a cod end comprising a stretched mesh of 45 mm. The medium-sized (200-400 mm) and larger (>400 mm) individuals of *P. auratus* were caught mainly using fish traps (consisting of 50 mm square steel mesh) and rod and reel fishing, respectively, whereas all *P. georgianus* >200 mm were caught using rod and reel and spear fishing. The clupeid *Sardinops sagax* was used as bait for both fish traps and rod and reel fishing, with the traps being set for 3h. Note that, because of legal fishing restrictions, *P. auratus* <400 mm TL, the minimum legal length (MLL) for retention, were not able to be obtained from the mid west coast.

6.1.2 Preparation of jaws and analyses of diets

After immersion in 100°C water for 15 min, the oral jaws of *P. auratus* and *P. georgianus* and the pharyngeal jaws of the latter species were removed from small and large individuals of both species, using a scalpel and fine tweezers. The jaws were prepared for examination by carefully removing the attached flesh with fine tweezers and brushes and then drying at 60°C for 6h.

Each fish was measured to the nearest 1 mm TL and its gut (stomach and intestine) dissected out and stored at -18°C. Each gut was subsequently defrosted and, when containing food, was placed in 100% ethanol for at least a week prior to further examination. The fullness of each gut was recorded, with values ranging from 1-10, i.e. 10 to 100% full. In the case of *P. auratus*, the fullness of the intestine, as well as of its stomach, was recorded because food was frequently found only in the intestine. The fullness of just the stomach of *P. georgianus* was recorded, however, as the stomach of this species always contained food when food was present in the gut.

The dietary items in the stomach and intestine of each *P. auratus,* and in the stomach of each *P. georgianus* in which there was food, were examined under a dissecting microscope and identified to the lowest taxonomic level possible, usually family or order, by employing one or more of the following taxonomic references; Shepherd and Thomas (1982ab), Hutchins and Swainston (1986), Coleman (1994), Lamprell and Healy (1998), Norman and Reid (2000), Wells and Bryce (2000), Jones and Morgan (2002), Wilson (2002), Poore (2004) and Edgar (2008). Cephalopods were identified to order using the descriptions of their beaks (Lu and Ickeringill, 2002). A combination of the morphology of the remnants of fish prey and of otoliths extracted from individual prey remnants enabled ca 6 and 60% of the fish prey of *P. auratus* and *P. georgianus,* respectively, to be identified to family. The far less successful identification rate with *P. auratus* is due to the majority of the gut contents used for the former species being located in the intestine and thus having undergone greater digestion than those of the latter species, which came exclusively from the stomach (see above). The use of otoliths to identify prey to the family level was undertaken employing the descriptions given by Rivaton and Bourett (1999) and Furlani et al. (2007) for the otoliths of different taxa and the substantial reference collection of otoliths for a range of fish species that was developed by E. Lek of Murdoch University in Western Australia.

Sardinops sagax, which was employed as bait, was distinguishable from the natural prey in the gut contents of the two species as its remnants could still clearly be seen to have been cut into pieces. Bait could thus readily be excluded from the dietary samples. As a preliminary analysis, using Analysis of Similarities (ANOSIM – Clarke, 1993), demonstrated that the dietary compositions of the stomachs and intestines of *P. auratus* were not significantly different (*P*>5%), the data for the contents of those two gut regions were pooled when both contained food.

The percentage frequencies with which each dietary item was found in the stomach and/or intestine of *P. auratus* and of the stomach of *P. georgianus* (%F) were recorded. The percentage volumetric contribution of each dietary item to the total volume of the stomach and/or intestinal contents (%V) was estimated visually with the aid of a grid-marked Petri dish (Hynes, 1950; Hyslop, 1980). Unidentifiable material, which on average contributed <15% of the overall dietary volume, was excluded from analyses. Each of the 96 dietary items identified in the gut contents of both species collectively was allocated to one of 33 broader taxonomic groups, subsequently referred to as dietary categories, the volumetric data for which were then used for multivariate analyses of the dietary compositions of the two species.

The mean percentage volumetric contributions of the various dietary categories to the diets of fish in each length class of both species, in each of the two regions in which they were sampled, were calculated and plotted as stacked bar graphs to examine visually the trends exhibited by the dietary compositions of each species as it increased with body size. Length class widths were set at 150 mm for *P. auratus* and 75 mm for *P. georgianus*, but with the smallest and largest individuals being grouped as <150 and >750 mm, respectively, for *P. auratus* and as <150 and >450 mm, respectively, for *P. georgianus*.

6.1.3 Multivariate analyses

The following general approach and specific procedures follow those described in detail by Lek et al. (2011). Individuals in each length class of *P. auratus* on the lower west and mid west coasts and of *P. georgianus* on the lower west and south coasts in each season were randomly sorted into groups of three to five, depending on the number of fish sampled. The percentage volumetric contributions of the different dietary categories in the guts of the resultant groups were then averaged and square root transformed prior to multivariate analyses.

The averaged and square root transformed volumetric dietary data were used to construct three Bray-Curtis similarity matrices, namely for each season and length class of (i) *P. auratus* on the lower west and mid west coasts, (ii) *P. georgianus* on the lower west and south coasts and (iii) both species on the lower west coast. These matrices were subjected to a series of a two-way and three-way crossed Permutational Analysis of Variance tests (PERMANOVA - Anderson et al., 2008) to assess, where appropriate, whether there were significant interactions in dietary compositions between length class, season, region and species, and, if so, to determine the extent of those interactions relative to that of each of the main effects. Note that the tests involving both length class and season for *P. auratus* on the mid west coast were not undertaken because individuals representing the two size classes of smallest fish could not be obtained (see earlier) and the possibility that there was a seasonal effect in this case is explored in the comparisons between the dietary compositions of *P. auratus* on the lower west and mid west coasts (see later). While only the values for *P* and pseudo-*F* in the PERMANOVA tests are given in the text, the full results of those tests are provided in Appendix 3. Note that type III sums of squares were used in all but one of the PERMANOVA analyses because the designs were generally unbalanced only at the replicate level. The one exception involved the comparison between the dietary compositions of *P. georgianus* on the lower west and south coasts, where, because the design was structurally less balanced due to the absence of data for several of the length class x season combinations in both regions, type I sums of squares were employed, and terms entered into the model in a specific order.

Separate two-way crossed Analyses of Similarities (ANOSIM - Clarke and Green, 1988; Clarke and Gorley, 2006) were used to determine the relative importance of the length class, season and/or region effects on the dietary compositions of *P. auratus* and *P. georgianus* for the same three similarity matrices as used in the PERMANOVA tests (see above). The ANOSIM average *R* value ($\bar{R}$) was computed for one factor (e.g. length class) removing the effect of the other factor (e.g. season) or the combined effects of two other factors (e.g. region and season).The magnitude of ANOSIM *R*-statistics typically range from 1, when the compositions of all samples within each group are more similar to each other than to any of the samples from other groups, down to ca 0, when the average similarity among and within groups do not differ (Clarke and Green, 1988; Clarke and Warwick, 2001). The resultant $\bar{R}$-statistics for region, length class, season and species (as appropriate) provide a robust, dimensionless and well-understood measure of the relative extents to which dietary composition is related to each of those factors.

The results of the statistical tests were visualised, as in classic univariate analyses, by 'means plots' of the effects of factors in different combinations. For multivariate analyses these are best defined as a non-metric multi-dimensional scaling (MDS) ordination on the resemblance matrix which determines 'distances among centroids' in the high-dimensional resemblance space (Anderson et al., 2008), though typically, as in this case, such an MDS plot will differ only marginally from an MDS plot based on the averages of the transformed data matrix for the relevant factor combinations. Here, centroid plots are used to display the mean changes in dietary composition over: (i) length classes for all seasons, (ii) length classes separately for pairs of seasons, (iii) seasons for pairs of regions averaged over length classes, (iv) length classes for pairs of regions averaged over season, (v) length classes for pairs of species averaged over season and (vi) seasons averaged over length classes for pairs of species.

In the case of the length class factor, note that ANOSIM (or PERMANOVA) analyses both test the null hypothesis of equality of all length classes in their effect on dietary composition against the unordered alternative that differing length classes have different effects, whereas the interpretation of the MDS plots makes much use of the ordering of length classes, often displaying a trajectory of increasing length. A supplementary test therefore becomes relevant when considering length class effects. The RELATE procedure in PRIMER (Clarke et al., 1993; Clarke and Gorley, 2006) tests the same null hypothesis as ANOSIM, but against the ordered alternative that dietary composition changes in a serial way through the increasing length classes. It is therefore an appropriate test in this case and, based on the same numbers of replicates, will be more powerful than ANOSIM for that ordered alternative (Somerfield et al., 2002). In the current context, given the presence also of a seasonal factor, the relevant test will be to use the same 'distances among centroids' matrix as exploited in the MDS plots, to carry out a RELATE test of the seriation (Clarke et al., 1993) of mean dietary composition with length class, in effect averaging over the seasonal data separately for each combination of species and region. As with the corresponding MDS plots, these tests have few points, either five or six length classes, and thus will only detect significant serial changes for which the RELATE ρ statistic is close to its upper limit of 1, representing a full serial change in dietary composition. They are, nonetheless, useful tests in this context, because they are the direct, and more accurate, counterpart to the visual information represented (sometimes imperfectly) in the MDS plots. For example, they result in a more realistic test of the length class differences in the case of *P. georgianus* on the south coast, where the effects are clearly seen in the corresponding ordination plots but are difficult to demonstrate when the natural ordering of length classes is ignored.

When the dietary composition was significantly related to a specific factor, two-way Similarity Percentages analysis (SIMPER – Clarke, 1993; Clarke and Gorley, 2006) was used to determine the dietary categories which typified and distinguished between the compositions of the fish diets, removing the (combined) effect of the other factors. In the few cases when, due to low levels of replication, the typifying and/or distinguishing dietary categories for an a priori group could not be determined using two-way SIMPER analyses, a one-way SIMPER analysis was employed.

6.2 AN INNOVATIVE STATISTICAL APPROACH TO CONSTRUCTING A READILY COMPREHENSIBLE FOOD WEB FOR A DEMERSAL FISH COMMUNITY

6.2.1 Sampling of fish and treatment of gut samples

The 35 demersal fish species, whose dietary data were used in the current study (Table 6.1), were collected from coastal marine waters along the lower west coast of Australia between Lancelin at ca 33°00 S and Cape Naturaliste at ca 33°30 S and in which these species are abundant. Each species was sampled by one or more of the following methods: otter trawling, rod and line fishing, long lining, gill netting, seine netting and spear fishing. The fish were placed on ice immediately after capture and the whole fish, or the carcass and gut contents when the fish had been filleted, were transported to the laboratory where they were frozen. The total length (TL) of each fish was measured to the nearest 1 mm and, when the gut contained food, it was removed and placed in 70% ethanol, except in the case of the larger guts which were first fixed in 10% formalin.

The dietary items in the guts of each fish were examined under a dissecting microscope and identified to the lowest taxonomic level possible. A total of 468 different taxa were identified in the gut contents of the 35 fish species. The percentage volumetric contribution of each dietary taxon to the total volume of the stomach and/or intestinal contents (%V) was estimated visually (Hynes, 1950; Hyslop, 1980). Unidentifiable material was not included in the analyses.

6.2.2 Structure of data

The dietary data, date of capture and total length of each individual of the 35 fish species were entered into a common database. As the vast majority of the dietary items typically were not able to be identified to species or genus, and frequently not to family, the dietary data for each individual were aggregated to a higher taxonomic level, usually order. The total number of orders or other higher taxa (47), subsequently referred to as prey taxa, was considered both manageable and appropriate for retaining crucial information on the relationships between the dietary composition of each species and its body size and time of year of capture.

The date of capture of each fish was assigned to the appropriate season, i.e. summer (December to February), autumn (March to May), winter (June to August) or spring (September to November). Length class intervals of 100 mm TL were chosen for all species, as they provided a sufficient but not excessive number of guts for each length class interval of each species to facilitate comparability in statistical analyses that involved intra- and interspecific data for dietary compositions. Total length classes in mm are as follows. 1 = <100, 2 = 100-199, 3 = 200-299, 4 = 300-399, 5 = 400-499, 6 = 500-599, 7= 600-699, 8 = 700-799, 9 = 800-899 and 10 = 900-999. Note that the body mass of fish was not considered as an alternative to total length as a measure of body size because a number of fish were obtained from fishers and fish markets as frames with the viscera intact and no accompanying data on body mass.

Table 6.1 The 35 demersal fish species whose diets were used to explore the trophic relationships between fish species and their prey on the lower west coast of Australia, together with the relevant publications or data sources.

Families	Species	Publications
Elasmobranchs		
Heterodontidae	*Heterodontus portusjacksoni*	Sommerville et al. (2011)
Myliobatidae	*Myliobatis australis*	Sommerville et al. (2011)
Rhinobatidae	*Aptychotrema vincentiana*	Sommerville et al. (2011)
Squatinidae	*Squatina australis*	Sommerville et al. (2011)
Urolophidae	*Trygonoptera mucosa*	Platell et al. (1998a)
	Trygonoptera personata	Platell et al. (1998a)
	Urolophus lobatus	Platell et al. (1998a)
	Urolophus paucimaculatus	Platell et al. (1998a)
Teleosts		
Atherinidae	*Atherinomorus ogilbyi*	Hourston et al. (2004)
Carangidae	*Pseudocaranx georgianus*	French et al. (2012)
	Pseudocaranx wrighti	Platell et al. (1997)
Clupeidae	*Spratelloides robustus*	Schafer et al. (2002)
Gerreidae	*Parequula melbournensis*	Platell et al. (1997)
Glaucosomatidae	*Glaucosoma hebraicum*	Platell et al. (2010)
Labridae	*Bodianus frenchii*	Platell et al. (2010)
Leptoscopidae	*Lesueurina platycephala*	Hourston et al. (2004)
Mullidae	*Upeneichthys lineatus*	Platell et al. (1998b)
	Upeneichthys stotti	Platell et al. (1998b)
Pempherididae	*Parapriacanthus elongatus*	Platell and Potter (1999)
	Pempheris klunzingeri	Platell and Potter (1999)
Platycephalidae	*Platycephalus longispinis*	Platell and Potter (1998)
Pleuronectidae	*Ammotretis elongatus*	Hourston et al. (2004)
	Pseudorhombus jenynsii	Schafer et al. (2002)
Scorpaenidae	*Maxillicosta scabriceps*	Platell and Potter (1998)
Serranidae	*Epinephelides armatus*	Platell et al. (2010)
Sillaginidae	*Sillaginodes punctata*	Hyndes et al. (1997) and Platell (unpublished data)
	Sillago burrus	Hyndes et al. (1997)
	Sillago robusta	Hyndes et al. (1997)
	Sillago schomburgkii	Hourston et al. (2004)
	Sillago vittata	Hyndes et al. (1997)
	Sillago bassensis	Hyndes et al. (1997)
Sparidae	*Pagrus auratus*	French et al. (2012)
	Rhabdosargus sarba	Ang (unpublished data)
Triglidae	*Lepidotrigla modesta*	Platell and Potter (1999)
	Lepidotrigla papilio	Platell and Potter (1999)

While season was included in the initial analyses, it was excluded from subsequent analyses aimed at identifying predator and prey guilds and constructing food webs for the following reasons. (1) The overall effect of season on dietary composition was shown by initial analyses to be relatively minor and less than those of the other two main effects, i.e. species and length class. (2) The effect of season on the dietary composition of each fish species studied on the lower west coast of temperate Australia (Table 6.1) was significant in a minority of cases and was almost invariably small and less than that of length class. Indeed, pronounced seasonal differences would not be expected on this coast because (a) water temperature does not change markedly during the year, with the mean monthly water temperatures ranging only from ca 18.5 to 22.5°C (Lek et al., 2012); (b) the difference between the minimum and maximum daylight hours is only ca 4 h (Geoscience Australia, 2012) and (c) there are no major seasonal upwellings that would lead to surges in productivity (Hanson et al., 2005). These features collectively account for productivity varying less markedly than in temperate waters elsewhere. For example, when measured in terms of carbon, primary production in the relatively oligotrophic waters off Perth on the lower west Australian coast ranges only from ca 0.3 to 0.6 g C m^{-2} day^{-1} (Hanson et al., 2005), compared with, for example, 0.5 to 17 g C m^{-2} day^{-1} in the western approaches to the English Channel (Boalch, 1987). (3) A breakdown of the data into seasonal components would mean that many species x length class x season groups would not contain sufficient data for each of those groups to facilitate reliable estimates of the species x length class group structuring; not to mention producing an unwieldy and unreliable table of results. (4) Furthermore, the inclusion of season as a component of the trophic guild structure, i.e. predator groups which have the same species at the same length in different predator guilds, would increase markedly the complexity of the plots of the relationships between the predators and their prey and thus reduce the effectiveness of the plots as a management tool for deciding conservation methods etc. for key predators and their prey. The decision to exclude season is consistent with the fact that, in detailed studies, the overall dietary composition of the fish communities of Puget Sound (USA), the upper shelf of south-eastern Australia and the mid-slope of southern Tasmania (Australia) did not change with season (Reum and Essington, 1988; Bulman et al., 2001; 2002).

It is reiterated that every attempt was made to obtain dietary data for a length class of each species from each season. If prey taxa are therefore important to a certain species x length class group (predator guild) during a particular season, the seasonal effect will still constitute part of the analysis determining that guild. Thus, the aim is to average the seasonal effects for good management reasons, rather than ignoring them, and thus ultimately to produce a more robust and parsimonious description of the food web.

6.2.3 Initial screening of dietary data

The data for all length class by season combinations for the 35 fish species, which contained at least three replicate fish, were extracted from the common database. As the number of replicates for each length class by season combination for each species varied greatly, the data set was unbalanced. The dietary data were therefore subjected to the following iterative process to explore whether this imbalance would influence the results. The volumetric contributions of the dietary items to each length class by season combination for each species were square root transformed and the resultant data employed to create a Bray-Curtis similarity matrix. A ‘distance among centroids’ matrix was calculated in PERMANOVA+ (Anderson et al., 2008), namely the distances between the centres of gravity of selected groups of points within the full-dimensional ‘Bray Curtis space’, in which points are located so that their inter-point distances (Euclidean) equate to Bray-Curtis dissimilarities in the original space of the transformed data matrix. These selected groups correspond to fish from each length class by season combination for each species.

It can be argued that this 'distances among centroids' matrix is the optimal description of the mean relationships among the dietary compositions of these groups. However, this matrix does have the significant disadvantage that it loses the link to the original scale of measurement of the data matrix, and is therefore not amenable to the subsequent, objective approach of defining higher-level group structures within both the predator and prey taxa, using the SIMPROF routine (Clarke et al., 2008) - see below. An alternative, which retains this crucial link, is to average the (transformed) data matrix itself into these same groups of fish species by length class by season, but this may have the potential to distort the true inter-group relationships because of the unbalanced group sizes. This is a result of the well-known 'species accumulation' effect, in which averages from larger numbers of replicates are likely to contain more species (here, prey taxa) and thus artefactually generate additional dissimilarity between groups of different sizes. In order to examine whether such distortion exists in this case, a simple model matrix was created using Euclidean distances between the numbers of replicates in each group. From the RELATE routine in PRIMER v6 (Clarke and Gorley, 2006), a Spearman correlation ρ was first calculated between this model matrix and the Bray-Curtis dissimilarities computed from the averages of the square root transformed dietary data for each group. A very weak relationship here ($\rho < 0.2$) is considered to indicate that the lack of balance in the numbers of replicates making up the averages was potentially not a confounding factor for subsequent analyses. As the first RELATE value exceeded 0.2, the original data matrix was therefore re-examined to identify, for each species, any length class by season combinations (groups) that contained only a small number (*n*) of replicates. Such combinations were successively removed ($n < 4$, $n < 5$, etc) until the RELATE ρ value fell below the designated threshold of 0.2.

In conjunction with the above threshold, the RELATE ρ statistic was then calculated between the optimal 'distances among centroids matrix' and the Bray-Curtis dissimilarities based on simple averaging of the transformed data, with a Spearman correlation approaching 0.9 considered to indicate a high degree of conformity between the information in these two matrices. These combined criteria were satisfied by retaining, for every species, all length class by season combinations that contained at least six replicates, the resulting RELATE correlations (ρ) between centroid and average matrices then being 0.88, whilst the average and count matrices were correlated at only the 0.19 level and the centroid and count matrices at only the 0.18 level.

For the retained species by length class by season combinations, a Bray-Curtis matrix was produced from the square-root transformed dietary volumetric data for all replicates in each combination. This matrix was then subjected to a series of two-way crossed ANOSIM tests (Clarke, 1993), in which one factor (e.g. predator species) was crossed with the combined levels of the two remaining factors (e.g. length class and season), thus removing the confounding effects of the latter. This analysis was carried out separately for each of the three factors, removing the effects of the other two, and the resultant global average *R* values were used to rank the factors in order of importance in determining the assemblage of prey items in the diets. The factor found to be of least importance, i.e. season, was ignored for subsequent analysis (see previous section for full rationale for this exclusion) and thus the resulting calculations employed 112 combinations of species and their length classes. This strengthened the number of replicates constituting each group, and the results of re-analysis of the relationships between centroid and averaged matrices, i.e. $\rho = 0.92$, and their relationship to sample size, i.e. $\rho = 0.12$ and $\rho = 0.17$, respectively, reinforced the validity of working with the averaged matrix in the subsequent analyses.

6.2.4 Identification of predator guilds

The dietary compositions for the various species x 100 mm length class combinations for the 35 fish species were then grouped statistically into predator guilds, using an objective form of cluster analysis. Specifically, the Bray-Curtis similarities from the above 112 group averages of volumetric dietary data, now regarded as the ‘samples’ and considered to be effectively free from sample-size bias, were subjected to hierarchical (Q-mode) cluster analysis using group-average linking, and tested using the SIMPROF routine in PRIMER v6 (Clarke and Gorley, 2006; Clarke et al., 2008). SIMPROF provides an objective means of defining, from the cluster dendrogram, the sets of species x length-class combinations for which there is no evidence of the samples within each set having any multivariate structure (e.g. further meaningful clustering of samples). This is achieved by a hierarchical series of tests on the nodes of the dendrogram, progressing down the tree to a finer level of classification of samples within a set only when there is evidence of remaining multivariate structure. These SIMPROF sets therefore defined the ‘trophic guilds’ of predators, each guild constituting different species and/or length-class combinations, such that similar diets are found within each set, and are significantly different from those in other sets.

A few of the resulting sets were outliers and, as they contained insufficient information for credible inclusion in the ensuing guild analyses (e.g. they consisted of only one length class of one species, and a low number of dietary samples), they were excluded from further consideration (see Results). The relationships between the remaining 14 predator guilds were then examined in the following two ways. Firstly, the Bray-Curtis resemblance matrix among samples (averaged data for each predator species by length class combination) was input to a SIMPER analysis in PRIMER v6 (Clarke, 1993; Clarke and Gorley, 2006) giving, for each guild, the percentage contributions that prey taxa made to the average within-guild similarity. From the full SIMPER tables, the prey taxa principally typifying each predator guild were extracted.

Secondly, the same Bray-Curtis similarities were used to construct a ‘distances among centroids’ matrix among the 14 predator guilds, using the PERMANOVA+ routine (Anderson et al., 2008). A 2-dimensional non-metric MDS plot of the relationships among these 14 centroids was then employed to display the gradient structure of trophic relationships among those various guilds. Subsequently, summary measures, such as the number of predator species by length class combinations making up each trophic guild, the total number of guts examined for these groups, and the values for Simpson diversity of the average prey assemblage for each guild were displayed as bubble plots on the 2-d nMDS ordination plot. The significance and extent to which the dietary relationships amongst predator guilds are mirrored in Simpson evenness was quantified by the RELATE routine (Clarke and Gorley, 2006), which, in this case, is a Spearman matrix correlation between dietary Bray-Curtis dissimilarities and (Euclidean) distances between the values for Simpson diversity, tested by permutation.

The main axis of the MDS ordination of predator guilds was also identified. Since axis orientations are essentially arbitrary in MDS, this is defined as the first axis of a principal component analysis of the 2-d MDS points, displayed in this case in the vertical direction, following the usual convention for displaying hierarchies or gradients, with the guilds containing the largest predators at the top of the plot.

6.2.5 Identification of prey guilds

The next step again involved SIMPROF, but this time to delineate each group of prey taxa (prey guilds) within which the relative contributions to the diets of the trophic (predator) guilds were similar. Therefore, after cluster analysis of the species x length class combinations and the subsequent deletion of three outlying predator guilds (see Fig. 7.8), 44 of the original 47 prey taxa remain, as the three other prey taxa only occurred in the deleted predator guilds. A ‘species resemblance’ matrix (Clarke and Warwick, 2001) can be defined between every pair of these prey taxa by standardising the averaged data matrix (of 44 prey taxa by 14 predator guilds) over the predator guilds, for each prey category (so that the values for each prey taxa sum to 100 over all predator guilds), and then calculating Bray-Curtis similarities between prey taxa. (Note that this method can be alternatively, and entirely equivalently described, as calculating Whittaker's Index of Association (Whittaker, 1952) on the species of the original (unstandardised) matrix). The resulting resemblances reflect the viewpoint of the prey; i.e. what is the percentage breakdown of each prey taxa across the predator guilds that consume it, and how similar are those percentage breakdowns for the 44 different prey taxa? This species resemblance matrix was subjected to group-average linked clustering (R-mode) in a manner similar to that used for the predator guilds (see earlier). In conjunction with the cluster analysis, a further run of the SIMPROF routine (Clarke et al., 2008) yields an objective grouping of the 44 prey taxa into 'prey guilds' (see Results for further details). Prey taxa within each such guild are those for which the null hypothesis of indistinguishability in their breakdown of percentage composition across the predator guilds cannot be rejected. Note that such 'species SIMPROF tests' can be undertaken in PRIMER v6 but not straightforwardly, because the default SIMPROF permutation procedure is not designed to carry out this novel analysis and will permute the data matrix incorrectly. It thus requires temporary switching of the definition of 'samples' and 'variables' to obtain the correct permutation distributions (Somerfield and Clarke, 2011).

The resemblance matrix used for the cluster analysis of the prey taxa was then employed, as described earlier for the predator guilds, to produce a nMDS plot of the 'distances among centroids' for the prey guilds and to determine the main axis of this plot. The common pattern of predation within each prey guild is then illustrated by simple line plots showing the percentage consumption of each prey taxa by each of the 14 predator guilds, with the predator and prey guilds each arranged as in their order on the main axis of their respective nMDS ordination plots.

6.2.6 Food webs

A food web that linked the 44 prey taxa to the 112 predator species x length class combinations would clearly be so complex that it would be uninformative. It is realistic, however, to produce a web relating the ten prey guilds to the 14 predator guilds. For this purpose, the volumetric percentage contributions of each prey taxa in a given prey guild are simply added, and the resultant values averaged across all species x length class combinations in each of the predator guilds. This enables a table to be constructed that provides the volumetric contribution of each prey guild to the diet of a 'typical' member of each predator guild. These data were then square-root transformed and rescaled so that, in an appropriate and clear visual manner, the lines linking the various predator and prey guilds varied linearly in thickness on a food web plot in proportion to the magnitude of the trophic interactions between those guilds.

Although the above food web comprises only cross-links between two discrete sets of objects, i.e. predator guild and prey guild, and no internal links within those guilds, it is still very complex. A more helpful and readily comprehensible representation of the relationships between the predator and prey guilds is a 'shade plot', which uses the same square-root transformed volumetric dietary data as employed for the above food web, but with rows and columns representing the prey and predator guilds, respectively, and the shading in each cell of this two-way layout being related on a continuous scale to the strength of the trophic interaction in this second simpler food web.

The sequence of the predator and prey guilds in both the traditional food web and the food web displayed as a shade plot follow those designated by their respective positions along the main axis (vertical alignment) in their respective nMDS ordination plots (see earlier).

7. RESULTS

7.1 RANKING OF LENGTH-CLASS, SEASONAL AND REGIONAL EFFECTS ON DIETARY COMPOSITIONS OF THE CO-OCCURRING PAGRUS AURATUS *(SPARIDAE) AND* PSEUDOCARANX GEORGIANUS *(CARANGIDAE)*

7.1.1 Jaws and dentition

The anterior part of the upper and lower jaws of *Pagrus auratus* each contain four pairs of prominent, pointed and re-curved canine teeth (Fig. 7.1a-d). Immediately inside those canines are numerous and very small teeth that grade into two rows of rounded and stout molariform teeth which run along the wide margins of both jaws.

The jaws of *Pseudocaranx georgianus* are far more slender than those of *P. auratus* and contain a single row of very small, pointed teeth that do not extend along the full length of the jaw margins (Fig. 7.1e-h). Unlike *P. auratus, P. georgianus* possesses pharyngeal jaws, which contain numerous small rounded teeth that are largest along the central longitudinal axis.

7.1.2 Overall dietary compositions

A large proportion of the guts of *P. auratus* and *P. georgianus* contained no food (Table 7.1), with the percentage of empty guts ranging from ca 70% for large *P. auratus* (i.e. >400 mm TL) on the mid west coast to ca 40% for *P. georgianus* on the south coast. The mean fullness of the guts with food ranged from 3.2 for *P. georgianus* on the lower west coast to 4.0 for large *P. auratus* on the same coast (Table 7.1).

Echinoderms, teleosts, crustaceans and molluscs made the greatest overall contributions to the diet of *P. auratus* on the basis of both their frequency of occurrence in the gut contents and their volumetric contributions to those contents (Table 7.1). Thus, for example, the most important of these major taxa (echinoderms) was ingested by as many as 78% of individuals <400 mm and contributed as much as 59% to the gut contents of those individuals.

While ophiuroids (belonging entirely to the family Ophiuridae) and echinoids were the two major echinoderm classes in the gut contents of *P. auratus*, the former was ingested far more frequently and made a far greater contribution to those of smaller fish (<400 mm) from the lower west coast than to those of large fish from both this region and the mid west coast (Table 7.1). The decapod component of the diet of *P. auratus* was always overwhelmingly dominated by crabs, which represented a number of different families, such as the Portunidae and the Majidae.

With the two most important dietary groups of molluscs consumed by *P. auratus* on the lower west coast, gastropods tended to be ingested slightly more frequently and in greater volumes by larger fish (i.e. >400 mm), whereas the reverse was the case with bivalves (Table 7.1). While polyplacophorans and cephalopods made a small but appreciable contribution to the diets of larger *P. auratus* from the lower west coast, these two groups were either absent or present in only small volumes in the gut contents of both small *P. auratus* from the lower west coast and of larger individuals from the mid west coast (Table 7.1).

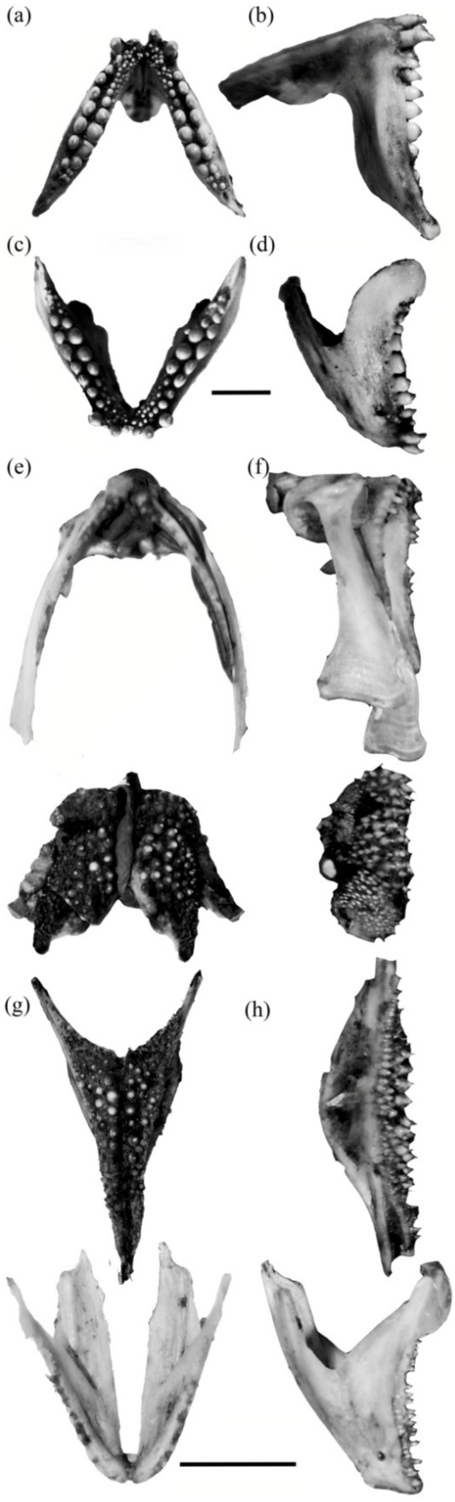


Figure 7.1 Plan and profile view of the upper (a,b) and lower (c,d) jaws of *Pagrus auratus*, respectively, and plan and profile view of the upper jaw and pharyngeal plate (e,f) and lower jaw and pharyngeal plate (g,h) of *Pseudocaranx georgianus*, respectively. Bar, 10 mm.

Table 7.1 Frequencies of occurrence (%F) and mean percentage contributions by volume (%V) of the major taxa (bold), dietary categories (*) and dietary items in the gut contents of different-sized *Pagrus auratus* in waters on the mid and lower west coasts of Australia and of *Pseudocaranx georgianus* in waters on the lower west and south coasts. Unid., unidentifiable.

Major taxa, dietary categories and dietary items	*P. auratus* Mid west >400 mm		*P. auratus* Lower west <400 mm		*P. auratus* Lower west >400 mm		*P. georgianus* Lower west		*P .georgianus* South	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Porifera*	**3.8**	**1.9**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Cnidaria*	**-**	**-**	**-**	**-**	**1.7**	**0.2**	**-**	**-**	**-**	**-**
Actiniaria	-	-	-	-	1.7	0.2	-	-	-	-
Gorgonacea	-	-	-	-	-	-	-	-	-	-
Sipuncula*	**1.3**	**0.2**	**-**	**-**	**3.3**	**0.5**	**-**	**-**	**-**	**-**
Polychaeta	**3.8**	**0.5**	**14.5**	**3.3**	**8.2**	**1.5**	**4.5**	**2.0**	**9.1**	**5.1**
Aphroditidae*	-	-	-	-	1.6	1.2	-	-	1.3	0.3
Pectinariidae*	3.8	0.5	14.5	3.3	6.6	0.3	3.2	1.6	3.9	1.7
Other Polychaeta*	-	-	-	-	-	-	1.3	0.4	5.2	3.1
Mollusca	**27.6**	**8.8**	**25.6**	**9.0**	**40.0**	**14.4**	**53.9**	**32.2**	**23.4**	**13.2**
Polyplacophora*	**-**	**-**	**1.2**	**0.3**	**6.6**	**2.6**	**0.6**	**0.4**	**1.3**	**0.1**
Gastropoda	**13.2**	**2.6**	**13.4**	**3.1**	**16.7**	**3.8**	**39.6**	**19.1**	**11.7**	**4.9**
Olividae*	5.1	1.5	1.2	-	1.6	-	-	-	1.3	0.3
Trochidae*	2.5	0.8	4.8	2.4	8.2	1.4	14.9	5.4	5.2	2.0
Littorinidae*	1.3	0.1	8.4	0.7	-	-	20.8	13.0	5.2	1.3
Other Gastropoda*	-	-	1.2	<0.1	8.3	1.6	1.3	0.1	2.6	0.8
Columbellidae	-	-	-	-	-	-	0.6	<0.1	1.3	0.7
Cypraeidae	-	-	-	-	1.6	0.1	-	-	-	-
Haliotidae	-	-	-	-	1.6	0.4	-	-	-	-
Naticidae	-	-	-	-	1.6	0.9	-	-	-	-
Turritellidae	-	-	1.2	<0.1	3.3	0.2	0.6	<0.1	1.3	0.1
Unid. Gastropoda	5.3	0.2	-	-	8.2	0.8	4.5	0.7	1.3	0.5
Bivalvia*	**11.8**	**4.2**	**14.4**	**5.6**	**10.0**	**4.3**	**15.6**	**7.1**	**9.1**	**5.8**
Mytilidae	-	-	-	-	-	-	1.9	1.9	-	-
Pectinidae	-	-	-	-	4.9	2.5	-	-	1.3	1.7
Pinnidae	3.8	1.5	-	-	-	-	0.6	-	-	-
Veneroida	2.5	0.1	2.4	0.5	1.6	0.2	-	-	-	-
Unid. Bivalvia	5.1	2.6	12.0	5.1	4.9	1.6	13.0	5.2	7.8	4.1
Cephalopoda	**9.2**	**2.0**	**-**	**-**	**16.4**	**3.7**	**5.2**	**5.6**	**2.6**	**2.4**
Octopoda*	1.3	0.2	-	-	6.6	1.4	0.3	0.4	2.6	2.4
Sepiida*	7.6	1.8	-	-	8.2	1.8	1.0	2.8	-	-
Teuthida*	-	-	-	-	1.6	0.5	1.3	2.4	-	-
Crustacea	**23.7**	**11.7**	**32.9**	**18.7**	**33.3**	**19.1**	**53.9**	**37.8**	**76.6**	**61.5**
Ostracoda*	-	-	-	-	-	-	6.5	1.5	10.4	1.7
Cumacea*	-	-	3.6	0.8	-	-	1.9	0.9	15.6	5.7
Isopoda*	2.5	0.4	1.2	0.4	3.3	2.5	7.1	1.9	24.7	10.1
Amphipoda*	1.3	0.9	2.4	2.2	-	-	20.8	6.7	45.5	28.1

Table 7.1 cont. on next page

Major taxa, dietary categories and dietary items	*P. auratus* Mid west >400 mm		*P. auratus* Lower west <400 mm		*P. auratus* Lower west >400 mm		*P. georgianus* Lower west		*P .georgianus* South	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Decapoda	**22.4**	**10.4**	**28.0**	**14.2**	**31.7**	**16.6**	**28.6**	**26.8**	**29.9**	**15.9**
Caridea*	-	-	2.4	2.2	1.6	0.8	17.5	10.1	13.0	4.9
Crabs	22.4	10.4	24.4	11.9	28.3	15.5	28.6	16.3	6.5	11.0
Larvae*	-	-	-	-	-	-	0.6	0.1	1.3	-
Adults*	22.4	10.4	24.4	11.9	28.3	15.5	28.6	16.2	19.5	11.0
Atelecyclidae	-	-	1.2	0.5	3.3	1.0	1.3	0.3	-	-
Majidae	2.5	0.7	7.2	3.6	1.6	-	2.6	0.8	1.3	0.1
Paguridae	5.1	0.9	2.4	0.4	8.2	3.5	1.3	0.1	5.2	2.0
Portunidae	7.6	4.0	2.4	1.7	11.5	7.1	2.6	2.0	10.4	8.2
Unid. crabs	11.4	4.8	12.0	5.7	11.5	3.9	22.7	13.0	5.2	0.7
Lobsters	-	-	1.2	0.1	3.3	0.3	-	-	-	-
Galatheoidea*	-	-	1.2	0.1	1.6	0.1	-	-	-	-
Achelata*	-	-	-	-	1.6	0.2	-	-	-	-
Unid. Decapoda	-	-	-	-	-	-	1.9	0.4	-	-
Unid. Crustacea	-	-	2.4	1.3	-	-	-	-	-	-
Echinodermata	**53.9**	**39.4**	**78.0**	**59.2**	**46.7**	**30.9**	**16.2**	**8.1**	**6.5**	**1.7**
Asteroidea*	**9.2**	**3.8**	**4.8**	**2.0**	**20.0**	**11.8**	**-**	**-**	**-**	**-**
Astropecten preissei	-	-	-	-	6.6	4.6	-	-	-	-
Luidia australiae	2.5	1.2	-	-	1.6	0.9	-	-	-	-
Stellaster inspinosus	3.8	1.4	-	-	-	-	-	-	-	-
Goniasteridae	-	-	-	-	1.6	0.3	-	-	-	-
Unid. Asteroidea	5.1	1.2	4.8	2.0	11.5	6.0	-	-	-	-
Ophiuroidea*	**6.3**	**3.8**	**63.9**	**43.8**	**9.8**	**3.0**	**5.8**	**2.2**	**6.5**	**1.7**
Echinoidea	**46.1**	**31.8**	**19.2**	**13.4**	**25.0**	**14.1**	**10.4**	**6.0**	**-**	**-**
Clypeasteroida*	-	-	-	-	1.6	1.8	-	-	-	-
Echinocardium cordatum	29.1	18.4	10.8	8.6	6.6	3.8	0.6	0.7	-	-
*Heliocidaris erythrogramma**	6.3	2.4	-	-	-	-	-	-	-	-
Other Echinoidea*	22.8	11.0	8.4	4.8	18.0	8.5	9.7	5.3	-	-
Holothuroidea*	**-**	**-**	**-**	**-**	**3.3**	**2.0**	**-**	**-**	**-**	**-**
Teleostei*	**53.9**	**38.4**	**18.3**	**9.8**	**50.0**	**29.3**	**19.5**	**19.9**	**16.9**	**18.3**
Atherinidae	-	-	-	-	-	-	8.4	10.7	7.8	10.5
Clinidae	-	-	-	-	-	-	2.6	1.7	-	-
Diodontidae	-	-	-	-	1.6	0.8	-	-	1.3	0.3
Gobiidae	-	-	-	-	-	-	-	-	1.3	0.2
Scorpaenidae	-	-	-	-	1.6	0.7	-	-	-	-
Syngnathidae	1.3	0.1	-	-	1.6	0.2	1.9	1.4	-	-
Tripterygiidae	1.3	0.1	-	-	-	-	0.6	0.3	-	-
Unid. Teleostei	53.2	38.1	18.1	9.8	47.5	27.6	6.5	5.8	6.5	7.3
Plant material*	-	-	-	-	9.8	4.1	-	-	-	-
Guts (*n*)	252		159		119		367		130	
Guts with food (*n*)	76		82		60		166		77	
Mean (SE) gut fullness	3.7 (0.2)		3.9 (0.2)		4.0 (0.2)		3.2 (0.2)		3.3 (0.2)	

In terms of both their frequency of ingestion and volumetric contribution to the guts, the most important contributors to the diets of *P. georgianus* on the lower west and south coasts were crustaceans, molluscs and then teleosts (Table 7.1). Among crustaceans, amphipods made a far greater volumetric contribution to the diets of fish on the south coast (28.1%) than lower west coast (6.7%), a trend paralleled by those for isopods and cumaceans. In contrast, the other main crustaceans in the diets of *P. georgianus*, i.e. carideans and crabs, contributed more to the dietary volume of fish on the lower west than south coasts, a trend followed, to varying degrees, by the main groups of mollusc (gastropods, bivalves and cephalopods) and echinoderms (echinoids) (Table 7.1).

7.1.3 Relationships between diets and body size

On the mid west coast, where smaller *P. auratus* could not be obtained, echinoids and teleosts were by far the most important contributors to the diets of this species and collectively contributed far more to those diets than to those of the corresponding size range of fish on the lower west coast (Fig. 7.2a). On the lower west coast, an increase in the body size of *P. auratus* was accompanied by a dramatic decline in the dietary contribution made by ophiuroids, from as high as ca 63% in the smallest fish, and an increase in that of teleosts, with asteroids becoming ingested by the larger individuals and contributing as much as 25% to the diets of the largest *P. auratus* (Fig. 7.2b). The dietary contributions of echinoids and gastropods tended initially to increase with body size and then decline in the larger individuals (Fig. 7.2b).

With *P. georgianus* from the lower west coast, the volumetric dietary contribution of teleosts and, to a lesser extent that of crabs, rose with increasing body size, whereas the reverse trend was exhibited by carideans (Fig. 7.2c). Cumaceans, isopods and bivalves were ingested by the smaller *P. georgianus* on this coast.

On the south coast, amphipods were present in relatively greater volumes in the stomach contents of all length classes of *P. georgianus* than in those from the lower west coast (Fig. 7.2c). As this species increased in body size on the south coast, the volumetric contributions of amphipods to the diet declined from their maxima of ca 25% in fish with lengths <300 mm to far lower levels in the largest fish (Fig. 7.2d). The dietary contributions of isopods also decreased with body size, while that of crabs increased and that of teleosts showed no conspicuous size-related trend. On the south coast, cumaceans were ingested only by those *P. georgianus* with lengths <300 mm (Fig. 7.2d).

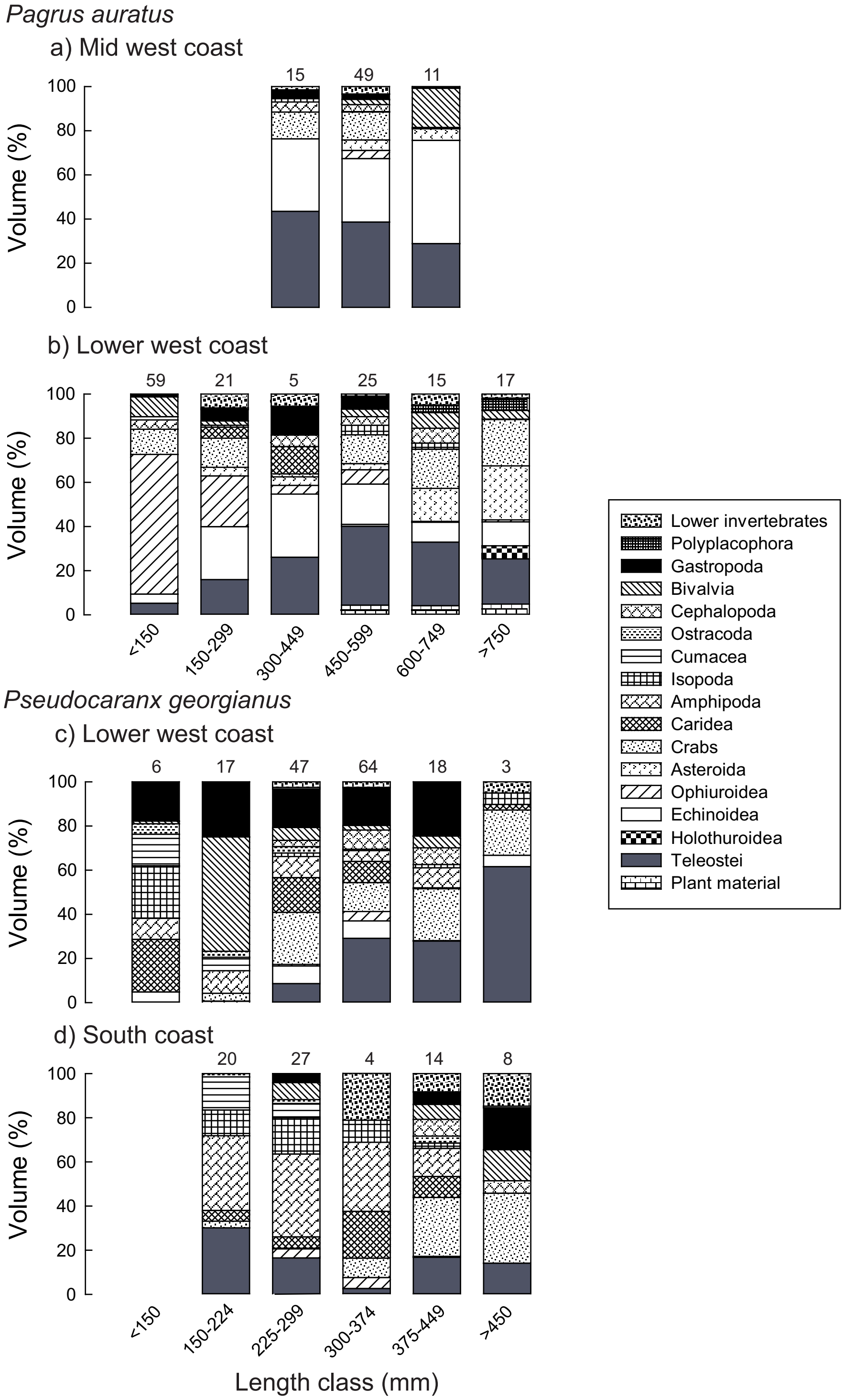


Figure 7.2 Stacked bar graphs showing mean percentage volumetric contributions (%V) of the dietary categories (see key) in the gut contents of the length classes of *Pagrus auratus* on the mid west and lower west coasts and of *Pseudocaranx georgianus* on the lower west and south coasts. Sample sizes are given above the stacked bar graphs for each length class. N.B. For visual clarity, a few dietary categories for closely-related taxa with small volumetric contributions have been pooled.

7.1.4 Analyses of dietary compositions of Pagrus auratus *on the lower west and mid west coasts*

PERMANOVA showed that, in relating dietary composition of *P. auratus* on the lower west coast to length class and season, there were significant main effects (pseudo-F=3.3 and 3.7 respectively, both P<0.01%) and a significant interaction between these two factors (pseudo-F=2.2, P=0.04%) (Appendix 3). Two-way crossed ANOSIM also showed that the dietary composition of *P. auratus* on this coast was significantly related to length class and season (both P=0.01%), with the global $\bar{R}$ of 0.63 for length class (removing the effect of season) being greater than the global $\bar{R}$ of 0.55 for season (removing the effect of length class). The interaction in PERMANOVA indicates, however, that these average values conceal some significant variations. Thus, one-way ANOSIM global R values for differences between seasons, computed separately for each length class, were significant for the first two length classes (R=0.85 and 0.65, both P<5%), but not for the other length classes (R=-0.05 to 0.15, all P>5%), thus accounting for the weighted average of 0.55 for the 2-way test.

On the ordination plot shown in Fig. 7.3a, most of the points representing the dietary samples for the length classes of *P. auratus* on the lower west coast in autumn and winter form a group in the centre of the plot, whereas those for spring and summer are more widely dispersed and located predominantly in the upper third of the plot. Because the trends exhibited by sequential length classes in each season cannot be readily visualised on Fig. 7.3a and the stress was relatively high, the data for autumn and winter and for spring and summer were plotted separately (Figs 7.3b,c). The points for the dietary samples of the sequential size classes represented in autumn and winter can then be seen to progress essentially from top to bottom on the ordination plot, but not in precisely the same manner (Fig. 7.3b). In contrast, the points for spring and summer each form more of a semi-circular pattern (Fig. 7.3c). This difference in the trends exhibited by sequential length classes in particularly autumn and winter vs spring and summer helps explain the interaction between length class and season, though the primary effect here is clearly the progressive trend in dietary composition across sequential length classes and, secondarily, the different average compositions of the diets between autumn/winter and spring/summer.

The results of SIMPER emphasise that the typifying and distinguishing prey of the diets of sequential length classes of *P. auratus* on the lower west coast progressed from ophiuroids and small crabs to teleosts and larger crabs, with asteroids becoming prevalent in the diet of the largest individuals (Table 7.2). While ophiuroids were an important typifying prey category of *P. auratus* on the lower west coast in each season, they were consumed in greater volumes in summer and autumn than in winter and spring (Table 7.3). The diets in summer were distinguished from those in autumn and spring by consistently greater volumes of crabs, while consistently greater volumes of the echinoid *Echinocardium cordatum* distinguished the diet in spring from that in each of the other seasons and the volumetric contributions of teleosts to the diets in autumn and winter were consistently greater than those in spring and summer (Table 7.3).

In comparisons between the dietary compositions of *P. auratus* on the lower west and mid west coasts, which were involved the three length classes that were represented in samples from both regions (see earlier), there were significant interactions between season and both length class (pseudo-F=2.0, P=0.4%) and region (pseudo-F=2.6, P=0.5%), but not between length class and region (pseudo-F=1.1, P=38.7%), and neither was the 3-way interaction significant (pseudo-F=0.6, P=66.8%) (Appendix 3). The main effect of length class was not significant. A two-way crossed ANOSIM test, employing season vs region (with length class being ignored as the size range of fish was incomplete; see earlier) demonstrated that the dietary composition of *P. auratus* changed with season ($\bar{R}$=0.50, P=0.1%) and region ($\bar{R}$=0.30, P=0.4%).

Table 7.2 Dietary categories that typify (shaded) the dietary compositions of sequential length classes of *Pagrus auratus* on the lower west coast of Australia and those which distinguish between the dietary compositions of those length classes (unshaded). In this table and Table 4, * denotes that the relative contribution of that dietary category is greater for the length class represented in the vertical column than in the horizontal row. Note that, because of limited replication, the typifying dietary categories for the 300-449 mm length class are derived using a one-way rather than two-way SIMPER analysis.

Length class (TL, mm)	<150	150-299	300-449	450-599	600-749	≥750
<150	Ophiuroidea Bivalvia					
150-299	Ophiuroidea* Crabs Teleostei Polychaeta Other Echinoidea Trochidae *E.cordatum*	Ophiuroidea Teleostei Crabs Polychaeta				
300-449	Ophiuroidea* Other Echinoidea Teleostei Crabs * Trochidae Asteroidea	Ophiuroidea* Crabs* Trochidae Other Echinoidea Asteroidea *E.cordatum**	Trochidae Polychaeta*			
450-599	Ophiuroidea* Teleostei Other Echinoidea Bivalvia* Other Gastropoda Crabs Trochidae	Ophiuroidea* Crabs* Other Echinoidea Polychaeta* Trochidae Other Gastropoda Bivalvia Asteroidea*	Sepiida Other Echinoidea Other Gastropoda Crabs Trochidae* Plant material Isopoda Asteroidea*	Teleostei Other Echinoidea Crabs		
600-749	Teleostei Ophiuroidea* Crabs Asteroidea Isopoda	Ophiuroidea* Asteroidea Crabs *E.cordatum** Plant material Polychaeta* Other Echinoidea* Holothuroidea	Trochidae* Teleostei Asteroidea Plant material Polyplacophora Polychaeta* Crabs	Asteroidea Crabs Ophiuroidea* Other Echinoidea* Octopoda Bivalvia Polychaeta *E.cordatum* Teleostei*	Teleostei Crabs	
≥750	Ophiuroidea* Teleostei Crabs Asteroidea Bivalvia* *E.cordatum* Holothuroidea	Ophiuroidea* Asteroidea Crabs *E.cordatum** Plant material Polychaeta Other Echinoidea Holothuroidea	Crabs Asteroidea Other Echinoidea* Trochidae* *E.cordatum* Clypeasteroidea Plant material	Other Echinoidea* Asteroidea Crabs *E.cordatum* Holothuroidea Ophiuroidea * Bivalvia Teleostei*	Asteroidea Crabs Polyplacophora* Teleostei* Octopoda* Polychaeta* Clypeasteroidea	Teleostei Asteroidea Bivalvia

Table 7.3 Dietary categories that typify (shaded) the dietary compositions of *Pagrus auratus* in sequential seasons on the lower west coast of Australia and those which distinguish between the dietary compositions in each pair of seasons (unshaded). * Denotes that the relative contribution of that dietary category is greater for the season represented in the vertical column than in the horizontal row.

Season	Summer	Autumn	Winter	Spring
Summer	Ophiuroidea Crabs			
Autumn	Crabs* Teleostei Ophiuroidea Bivalvia Amphipoda *E. cordatum*	Ophiuroidea Teleostei Bivalvia Crabs Other Echinoidea		
Winter	Clypeasteroidea* Teleostei Asteroidea Bivalvia Crabs Isopoda* Polyplacophora Ophiuroidea*	Crabs Teleostei* *E. cordatum* Asteroidea Bivalvia Ophiuroidea* Sepiida Other Echinoidea Plant material	Teleostei Crabs Asteroidea Ophiuroidea Bivalvia Sepiida	
Spring	Crabs* Littorinidae *E. cordatum* Asteroidea Plant material Caridea Amphipoda*	Teleostei* Ophiuroidea* Crabs* *E. cordatum* Littorinidae Bivalvia*	Plant material Polyplacophora Teleostei* Crabs* Bivalvia* Asteroidea* *E. cordatum*	Ophiuroidea *E. cordatum*

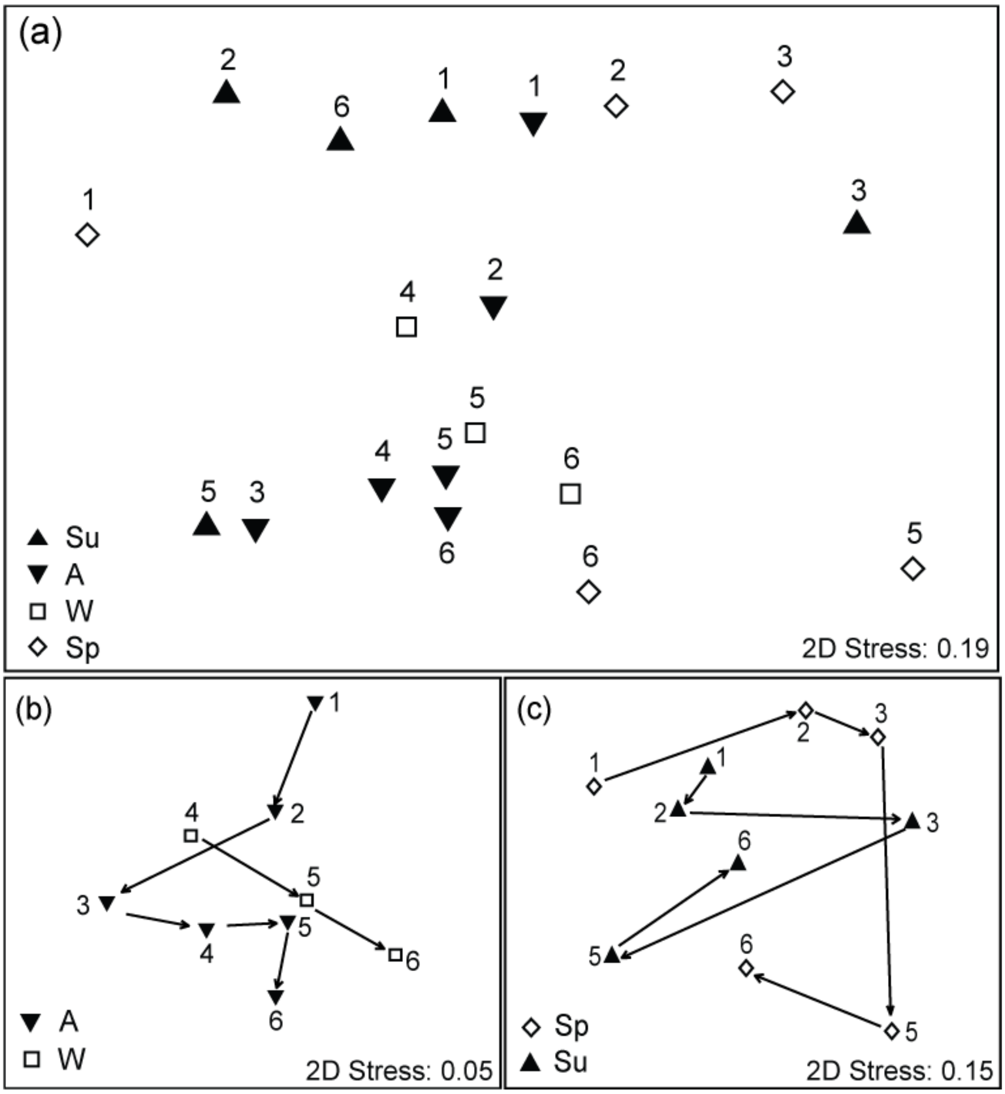


Figure 7.3 Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pagrus auratus* caught seasonally on the lower west coast. Plot (a) is derived from data for all seasons and length classes, while (b) is derived from data for autumn and winter and (c) is derived from data for spring and summer. 1 = <150 mm, 2 = 150-299 mm, 3 = 300-449 mm, 4 = 450-599 mm, 5 = 600-749 mm, 6 = ≥750 mm. In this and Figs 7.4, 7.6 and 7.7, Su, summer, A, autumn; W, winter; Sp, spring.

The PERMANOVA interaction suggests that the average *R* of 0.50 for season may conceal some variability in the seasonal effects for the two regions, which is consistent with the fact that 1-way ANOSIMs carried out separately for each region yielded *R* values for the seasonal effect of 0.57 (*P*=0.1%) for the mid west coast and 0.39 (*P*=1.4%) for the lower west coast.

One-way SIMPER analysis showed that the diets of *P. auratus* on the mid west coast were typified by the consistent presence of substantial volumes of teleosts and other echinoids in autumn, winter and spring and of crabs in the latter two seasons. The diets during autumn were distinguished from those in winter and spring by consistently greater contributions of *E. cordatum* and consistently lower contributions of other echinoids and crabs, whereas those in winter were distinguished from those in spring by a greater consumption of teleosts and crabs and smaller contributions by other echinoids and amphipods.

On the nMDS ordination plot shown in Fig. 7.4a, the dietary samples for *P. auratus* in each season on the lower west coast lie to the left of those for each season on the mid west coast. The points for the dietary samples arguably follow a better defined cyclic progression for fish on the lower west than mid west coasts, but primarily the change is of a smaller scale and in a different direction, which accounts for the season x region interaction. Turning to the nMDS ordination employing the three length classes in each of the four seasons (Fig. 7.4b), the dominant feature is the much smaller change in diet over the length classes in autumn and winter than in summer and spring, which explains the interaction seen between season and length class in the PERMANOVA analysis.

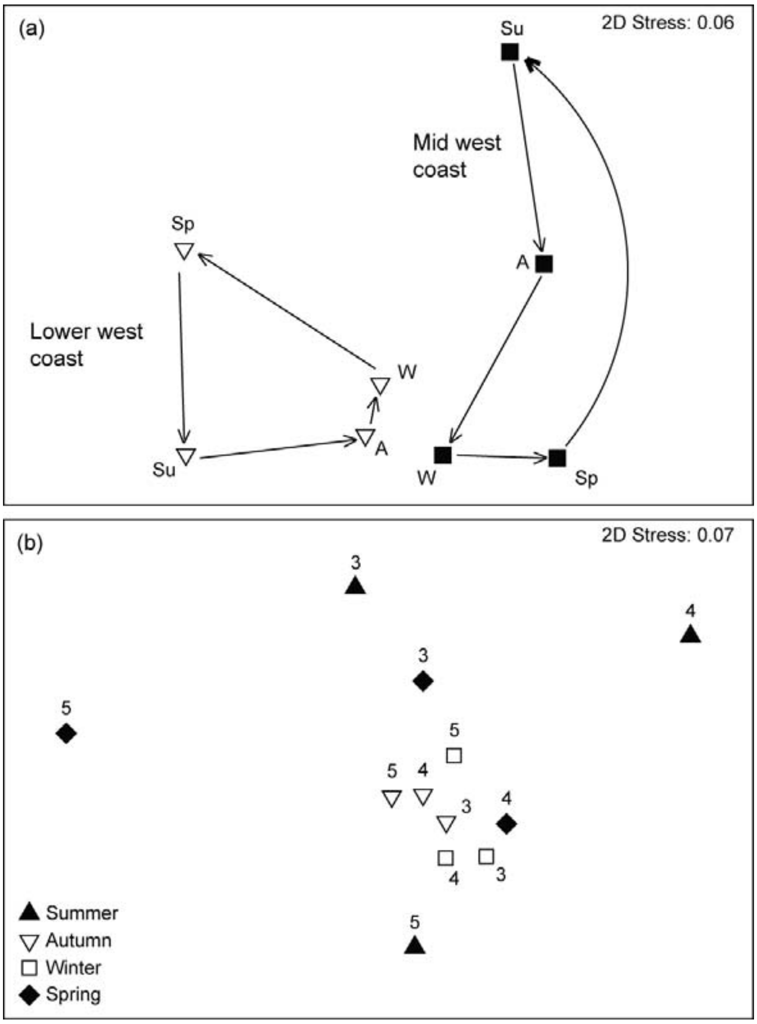


Figure 7.4 Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of *Pagrus auratus* caught seasonally on the lower west and mid west coasts, separated firstly by (a) season and region and then (b) season and length class. Comparisons were restricted to the length classes of fish represented in both regions, i.e. 3 = 300-449, 4 = 450-599 and 5 = 600-749 mm.

The Teleostei was the most important typifying dietary category for *P. auratus* on both the mid west and lower west coasts. The diets of *P. auratus* from the mid west coast were distinguished from those on the lower west coast by consistently greater contributions of *E. cordatum* and other echinoids and a more reduced range of prey, whereas the reverse trend applied to asteroids, trochids and ophiuroids.

7.1.5 Analyses of dietary compositions of Pseudocaranx georgianus *on the lower west and south coasts*

PERMANOVA showed that, in the case of the dietary compositions of *P. georgianus* on the lower west coast, there was no significant interaction between length class and season (pseudo-*F*=1.2, *P*=12.1%) (Appendix 3). Two-way crossed ANOSIM showed that the dietary composition of *P. georgianus* on this coast was significantly related to length class ($\bar{R}$=0.20, *P*=1.7%) but not season ($\bar{R}$=0.05, *P*=23.9%). SIMPER emphasised that the size-related change in diet reflected a sequential progressive shift from the ingestion of substantial volumes of bivalves to crabs and littorinid gastropods and also teleosts by the larger fish (Table 7.4).

There was also little evidence of an interaction between length class and season with the dietary composition of *P. georgianus* on the south coast (pseudo-*F*=1.6, *P*=6.2%) (Appendix 3). Here, however, two-way crossed ANOSIM demonstrated that dietary composition was related to season ($\bar{R}$=0.49, *P*=0.2%) but not length class ($\bar{R}$=0.13, *P*=14.1%). Nonetheless, pulling together the length class information from the two regions, the nMDS ordination (Fig. 7.5) shows an essentially similar picture for the dietary samples of sequential length classes of *P. georgianus,* with both progressing from left to right across the plot, but with the pattern being weaker for the south coast region (non-significant in the ANOSIM test though marginally significant at the *P*=3.5% level for the RELATE seriation test corresponding to the MDS ordination plot in Fig. 7.5). Amphipods were one of the two most important typifying dietary categories ingested by *P. georgianus* in summer, autumn and winter on the south coast. Consistently greater volumes of bivalves characterised the diets in spring from those in all other seasons and the same was true for amphipods in summer vs all other seasons and for teleosts in winter vs summer, autumn and spring.

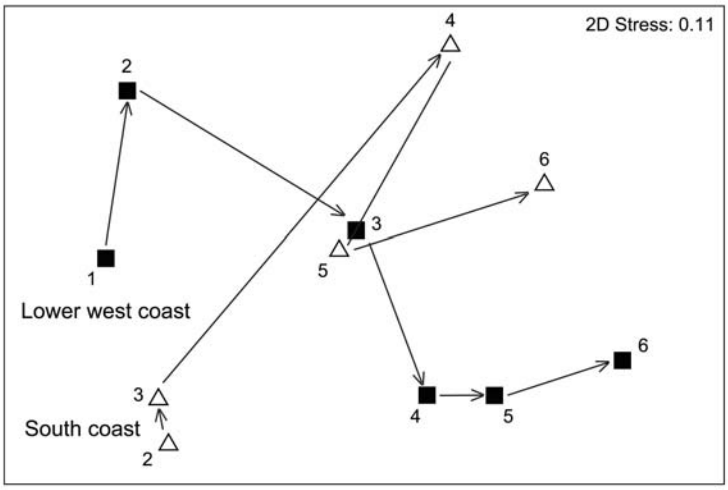


Figure 7.5 Centroid nMDS ordination plot, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pseudocaranx georgianus* caught seasonally from the lower west and south coasts. 1 = <150 mm; 2 = 150-224 mm; 3 = 225-299 mm; 4 = 300-374 mm; 5 = 375-449 mm; 6 = ≥450 mm.

Table 7.4 Dietary categories that typify (shaded) the dietary compositions of sequential length classes of *Pseudocaranx georgianus* on the lower west coast of Australia and those which distinguish between the dietary compositions of those length classes (unshaded). Note that, because of limited replication, the typifying dietary categories for the diets of fish comprising the >150 and ≥450 mm length classes and the comparison between the diets of those two length classes, are based on the results of a one-way rather than two-way SIMPER analysis.

Length class (mm, TL)	<150	150-224	225-299	300-374	375-449	≥450
<150	Trochidae					
150-224	Trochidae* Cumacea* Ostracoda* Amphipoda Isopoda* Caridea* Other Echinoidea*	Bivalvia				
225-299	Crabs Isopoda* Trochidae* Caridea Amphipoda Teleostei Bivalvia	Bivalvia* Caridea Amphipoda Crabs Other Echinoidea Ostracoda Cumacea	Crabs Caridea Amphipoda Bivalvia Littorinidae			
300-374	Teleostei Cumacea* Crabs Ostracoda* Other Echinoidea Isopoda* Caridea* Amphipoda Trochidae*	Bivalvia* Trochidae* Teleostei Amphipoda* Crabs Cumacea Littorinidae Caridea	Teleostei Crabs* Caridea Littorinidae Other Echinoidea Amphipoda* Trochidae Bivalvia	Teleostei Littorinidae Crabs Caridea Amphipoda Trochidae		
375-449	Crabs Cumacea* Teleostei Littorinidae Trochidae* Ostracoda* Other Echinoidea*	Crabs Teleostei Bivalvia* Trochidae* Cumacea* Littorinidae Amphipoda* Ostracoda*	Teleostei Littorinidae Amphipoda Crabs Caridea* Other Echinoidea Bivalvia	Teleostei Littorinidae Crabs Caridea* Bivalvia Sepiida	Crabs Teleostei Littorinidae	
≥450	Teleostei Crabs Cumacea* Isopoda* Caridea* Trochidae* Ostracoda* Other Echinoidea	Teleostei Bivalvia* Polychaeta Isopoda Other Echinoidea	Teleostei Caridea* Other Echinoidea Amphipoda Isopoda Crabs	Littorinidae* Teleostei Crabs Caridea* Other Echinoidea Polychaeta Amphipoda*	Teleostei Caridea Littorinidae* Polychaeta Bivalvia	Teleostei Crabs

In comparisons that employed the dietary data for *P. georgianus* from both the lower west and south coasts, there were significant interactions between length class and both region and season, though weak in the latter case (pseudo-*F*=2.1, *P*=0.4% and pseudo-*F*=1.4, *P*=2.9%, respectively) (Appendix 3). Two-way crossed ANOSIMs showed that the dietary composition of *P. georgianus* was most strongly related to region ($\bar{R}$=0.43, *P*=0.1%), with much weaker relationships to length class ($\bar{R}$=0.18, *P*=1.1%) and season ($\bar{R}$=0.16, *P*=0.5%).

Although the points for the dietary samples of sequential length classes of *P. georgianus* from both regions progressed from left to right on the ordination plot shown in Fig. 7.5, the lines connecting the sequential points for the two regions transect and tend to pass downwards on the lower west coast and upwards on the south coast, thereby accounting for the stronger of the two interactions, i.e. that between length class and region.

As the multiplicity of points on Fig. 7.6a made it difficult to identify the trends exhibited by the various length classes in the four seasons, the data for autumn and winter were analysed and plotted separately from those for spring and summer (Figs 7.6b,c), thereby substantially reducing the stress to lower levels in both representations. While the points for the dietary samples for sequential length classes from autumn and winter progress together down the ordination plot shown in Fig. 7.6b, those from spring and summer (Fig. 7.6c) tend to work in opposite directions, reflecting the weak interaction between length class and season.

While crabs and amphipods were important typifying dietary categories for *P. georgianus* on both coasts, relatively greater volumes of crabs (and also of teleosts) were particularly important in distinguishing the diets of fish from the lower west and south coasts, and the reverse was true for amphipods.

7.1.6 Comparisons between the diets of Pagrus auratus *and* Pseudocaranx georgianus *on the lower west coast*

In the case of comparisons based on the dietary data for co-occurring *P. auratus* and *P. georgianus* on the lower west coast, PERMANOVA showed that each two way interaction and the three way interaction involving all three factors, i.e. length class, species and season, were significant, though the 3-way interaction was weak (pseudo-*F*=1.5, *P*=3.7%); other terms were significant at least at the 0.5% level, with the species effect having easily the largest pseudo-*F* value, i.e. 6.6 (*P*<0.01%) (Appendix 3). Two-way crossed ANOSIM, employing, in turn, the dietary data for each of the above effects vs the other two combined, yielded global $\bar{R}$ values of 0.51 for species, 0.35 for length class and 0.19 for season (all significant at least at the *P*<0.2% level).

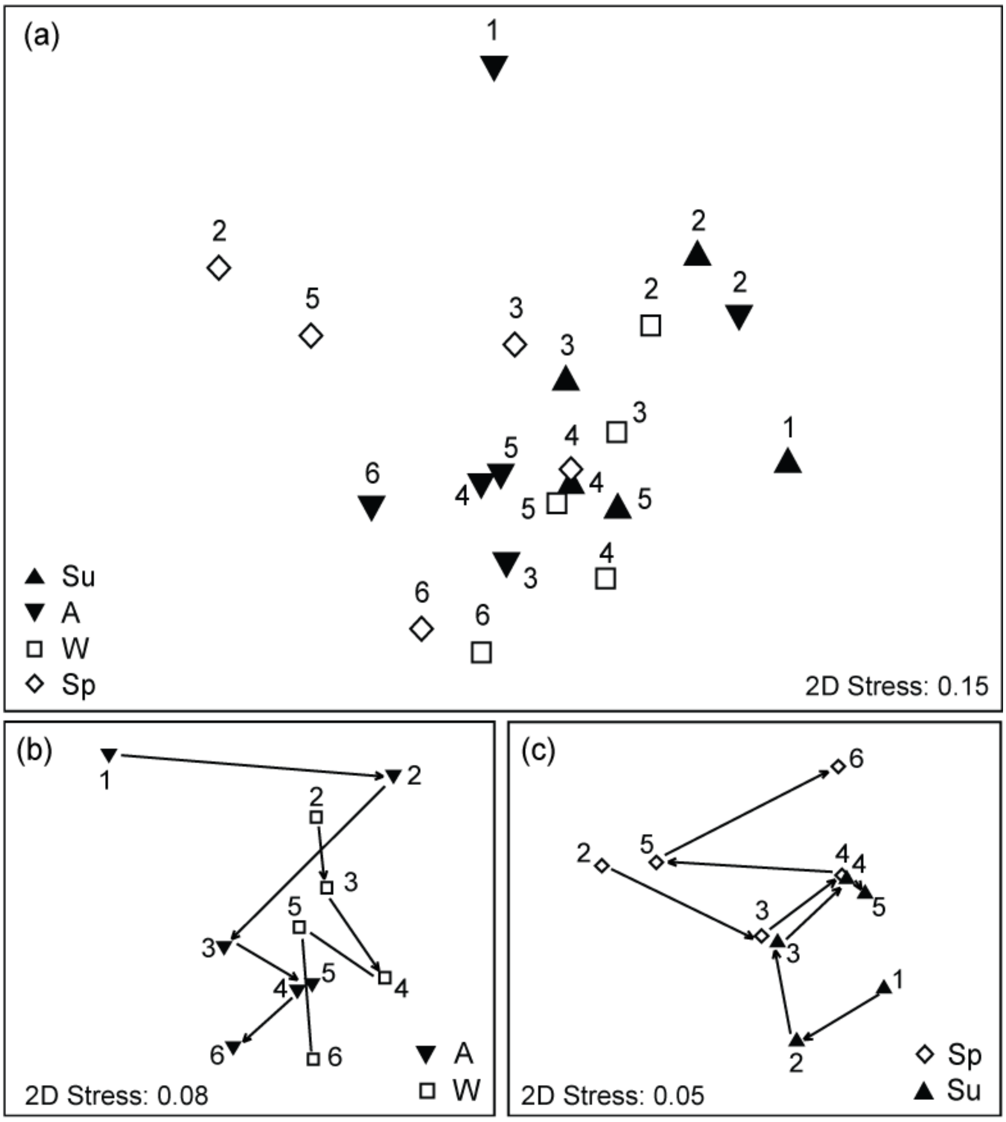


Figure 7.6 Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pseudocaranx georgianus* caught seasonally on the lower west and south coasts. Plot (a) is derived from data for all seasons and length classes, while (b) is derived from data for autumn and winter and (c) from spring and summer. 1=<150 mm; 2=150-224 mm; 3=225-299 mm; 4=300-374 mm; 5=375-449 mm; 6=≥450 mm.

The lines connecting the dietary samples for sequential length classes of *P. auratus* and *P. georgianus* on the ordination plot shown in Fig. 7.7a both progress essentially from left to right and do not transect each other, illustrating the large difference in the dietary compositions of those two species. However, the two sets of lines do not follow precisely the same parallel trends, which account for the interaction between length class and species (pseudo-*F*=2.2, *P*=0.02%) (Appendix 3). The RELATE procedure, computed from the distances among centroids matrix underlying the ordination plots in Figs 7.5 and 7.7a, showed that the dietary composition is significantly related, in a serial manner, to length class in the case of both *P. auratus* (ρ=0.79, *P*=0.3%) and *P. georgianus* (ρ=0.75, *P*=0.8%) on the lower west coast. The corresponding seriation test to the ordination for *P. georgianus* on the south coast (Fig. 7.5) gave a similar ρ value of 0.76 (*P*=3.5%).

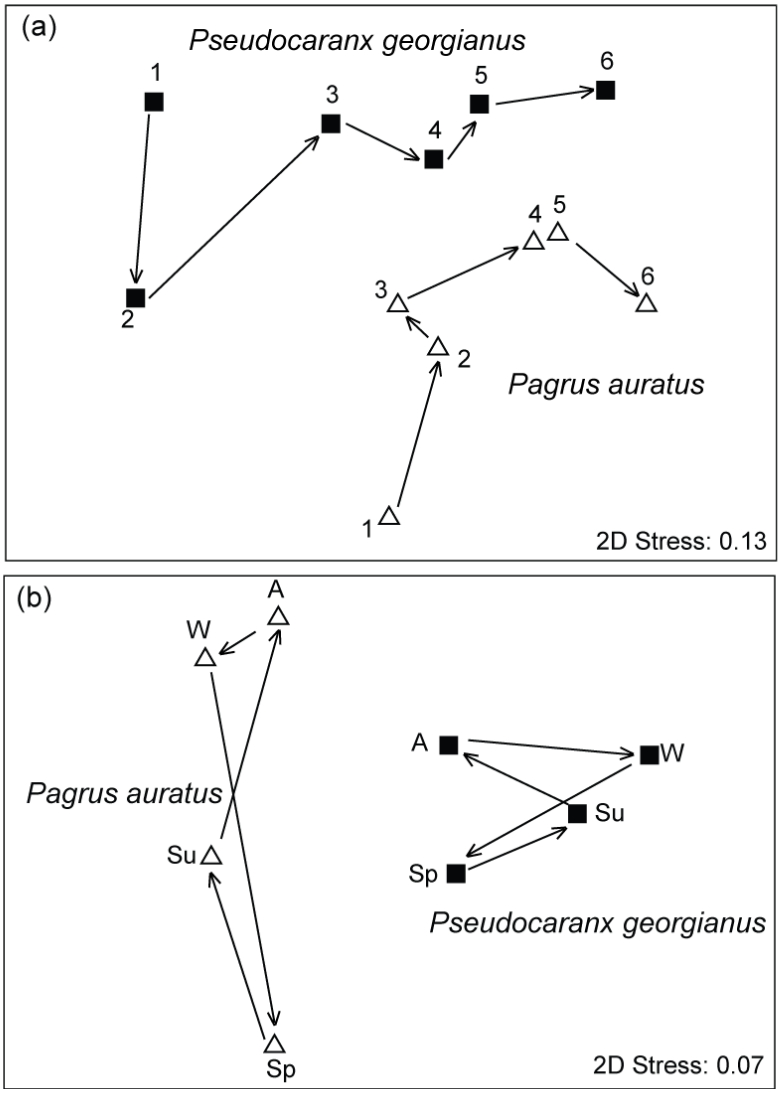


Figure 7.7 Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of co-occurring *Pagrus auratus* and *Pseudocaranx georgianus* on the lower west coast, separated firstly by (a) species and length class and then (b) species and season. Length classes are as follows; for *P. auratus* 1 = <149 mm; 2 = 150-299 mm; 3 = 300-449 mm; 4 = 450-599 mm; 5 = 600-749 mm; 6 = ≥750 mm; for *P. georgianus* 1 = <150 mm; 2 = 150-224 mm; 3 = 225-299 mm; 4 = 300-374 mm; 5 = 375-449 mm; 6 = ≥450 mm.

The large interspecific differences, seen with length class on Fig. 7.7a, are also apparent in the MDS ordination plot showing the seasonal patterns exhibited by the dietary compositions of the two species (Fig. 7.7b). However, they progress in somewhat different directions and on clearly different scales of change, illustrating the significant interaction between species and season (pseudo-*F*=2.6, *P*=0.02%) (Appendix 3).

Consistently large contributions by crabs and teleosts were very important in typifying the diets of both *P. auratus* and *P. georgianus* on the lower west coast of Australia. The diets of *P. auratus* were distinguished, however, from those of *P. georgianus,* by consistently greater contributions of ophiuroids (particularly by smaller individuals, see also Table 7.1), asteroids and *E. cordatum,* and consistently lower contributions of littorinids, other echinoids, amphipods and carideans.

7.2 AN INNOVATIVE STATISTICAL APPROACH TO CONSTRUCTING A READILY COMPREHENSIBLE FOOD WEB FOR A DEMERSAL FISH COMMUNITY

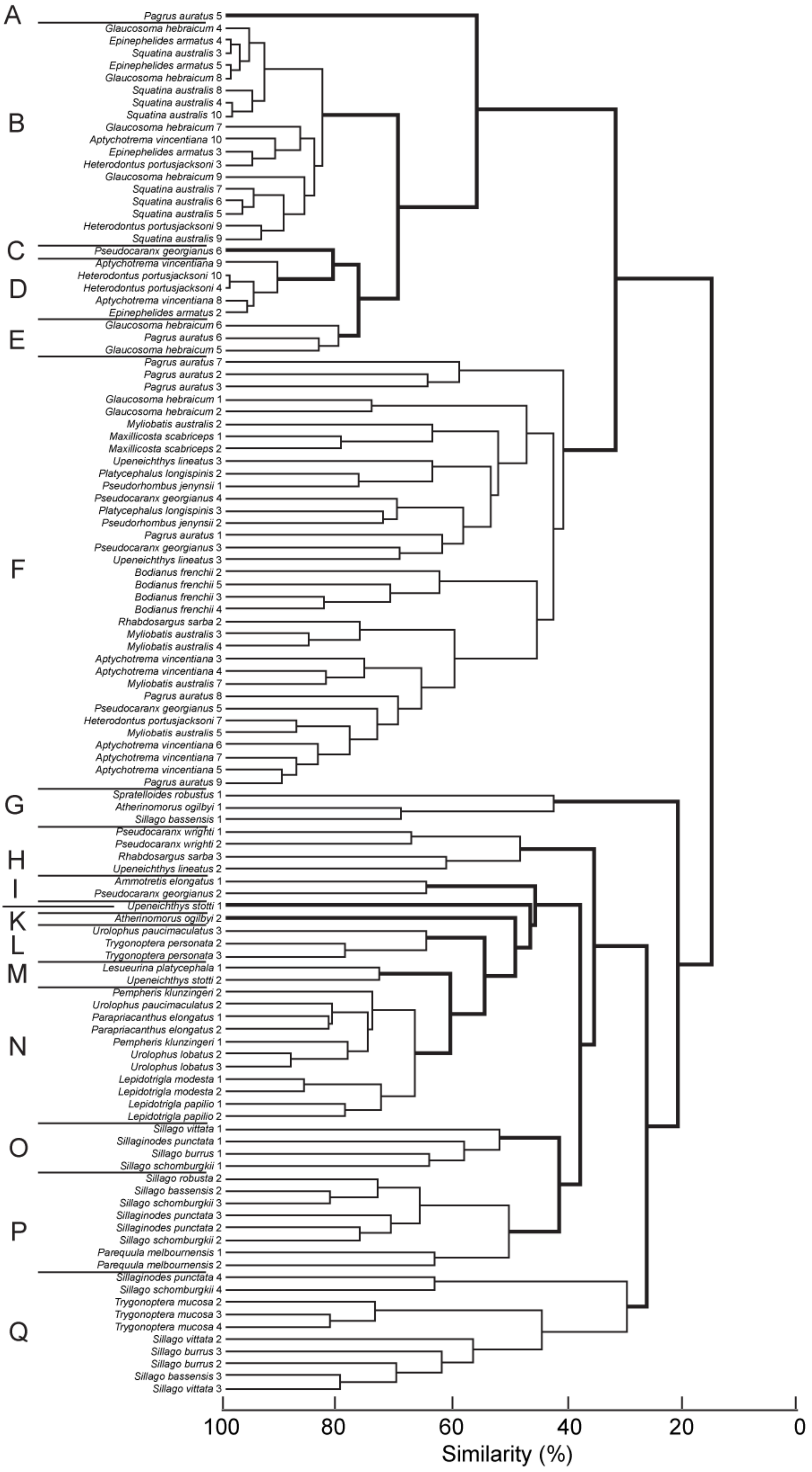
7.2.1 Identifying predator guilds and their typifying prey species

The cluster dendrogram, derived from the Bray-Curtis similarity matrix constructed from the volumetric dietary data for the length classes of each species, is shown in Fig. 7.8. The subjection of these dietary data to SIMPROF separated the 112 species x length class combinations into 17 predator guilds, designated as A to Q, which were significantly different from each other using a sequence of $P < 5\%$ level tests, among which there were four outliers (Fig. 7.8). Although one of the outliers (guild K) comprised a single species x length class combination, it contained as many as 37 replicates and was therefore considered a bona fide guild and thus retained for subsequent analyses. The three other outliers (guilds A, C and J) each contained only one species x length class combination and few replicates and were thus not included in subsequent analyses. There was thus data for a total of 14 predator guilds for analysis.

On the ordination plot, derived from the volumetric dietary data for the above 14 predator guilds, the points for those guilds followed a broadly downward progression from B at the top to I at the bottom (Fig. 7.9a). Major artefactual effects on this plot can be ruled out for the following reasons. The number of species by length class combinations in each predator guild, as reflected in the relative sizes of the bubbles for each guild in Fig. 7.9b, showed no overall tendency to change consistently with its position on that ordination plot. Likewise, there was no evidence that the total number of guts examined for dietary analyses varied with position on the same ordination plot (Fig. 7.9c). Thus, in keeping with the earlier RELATE tests (see the Methods section 6.2.3 on Initial Screening of Dietary Data), the order in which the predator guilds are distributed in the vertical axis in Fig. 7.9 is related neither to the number of species by length class groups in each predator guild nor to the number of individual guts in those guilds.

The vertical sequence of the 14 predator guilds in Fig. 7.9a is given in Table 7.5, commencing with guild B and ending with predator guild I. This sequence progresses from the larger individuals of the larger species, such as the teleosts *Epinephelides armatus* and *Glaucosoma hebraicum* and the elasmobranchs *Heterodontus portusjacksoni* and *Squatina australis* (predator guilds B and D), to the smallest individuals of four sillaginid species (predator guild O) and to smaller individuals of *P. georgianus* and the small species *Ammotretis elongatus* (predator guild I).

Figure 7.8 ‘Q-mode’ cluster dendrogram, derived from the Bray-Curtis similarity matrix constructed from the volumetric dietary data for the length classes of each fish species for which there were such data. The thick lines designate the species x length class combinations that were separated by SIMPROF into a series of groups (predator guilds) whose dietary compositions differed. Note that three of the four outliers (A, C and J) contained a single species x length class combination and were not included in further analysis (see text for full rationale). Full generic names for each fish species are provided in Table 7.6.


A
Pagrus auratus 5
Glaucosoma hebraicum 4
Epinephelides armatus 4
Squatina australis 3
Epinephelides armatus 5
Glaucosoma hebraicum 8
Squatina australis 8
Squatina australis 4
Squatina australis 10
B
Glaucosoma hebraicum 7
Aptychotrema vincentiana 10
Epinephelides armatus 3
Heterodontus portusjacksoni 3
Glaucosoma hebraicum 9
Squatina australis 7
Squatina australis 6
Squatina australis 5
Heterodontus portusjacksoni 9
Squatina australis 9
C
Pseudocaranx georgianus 6
Aptychotrema vincentiana 9
Heterodontus portusjacksoni 10
D
Heterodontus portusjacksoni 4
Aptychotrema vincentiana 8
Epinephelides armatus 2
E
Glaucosoma hebraicum 6
Pagrus auratus 6
Glaucosoma hebraicum 5
Pagrus auratus 7
Pagrus auratus 2
Pagrus auratus 3
Glaucosoma hebraicum 1
Glaucosoma hebraicum 2
Myliobatis australis 2
Maxillicosta scabriceps 1
Maxillicosta scabriceps 2
Upeneichthys lineatus 3
Platycephalus longispinis 2
Pseudorhombus jenynsii 1
Pseudocaranx georgianus 4
Platycephalus longispinis 3
Pseudorhombus jenynsii 2
Pagrus auratus 1
Pseudocaranx georgianus 3
Upeneichthys lineatus 3
F
Bodianus frenchii 2
Bodianus frenchii 5
Bodianus frenchii 3
Bodianus frenchii 4
Rhabdosargus sarba 2
Myliobatis australis 3
Myliobatis australis 4
Aptychotrema vincentiana 3
Aptychotrema vincentiana 4
Myliobatis australis 7
Pagrus auratus 8
Pseudocaranx georgianus 5
Heterodontus portusjacksoni 7
Myliobatis australis 5
Aptychotrema vincentiana 6
Aptychotrema vincentiana 7
Aptychotrema vincentiana 5
Pagrus auratus 9
G
Spratelloides robustus 1
Atherinomorus ogilbyi 1
Sillago bassensis 1
H
Pseudocaranx wrighti 1
Pseudocaranx wrighti 2
Rhabdosargus sarba 3
Upeneichthys lineatus 2
I
Ammotretis elongatus 1
Pseudocaranx georgianus 2
J
Upeneichthys stotti 1
K
Atherinomorus ogilbyi 2
L
Urolophus paucimaculatus 3
Trygonoptera personata 2
Trygonoptera personata 3
M
Lesueurina platycephala 1
Upeneichthys stotti 2
N
Pempheris klunzingeri 2
Urolophus paucimaculatus 2
Parapriacanthus elongatus 1
Parapriacanthus elongatus 2
Pempheris klunzingeri 1
Urolophus lobatus 2
Urolophus lobatus 3
Lepidotrigla modesta 1
Lepidotrigla modesta 2
Lepidotrigla papilio 1
Lepidotrigla papilio 2
O
Sillago vittata 1
Sillaginodes punctata 1
Sillago burrus 1
Sillago schomburgkii 1
P
Sillago robusta 2
Sillago bassensis 2
Sillago schomburgkii 3
Sillaginodes punctata 3
Sillaginodes punctata 2
Sillago schomburgkii 2
Parequula melbournensis 1
Parequula melbournensis 2
Q
Sillaginodes punctata 4
Sillago schomburgkii 4
Trygonoptera mucosa 2
Trygonoptera mucosa 3
Trygonoptera mucosa 4
Sillago vittata 2
Sillago burrus 3
Sillago burrus 2
Sillago bassensis 3
Sillago vittata 3
100
80
60
40
20
0
Similarity (%)

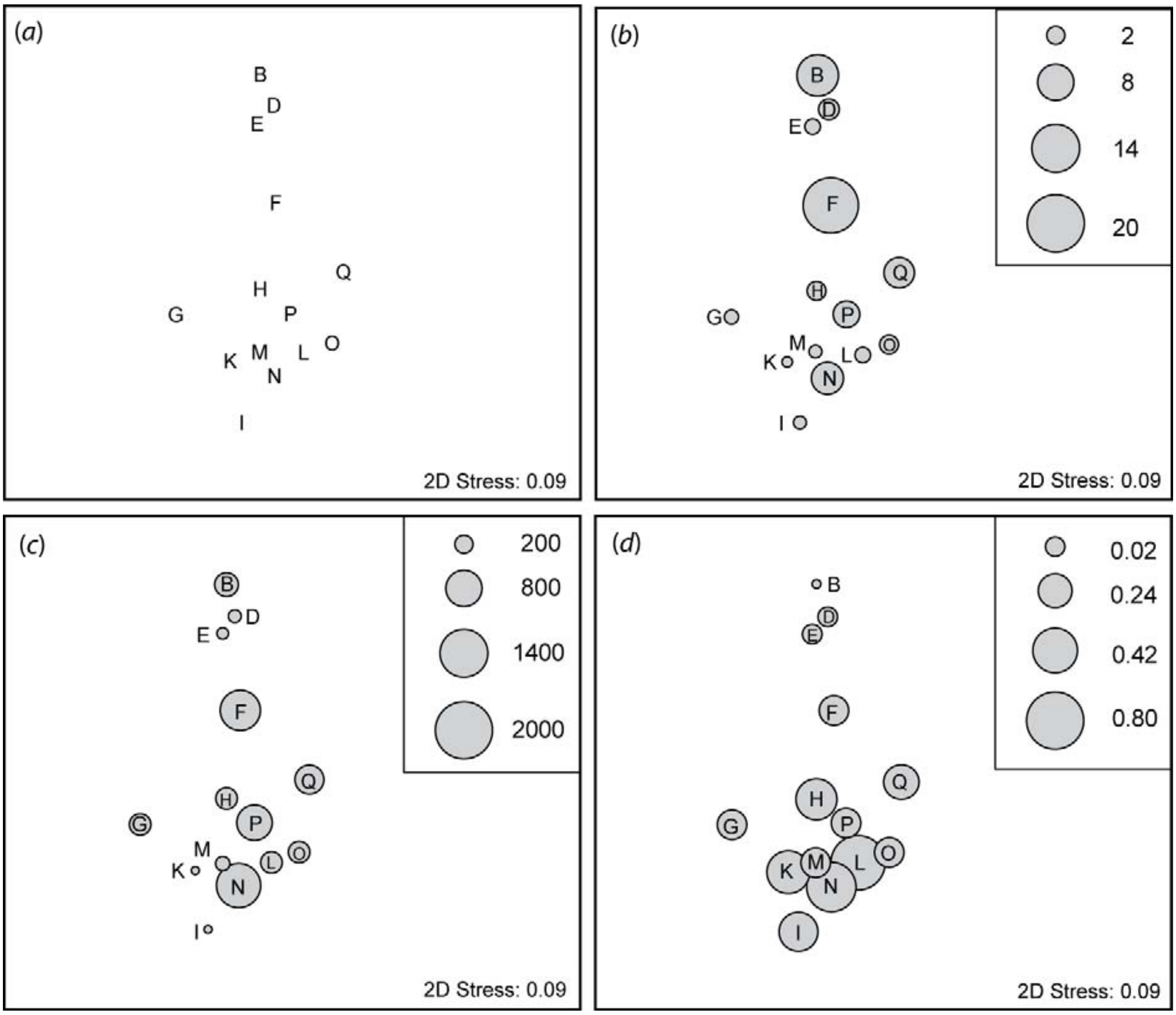


Figure 7.9 Centroid nMDS ordination plots of predator guilds, derived from a Bray-Curtis matrix of the volumetric contributions of the prey taxa to each 'sample' (species x length class combination) within the various predator guilds (a) and with the bubbles superimposed on the points for each predator guild being proportional to (b) the number of species x length class combinations representing each guild, (c) the total number of guts examined for each guild and (d) Simpson's diversity index for each guild.

Table 7.5 The predator guilds identified among the 35 demersal fish species by SIMPROF, together with their typifying prey taxa and the percentage contributions made by each of those categories to the average similarity of the dietary composition of each predator guild (as identified by SIMPER). Note that each predator guild comprises groups of species x length class combinations. Length classes in mm are as follows. 1 = <100, 2 = 100-199, 3 = 200-299, 4 = 300-399, 5 = 400-499, 6 = 500-599, 7 = 600-699, 8 = 700-799, 9 = 800-899 and 10 = 900-999.

Predator species	Length class (mm)	Predator guild	Prey taxa	Percentage similarity contribution
Aptychotrema vincentiana	10	B	Teleostei	97
Epinephelides armatus	3-5			
Glaucosoma hebraicum	4,7-9			
Heterodontus portusjacksoni	3,9			
Squatina australis	3-10			
Aptychotrema vincentiana	8,9	D	Teleostei	62
Epinephelides armatus	2		Other Decapoda	37
Heterodontus portusjacksoni	4,10			
Pagrus auratus	6	E	Teleostei	67
Glaucosoma hebraicum	5,6		Other Decapoda	22
Aptychotrema vincentiana	3-7	F	Other Decapoda	67
Bodianus frenchii	2-5		Teleostei	18
Glaucosoma hebraicum	1,2			
Heterodontus portusjacksoni	7			
Maxillicosta scabriceps	1,2			
Myliobatis australis	2-5,7			
Pagrus auratus	1-3,7-9			
Platycephalus longispinis	2,3			
Pseudocaranx georgianus	3-5			
Pseudorhombus jenynsii	1,2			
Rhabdosargus sarba	2			
Upeneichthys lineatus	3			
Sillaginodes punctata	4	Q	Sedentaria	40
Sillago bassensis	3		Errantia	31
Sillago burrus	2,3			
Sillago schomburgkii	4			
Sillago vittata	2,3			
Trygonoptera mucosa	2-4			
Pseudocaranx wrighti	1,2	H	Other Decapoda	37
Rhabdosargus sarba	3		Amphipoda	23
Upeneichthys lineatus	2		Tanaidacea	20

Table 7.5 cont on next page

Predator species	Length class (mm)	Predator guild	Prey taxa	Percentage similarity contribution
Parequula melbournensis	1,2		Amphipoda	40
Sillaginodes punctata	2,3		Errantia	31
Sillago bassensis	2			
Sillago robusta	2			
Sillago schomburgkii	2,3			
Atherinomorus ogilbyi	1	G	Calanoida	69
Sillago bassensis	1		Amphipoda	14
Spratelloides robustus	1		Cladocera	11
Sillaginodes punctata	1	O	Harpacticoida	48
Sillago burrus	1		Errantia	19
Sillago schomburgkii	1		Amphipoda	16
Sillago vittata	1			
Lesueurina platycephala	1	M	Amphipoda	39
Upeneichthys stotti	2		Mysidacea	21
			Cumacea	14
			Isopoda	12
Trygonoptera personata	2,3	L	Errantia	25
Urolophus paucimaculatus	3		Amphipoda	20
			Caridea	19
			Sedentaria	14
			Mysidacea	13
Atherinomorus ogilbyi	2	K	Amphipoda	85
Lepidotrigla modesta	1,2	N	Mysidacea	31
Lepidotrigla papilio	1,2		Amphipoda	27
Parapriacanthus elongatus	1,2		Cumacea	14
Pempheris klunzingeri	1,2		Caridea	11
Urolophus lobatus	2,3			
Urolophus paucimaculatus	2			
Ammotretis elongatus	1	I	Cumacea	56
Pseudocaranx georgianus	2		Amphipoda	44

The use of SIMPER demonstrated that the typifying prey taxa of the guilds at the top of Table 7.5 (B, D and E) comprise the largest prey, i.e. teleosts and other decapods (mainly brachyuran crabs), whereas those of predator guilds at the bottom of that table comprise the smaller prey, such as cumaceans, amphipods and mysids. The data in Table 7.5 also emphasise that the predator guild of the larger species can change markedly and progressively with increasing body size. This phenomenon is exemplified by *P. georgianus,* with its predator guild shifting from I for its smaller individuals, to F, near the top for its largest individuals (Table 7.5).

Bubbles, whose sizes represent the magnitude of the values for Simpson's Diversity Index, were superimposed on the points for the predator guilds in the ordination plot shown in Fig. 7.9a (Fig. 7.9d). The trends exhibited by bubble size demonstrated that the diets were less diverse for predator guilds in the upper part of the plot (B, D, E and F), which represented the larger individuals of the larger fish species, than for all of those in the lower part of the plot and sometimes markedly so (guilds I, N, L and K) and which represented the smaller individuals of large species and the smaller fish species. The apparent pattern of increase in bubble size from top to bottom of the ordination plot is statistically established by the RELATE test between the (Bray-Curtis) resemblance matrix for diets of the predator guilds and the (Euclidean) distances between Simpson diversity values, which gives a matrix correlation of $\rho = 0.32$, $P < 1\%$.

7.2.2 Identifying prey guilds and their relationships to predator guilds

Cluster analysis of the volumetric contribution of each prey taxon to the diets of each predator guild, expressed as a percentage of the total volumetric consumption of that prey taxon by all predator guilds collectively, allied with the use of SIMPROF, yielded 12 groups (a-l) whose compositions were significantly different from each other in a series of 5% level tests (Fig. 7.10). Some prey guilds comprised relatively similar types of prey. For example, all groups of insects were located in prey guild c, all cephalopods and teleosts in guild g, and guild l contained one cluster comprising small epibenthic crustaceans, e.g. cumaceans, amphipods and mysids etc., and another the two main groups of polychaetes, i.e. Errantia and Sedentaria (Fig. 7.10).

On the centroid ordination plot, derived from the same data as employed for the above cluster analysis, the points for prey guilds e, f, d and g lie at the top, those for h, j, k and l in the middle and those for i, c and b at the bottom, with prey guild a lying far to the left (Fig. 7.11). At one extreme, prey guilds e, f and d comprised the largest of the sedentary prey that were consumed by the 35 fish species, e.g. spatangoid echinoderms and archaeogastropod and mytiloid molluscs, whereas, at the other extreme, prey guilds i, c and b comprised small planktonic crustaceans and insect larvae.

The patterns displayed by the line plots in Fig. 7.12 emphasise that the relationships between the percentage consumption of each prey taxon within each prey guild are similar. Thus, the prey taxa in prey guilds e and f were consumed very largely only by one or both of predator guilds E and F, whereas those in prey guilds c and b were ingested almost exclusively by one or both of predator guilds G and K, which, in these cases, comprised the small individuals of sillaginid species and the small species *Atherinomorus ogilbyi* and *Spratelloides robustus* (Table 7.5, Fig. 7.12). In contrast, prey guild l was consumed by a wide range of predator guilds.

7.2.3 Food webs

Some trophic interactions can be clearly identified between certain predator and prey guilds in the food web shown in Fig. 7.13, and particularly at the top and bottom of that web. Thus, for example, the thickness of the lines relating predator guild B with the various prey guilds emphasise that the members of this guild feed predominantly on prey guild g and likewise the members of predator guild I feed largely on members of prey guild l. The trophic relationships are far more difficult to detect, however, in the middle part of the food web, where there is extensive criss-crossing of lines between many of the predator and prey guilds (Fig. 7.13).

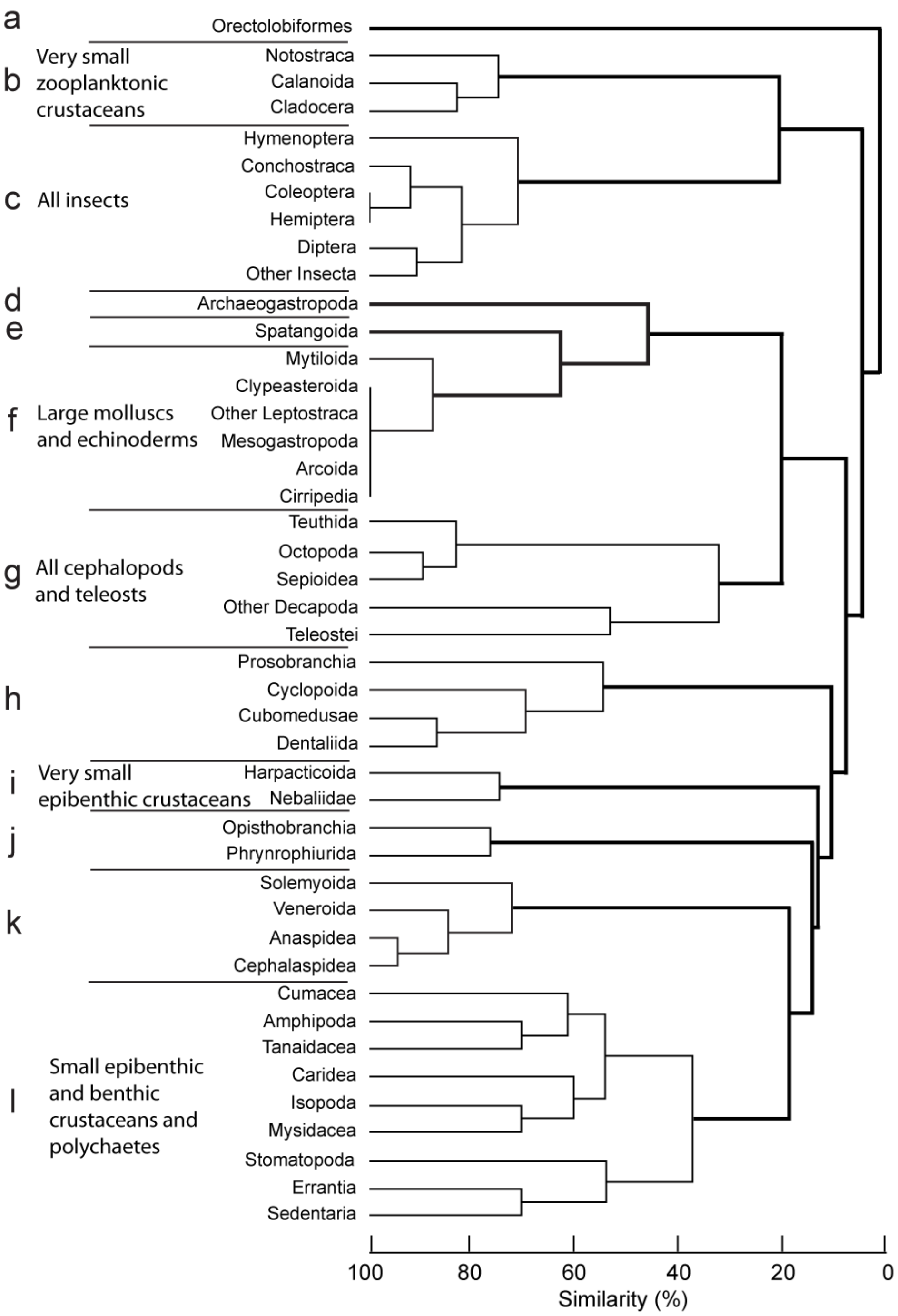


Figure 7.10 ‘R-mode’ cluster dendrogram of prey taxa, derived from the Bray-Curtis ‘species’ similarity matrix constructed from the standardised (percentage) volumetric contribution of each prey taxa to the predator guilds. The thick lines designate the prey taxa that were separated by SIMPROF into a series of prey groups whose members did not exhibit a significantly different internal pattern of contributions across the predator guilds and were thus considered to constitute prey guilds.

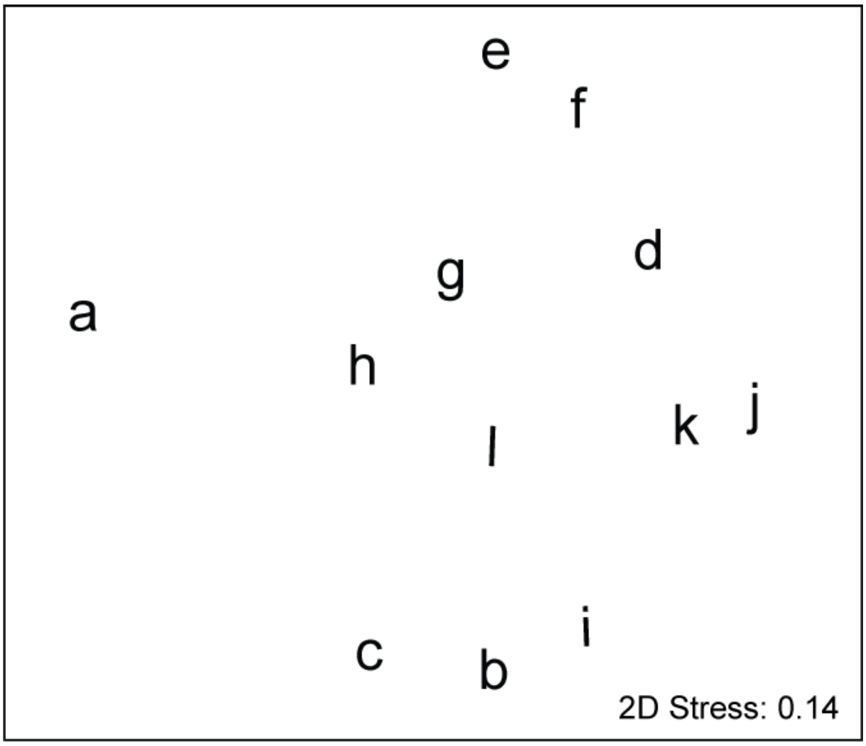


Figure 7.11 Centroid nMDS ordination plot of prey guilds, derived (as in Fig. 7.10) from the Bray-Curtis matrix of the standardised volumetric contribution of each prey taxa to the diets of each predator guild. See Fig. 7.11 for a list of the prey taxa that comprise each prey guild.

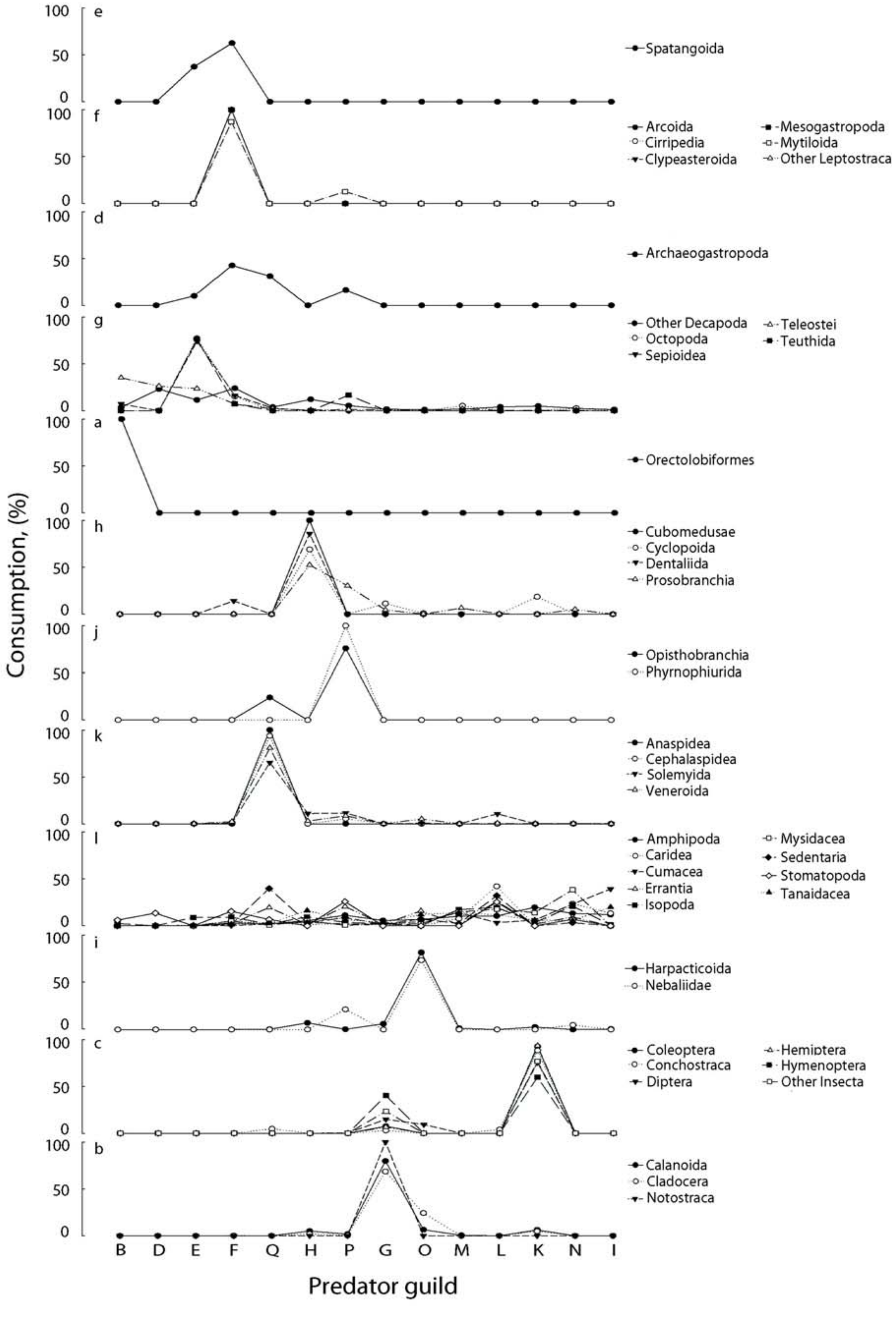


Figure 7.12 Line plots showing the pattern of consumption of each prey taxon, relative to its total consumption, across the 14 predator guilds. The predator and prey guilds are both listed according to their order on the vertical axes of their respective nMDS ordination plots (see Figs 7.9a and 7.11).

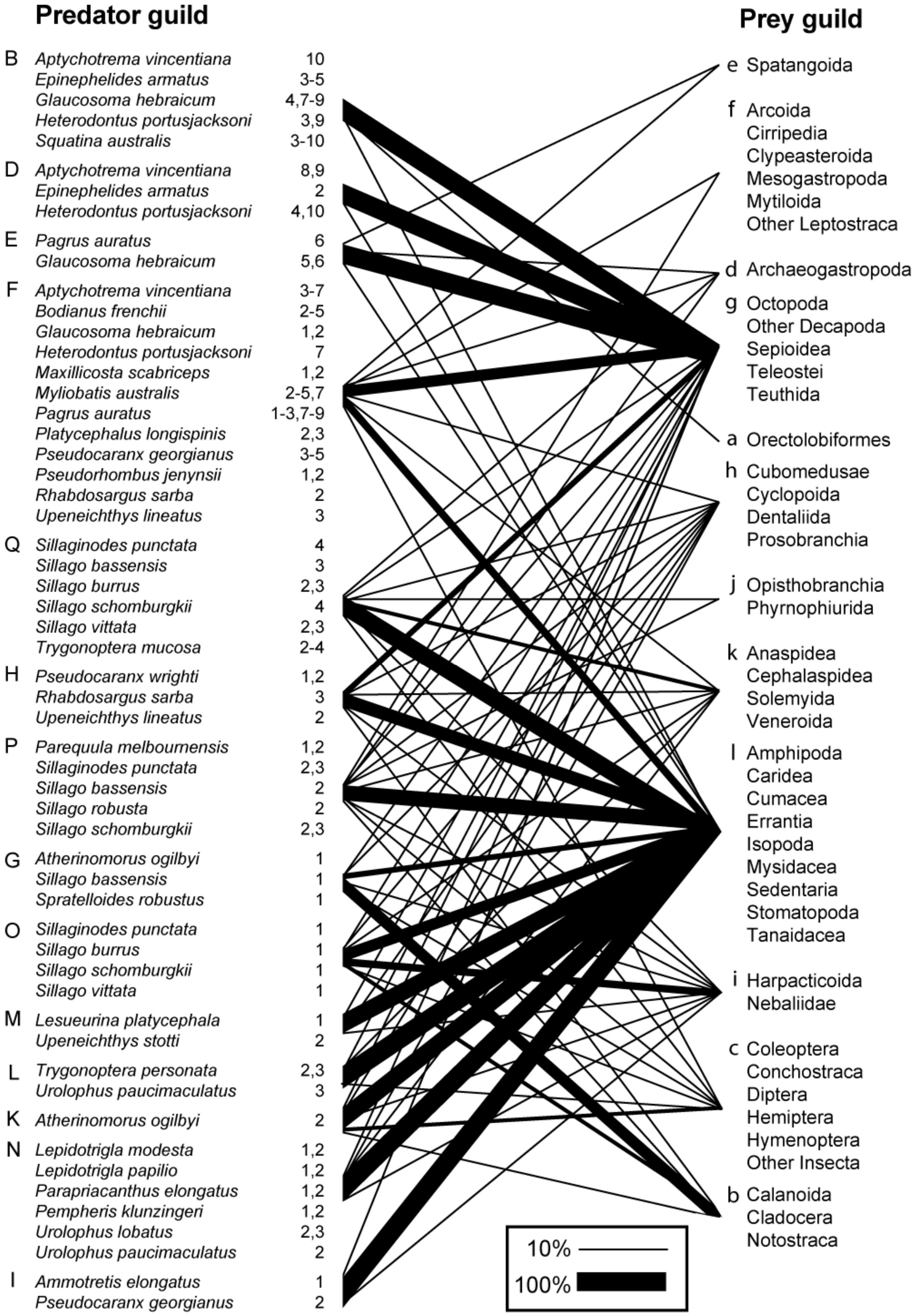


Figure 7.13 Traditional food web showing the trophic linkages between the predator and prey guilds. The thickness of the links represent the relative strengths of the relationships.

The colour of the shading for the relationship between each predator guild and prey guild in the shade plot shown in Fig. 7.14 reflects the magnitude of the interaction between those two guilds, with the predator and prey guilds each being arranged in the sequences designated by the results of the ordinations described earlier and shown in Figs 7.9a and 7.11, respectively. The trends emphasise that the extent of the interaction between the prey guilds and the predator guilds broadly shifts in a diagonal direction from top left to bottom right of the plot. Fig. 7.14 also illustrates very clearly that some prey, such as those belonging to g and l, are consumed by the members of all predator guilds, whereas others, such as those representing e, f and a, are ingested by only one or two predator guilds. Furthermore, prey guilds h and k are fed on by predators in the centre of the hierarchy. The plot also emphasises that predator guilds such as B and I fed on only three prey guilds, whereas, at the other extreme, predator guild P fed on a wide spectrum of prey guilds (Fig. 7.14).

Prey guild

e Spatangoida

f Arcoida
Cirripedia
Clypeasteroida
Mesogastropoda
Mytiloida
Other Leptostraca

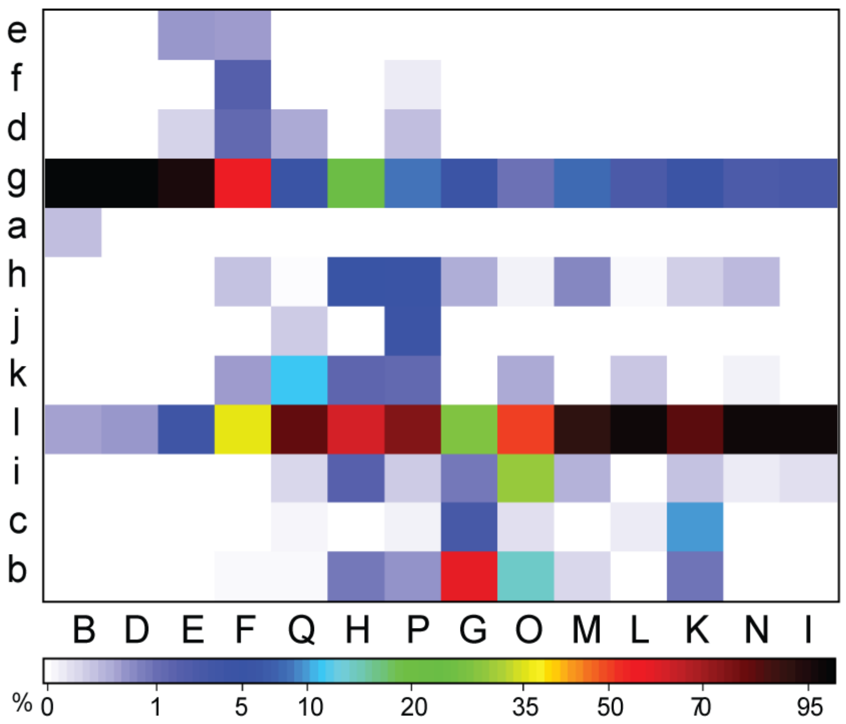
d Archaeogastropoda

g Octopoda
Other Decapoda
Sepioidea
Teleostei
Teuthida

a Orectolobiformes

h Cubomedusae
Cyclopoida
Dentaliida
Prosobranchia

j Opisthobranchia
Phyrnophiurida



Prey guild

k Anaspidea
Cephalaspidea
Solemyida
Veneroida

l Amphipoda
Caridea
Cumacea
Errantia
Isopoda
Mysidacea
Sedentaria
Stomatopoda
Tanaidacea

i Harpacticoida
Nebaliidae

c Coleoptera
Conchostraca
Diptera
Hemiptera
Hymenoptera
Other Insecta

b Calanoida
Cladocera
Notostraca

Predator guild

B	*Aptychotrema vincentiana*	10
	Epinephelides armatus	3-5
	Glaucosoma hebraicum	4,7-9
	Heterodontus portusjacksoni	3,9
	Squatina australis	3-10
D	*Aptychotrema vincentiana*	8,9
	Epinephelides armatus	2
	Heterodontus portusjacksoni	4,10
E	*Pagrus auratus*	6
	Glaucosoma hebraicum	5,6

Predator guild

F	*Aptychotrema vincentiana*	3-7
	Bodianus frenchii	2-5
	Glaucosoma hebraicum	1,2
	Heterodontus portusjacksoni	7
	Maxillicosta scabriceps	1,2
	Myliobatis australis	2-5,7
	Pagrus auratus	1-3,7-9
	Platycephalus longispinis	2,3
	Pseudocaranx georgianus	3-5
	Pseudorhombus jenynsii	1,2
	Rhabdosargus sarba	2
	Upeneichthys lineatus	3
Q	*Sillaginodes punctata*	4
	Sillago bassensis	3
	Sillago burrus	2,3
	Sillago schomburgkii	4
	Sillago vittata	2,3
	Trygonoptera mucosa	2-4

H	*Pseudocaranx wrighti*	1,2
	Rhabdosargus sarba	3
	Upeneichthys lineatus	2
P	*Parequula melbournensis*	1,2
	Sillaginodes punctata	2,3
	Sillago bassensis	2
	Sillago robusta	2
	Sillago schomburgkii	2,3
G	*Atherinomorus ogilbyi*	1
	Sillago bassensis	1
	Spratelloides robustus	1
O	*Sillaginodes punctata*	1
	Sillago burrus	1
	Sillago schomburgkii	1
	Sillago vittata	1

Predator guild

M	*Lesueurina platycephala*	1
	Upeneichthys stotti	2
L	*Trygonoptera personata*	2,3
	Urolophus paucimaculatus	3
K	*Atherinomorus ogilbyi*	2
N	*Lepidotrigla modesta*	1,2
	Lepidotrigla papilio	1,2
	Parapriacanthus elongatus	1,2
	Pempheris klunzingeri	1,2
	Urolophus lobatus	2,3
	Urolophus paucimaculatus	2
I	*Ammotretis elongatus*	1
	Pseudocaranx georgianus	2

Figure 7.14 A shade plot showing the relative magnitudes of the trophic linkages between the predator and prey guilds, with the total consumption of all members of prey guild ‘x’ making up percentage *p* of the diet of the average member of predator guild ‘X’, where the colour shading represents the value of *p* (see colour legend), ranging from *p*=0 (white) to *p*=100% (black).

8. DISCUSSION

8.1 RANKING OF LENGTH-CLASS, SEASONAL AND REGIONAL EFFECTS ON DIETARY COMPOSITIONS OF THE CO-OCCURRING PAGRUS AURATUS *(SPARIDAE) AND* PSEUDOCARANX GEORGIANUS *(CARANGIDAE)*

8.1.1 Influence of body size and season on the dietary composition of Pagrus auratus

The $\bar{R}$-statistic values in a two-way crossed ANOSIM test, using data for the wide size range of *Pagrus auratus* collected from the lower west coast of Australia, demonstrate that the dietary composition of this sparid was strongly related to both body size (length class) and season in this region, with the former factor having a slightly greater influence. These size-related changes were largely driven by a very pronounced and progressive shift in the size and type of prey from small ophiuroid echinoderms (brittle stars) by the smallest individuals to substantial consumptions of brachyuran crabs, teleosts and echinoid echinoderms (sea urchins) and ultimately also asteroid echinoderms (starfish) by the largest individuals. The ingestion of very large amounts of small and slow-moving ophiuroids by small *P. auratus* contrasts with the situation elsewhere, with these echinoderms never being found in the gut contents of such *P. auratus* in a gulf in South Australia (Saunders et al., 2012) and only occasionally in a gulf and estuary in New Zealand (Colman, 1972; Usmar, 2011).

The above comparisons imply that, on the lower west coast of Australia, ophiuroids are either especially abundant and/or there is a shortage of alternative prey for this size class of *P. auratus*. Elsewhere, the dominant prey taxa of small *P. auratus* were polychaetes and, to a lesser extent, small teleosts and various crustaceans (particularly brachyuran crabs) in a south Australian gulf (Saunders et al., 2012), polychaetes, mysids and amphipods in a New Zealand gulf (Colman, 1972) and carideans, mysids and crabs in a New Zealand estuary (Usmar, 2011). These comparisons strongly suggest that small *P. auratus* are readily able to adjust their feeding behaviour to target the most available prey in their environment, a form of “opportunism” characteristic of the Sparidae (Mariani et al., 2002; Chuwen et al., 2007).

Ophiuroids are abundant in Cockburn Sound (Marsh, 1978), where the majority of the small *P. auratus* were caught, and also over soft substrata in the waters of eastern Tasmania, where they likewise make a large contribution to the diet of two of the fish species studied in that environment (Blaber and Bulman, 1987; Blaber et al., 1987). Although brittle stars have a relatively low calorific value (Blaber et al., 1987), their high abundance over sand and hard structures in some waters (Shepherd and Thomas, 1982a) implies that they still potentially provide a substantial food source for fish species in those waters (Blaber et al., 1987; Packer et al., 1994). Furthermore, as their arms possess contrasting bands of colour (Edgar, 2008) and are “upraised and moving” when feeding, they would be particularly visible and accessible to fish predators (Blaber et al., 1987). As potential alternative prey for small *P. auratus*, e.g. polychaetes and amphipods, are relatively abundant in Cockburn Sound (Oceanica, 2007), it is proposed that brittle stars are targeted by small snapper in Cockburn Sound, because those echinoderms would be particularly visible in the turbid waters of this embayment. From this and the previous comparisons, it could also be inferred that the smaller individuals of *P. auratus* are also feeding to a large extent on the prey that occur over soft substrata (see also Saunders et al., 2012),

Although, on the lower west coast of Australia, the increased ingestion of teleosts and crabs by *P. auratus,* as this predator increases in size, parallels that recorded for this sparid in a gulf and estuary in New Zealand, the other major prey of the larger fish in these regions differ conspicuously in some respects (Colman, 1972; Usmar, 2011). Thus, whereas the stomach contents of medium-sized *P. auratus*, i.e. 300-599 mm TL, on the lower west coast of Australia contained substantial volumes of sea urchins, these echinoderms were either rarely or never ingested by *P. auratus* of that size in those New Zealand waters (Colman, 1972; Usmar, 2011). As large starfish, such as *Astropecten preissei,* were only ingested by the larger fish on the lower western Australian coast, i.e. >600 mm (which exceeded the length of *P. auratus* in the two New Zealand water bodies), these echinoderms represent the culmination of the size-related changes in diets in those waters. While a pronounced and progressive size-related shift towards the consumption of larger and/or more robust prey is characteristic of a wide range of other sparids in different environments throughout the world (e.g. Tancioni et al., 2003; Platell et al., 2007; Santic et al., 2010, 2011), the ingestion of substantial volumes of both starfish and sea urchins by *P. auratus* on the lower west coast of Australia is atypical for a sparid.

Although the overall dietary composition of *P. auratus* on the lower west coast changed with season, these changes were largely attributable to those exhibited by smaller fish and due, in particular, to the consumption of relatively greater volumes of ophiuroids in summer and autumn than in winter and spring. These seasonal changes are consistent with the fact that, elsewhere, the abundance of ophiuroids alters markedly with season, due to their recruitment varying as a result of spawning peaking at a particular time of the year and/or to migratory movements (Packer et al., 1994; Hinz et al., 2004). In contrast to the situation on the lower west coast, the diets of medium and large *P. auratus* on the mid west coast underwent conspicuous seasonal changes. The relatively greater consumption of brachyuran crabs by these *P. auratus* in winter and spring than in summer and autumn may be due to the 0+ age class *Portunus armatus* (Brachyura) in Western Australia having reached a sufficiently large size by the former seasons to provide a suitable food source (Potter et al., 1983). Seasonal differences in the diets of the co-occurring *Pagellus erythrinus* and *Pagellus acarne* and of another sparid *Lithognathus mormyrus* in the Mediterranean were also considered to be related, at least in part, to seasonal changes in prey abundance (Kallianiotis et al., 2005; Fanelli et al., 2011).

8.1.2 Influence of body size and season on the dietary composition of Pseudocaranx georgianus

Two-way crossed ANOSIM tests demonstrated that, while the diet of *Pseudocaranx georgianus* was influenced significantly by length class ($\bar{R}$=0.20) and not season ($\bar{R}$=0.05) on the lower west coast, the reverse was true for the south coast, with the $\bar{R}$-statistic for length class being only 0.13, whereas that for season was 0.49. The largely progressive shift in the points for the dietary compositions of successive length classes of *P. georgianus* on the ordination plots for the lower west coast (Figs 7.5, 7.7) and the results of the RELATE procedure (ρ=0.75, *P*=0.8%) demonstrate that the diet of this carangid changes in a mainly sequential manner with increasing body size. This represents a shift from the consumption of small benthic prey, such as isopods, carideans and small bivalve molluscs, to larger prey such as small crabs and small teleosts, a trend that largely follows that exhibited by another carangid, *Caranx bucculentus* (Brewer et al., 1989).

Although the trends exhibited by the points on the ordination plot in Fig. 7.5 indicated that the dietary composition of *P. georgianus* on the south coast also changed progressively with increasing body size, the dietary categories responsible for that trend differed markedly from those on the lower west coast. Thus, on the south coast, it reflected in particular, a decline in the importance of isopods, amphipods and cephalopods and an increase in the importance of crabs rather than teleosts. This regional difference presumably reflects a combination of differences in the relative abundances of the potential prey of this species on the two coasts and the ability of *P. georgianus* to feed opportunistically. The corresponding $\bar{R}$-statistic value for length class for the south coast was even lower (0.13) than for the lower west coast, suggesting that such opportunistic behaviour may be even more pronounced on this coast.

The small *P. georgianus*, i.e. <220 mm TL, correspond to the length range of the morphologically very similar but far smaller *Pseudocaranx wrighti*, with which it co-occurs on the lower west coast of Australia (Hyndes et al., 1999). The consumption by the smaller *P. wrighti,* i.e. <160 mm, of substantial volumes of mysids, copepods and zoeae/megalopae (Platell et al., 1997), imply that these *P. wrighti* feed within the water column and thus, in this respect, differ from those of *P. georgianus*, which, when of that size, feed predominantly on prey associated with the substrate. As it increases to its maximum size, *P. wrighti* ingests substantial amounts of polychaetes and echinoderms (Platell et al., 1997), dietary categories that were not ingested by *P. georgianus* of comparable size. There is thus a very conspicuous partitioning of food resources among these co-occurring and abundant congeners.

The marked seasonal changes in the dietary composition of *P. georgianus* on the south coast were due largely to a marked increase in the ingestion of amphipods during summer, which implies that the abundance of these invertebrates increases greatly in that season. Such a conclusion is consistent with the flatfish *Buglossidium luteum* feeding to a greater extent on amphipods in summer, which coincided with the numbers of this prey increasing in the benthos (Schückel et al., 2011). The lack of a seasonal change in the diet of *P. georgianus* on the lower west coast presumably reflects a less pronounced increase in the relative abundances of amphipods and/or less marked seasonal differences between the abundances of other prey sources.

8.1.3 Regional comparisons of dietary compositions of Pagrus auratus *and* Pseudocaranx georgianus

The main dietary categories consumed by the medium and large sized *P. auratus* on the lower west and mid west coasts were shown to be the same, and the Teleostei was the main typifying dietary category for this sparid on both coasts. However, the $\bar{R}$-statistic value of 0.30 for region in the ANOSIM comparisons between region and season, demonstrates that the dietary compositions of this species in these two regions were conspicuously different, although this difference was not as pronounced as the overall seasonal effect, for which the $\bar{R}$-statistic was 0.50. The regional difference was due, in particular, to relatively greater dietary contributions by both *Echinocardium cordatum* and other echinoids and a narrower range of prey on the mid west than lower west coast, presumably reflecting differences in the compositions of the potential prey in the two regions.

The above conspicuous regional differences in the diet of *P. auratus*, together with the seasonal changes in particularly the diet of the smaller individuals on the lower west coast, imply that this species is able to respond effectively to changes that arise through spatial and temporal differences in potential prey. In this context, certain sparid species in the Mediterranean can exhibit a generalist feeding behaviour in one locality and yet focus on a small suite of prey in another locality where the range of prey is presumably far more restricted (Mariani et al., 2002). In a large gulf in Australia, the feeding of 0+ snapper likewise varied within a large gulf which is considered to reflect differences in prey availability (Saunders et al., 2012). Furthermore, certain sparids can even consume large amounts of macrophytes, and their associated epiphytes, when such plant material is abundant, and yet in some cases are carnivorous in other localities (cf Blaber, 1974; Whitfield, 1980; Sarre et al., 2000; Chuwen et al., 2007; Sheppard et al., 2012).

The marked regional differences between the major dietary taxa of *P. georgianus* on the lower west coast (mainly teleosts, crabs, carideans and small gastropods) and south coast (mainly isopods, amphipods, bivalves and cumaceans) contrasts markedly with the lack of any such regional difference with the labrid *B. frenchii* (Platell et al., 2010). This implies that the type of prey ingested by *P. georgianus* varies to a greater degree in response to variations in the abundances of potential prey, and is thus more opportunistic in its feeding behaviour, than *B. frenchii*.

8.1.4 Comparisons between the dietary compositions of co-occurring Pagrus auratus *and* Pseudocaranx georgianus *on the lower west coast*

The global $\bar{R}$-statistic of 0.51 for the comparison between the dietary compositions of *P. auratus* and *P. georgianus* on the lower west coast of Australia is substantially greater than the corresponding overall value of 0.35 for length class and even more particularly the 0.19 for season. This emphasises that, when those species co-occur on that coast, their diets differ markedly, a feature due, overall, to a relatively greater or exclusive ingestion of ophiuroids (brittle stars), asteroids (starfish) and *E. cordatum* (heart urchins) by *P. auratus* and the reverse trend for littorinids (small gastropods), other echinoids (other sea urchins), amphipods and carideans (shrimps). There is, however, a marked overlap in the suite of dietary categories ingested by both of these carnivorous predators, a feature emphasised by the fact that crabs and teleosts were among the most important typifying dietary categories in the stomach contents of both species.

From the above, it is evident that the prey of *P. auratus* comprises a number of taxa that possess either hard and/or protective shells/exoskeletons, e.g. large crabs and sea urchins, or are structurally robust, e.g. starfish. However, as these prey are represented in the gut contents by clearly identifiable small or large fragments, they are initially broken into smaller components which thereby helps them to be ingested. This process is facilitated by the possession of prominent canines for seizing the prey and two rows of strong, rounded molariform teeth on both the upper and lower jaws (Fig. 7.1a-d) to crush the prey through employing a jaw-lever mechanism, which maximises the biting force applied to the jaw (Wainwright and Richard, 1995).

In contrast to *P. auratus,* the diet of *P. georgianus* comprises a greater volume of prey that tend to be smaller, e.g. amphipods, cumaceans, ostracods, small gastropods and small crabs, which is reflected in the presence of far smaller teeth and weaker oral jaws (Fig. 7.1e-h). The weakness of the oral jaws is partly compensated for, however, by the possession of robust and rounded teeth on its pharyngeal jaws, which enables small hard-shelled organisms to be crushed. Thus, *P. auratus* belongs to the feeding category designated by Wainwright and Richard (1995) as biters, whereas *P. georgianus* is essentially a suction feeder.

In summary, the combined use of ANOSIM, MDS ordination and the RELATE procedure demonstrates that the dietary compositions of *P. auratus* and *P. georgianus* were invariably influenced significantly by body size (length class) and region and, with the exception of *P. georgianus* on the lower west coast, also by season. However, the extents and rank orders of those influences differ between those two carnivorous species, while the seasonal effect can be restricted to fish of a certain size range. Furthermore the dietary compositions of these two species differed conspicuously between regions and markedly so in the case of *P. georgianus*. The results imply that *P. auratus* and *P. georgianus* are, to a certain extent, opportunistic feeders, which would account for the success of these species in different regions and, in turn, suggest that they would be relatively resistant to at least any moderate changes in prey composition brought about by anthropogenic effects, including climate change. Furthermore, although some prey are common to both *P. auratus* and

P. georgianus, their dietary compositions are demonstrably distinct when these species co-occur and are abundant, thereby reducing the potential for competition for food resources. The results and comparisons emphasise the need for caution when attempting to extrapolate regarding the extent of the influence of the above factors on dietary compositions on fish species in general.

8.2 AN INNOVATIVE STATISTICAL APPROACH TO CONSTRUCTING A READILY COMPREHENSIBLE FOOD WEB FOR A DEMERSAL FISH COMMUNITY

8.2.1 Relationships between predator guilds and prey taxa

This study has used a range of statistical analyses and approaches to develop a food web that can readily be used by scientists and managers to understand the strengths of the relationships between a suite of abundant demersal fish predators and their prey in a coastal ecosystem. The construction of this sound food web was facilitated by the availability of comprehensive quantitative dietary data for a wide size range of 35 demersal fish species caught seasonally on the lower west coast of Australia. The employment of the recently-developed SIMPROF technique (Clarke et al., 2008) enabled the predator and prey guilds to be identified statistically and without any a priori hypotheses, with the prey guilds being identified using an innovative version of this SIMPROF test. The use of nMDS ordination enabled the hierarchical structure of both the predator and prey guilds to be determined objectively and thus facilitate the matching of the components of those two hierarchies in the form of a shade plot, which illustrates, in an effective and visual manner, the magnitudes of the relationships between each predator guild and prey guild. It is recognised that this shade plot focuses on those relationships and does not incorporate data for lower levels in the food web, i.e. the relationships between primary consumers and primary producers.

The statistical identification of those fish species x length class combinations, whose diets were similar and differed from other such combinations, reduced the number of such combinations in the data matrix (112) to a far more manageable number of predator guilds (14), while retaining the resolution required for making meaningful dietary comparisons. The construction of these predator guilds was thus not subjective and avoided the ad hoc methods, which, as pointed out by Luczkovich et al. (2002), have frequently been used to aggregate predators into trophic guilds. While the type of boot-strapping approach developed by Jaksic and Medel (1990), and used by Garrison and Link (2000) in their dietary studies, also provides an objective method for distinguishing between dietary groups, it produces only a single cut off for the full data set, whereas the use of cluster analysis with SIMPROF has the advantage of testing for significance between the different species x length class combinations that represent the various nodes within the dendrogram.

It was particularly striking that, when the centroids of the dietary data for the predator guilds were subjected to nMDS ordination, the main axis of those guilds was aligned on the ordination plot from the larger individuals of the largest fish species at one extreme and the smaller individuals of the larger species and all individuals of the smallest species at the other. When that main axis was aligned to the vertical, the composition of the prey changed progressively from those of the larger predators at the top of the plot to those of the smaller predators at the bottom of the plot, thereby constituting a trophic hierarchy. The larger individuals of the fish predators tended to feed predominantly on other teleosts and other large prey, such as members of the Decapoda, and, in particular, brachyuran crabs, while small fish ingested a wide range of small crustaceans, including amphipods, mysids, cumaceans and carideans (see Platell et al., 1997, 1998a,b; 2010; Platell and Potter, 1998, 1999, 2001; Sommerville et al., 2011; French et al., 2012 for comprehensive dietary data for the separate species). This trend was reflected in an increase in the diversity of the diet from the top to the bottom of the hierarchy.

The hierarchical arrangement of the predator guilds, in combination with the distribution of the length class groups for each predator species within those guilds, demonstrates that, as several species of predator increase in body size, they progress sequentially upwards by at least one guild in the trophic hierarchy and sometimes far more (Table 7.5). A particularly extreme example is provided by the carangid *P. georgianus*, which belongs to predator guild I when small and thus feeds mainly on cumaceans and amphipods, and to predator guild F when large and therefore feeds predominantly on other decapods (mainly brachyurans) and teleosts. It was also noteworthy that the two largest of the six sillaginids, *Sillaginodes punctata* and *Sillago schomburgkii*, underwent a similar progressive upward shift in the trophic hierarchy from predator guild O when small to guild P when of moderate size and finally to Q when large. Thus, the most important typifying prey taxa were initially harpacticoid crustaceans, and then amphipod crustaceans and finally sedentary polychaetes with the largest individuals (Table 7.5). These size-related shifts in the main prey taxa of large species from one predator guild to one or more further guilds would reduce the potential for intra-specific competition for food resources by these species. This conclusion parallels that drawn by exploring the trends exhibited by the diets of individual species as they increase in size (Hyndes et al., 1997; French et al., 2012), recognising that, in the case of *S. punctata*, such competition would also be reduced by the tendency for larger fish to move into deeper waters and around reefs (Hyndes et al., 1998), a movement pattern exhibited by numerous fish species.

In contrast to the above trends, some larger species, such as *Myliobatis australis* and *Bodianus frenchii*, remained throughout life in the same predator guild (F) and the same was very largely true for *P. auratus,* with the typifying prey species of this guild comprising other decapods (mainly brachyurans) and teleosts. This lack of distinction between the predator guilds for the various length classes of these large fish species is considered valid because the number of prey taxa used was substantial (44). Indeed, that number, although similar to that of a recent compilation of dietary data for 76 fishes in north-western Australia (Farmer and Wilson, 2011), was far greater than the 8 and 26 employed in comparable studies by Reum and Essington (2008) and Akin and Winemiller (2006), respectively. While it should be recognised that the overall compositions of the diets of these species did change with increasing body size when using a finer taxonomic scale (Platell et al., 2010; Sommerville et al., 2011; French et al., 2012), the use of those finer taxonomic scales for the dietary categories in the present study would have produced a prohibitively large number of predator guilds for the analyses employed in the current study and thus mitigated against the construction of a readily comprehensible food web.

8.2.2 Food webs, including identification and characteristics of prey guilds

Until now, the discussion has largely focused on how food resources are partitioned among demersal fish species on the lower west coast of Australia, taking into account the size of the fish. The emphasis now shifts to exploring the ways in which food resources are shared among the various fish predator guilds. This was achieved by identifying the various groups of prey taxa, which had each been shown statistically to share common patterns of predation across one or more predator guilds. This was achieved by using a novel ‘switching’ approach within SIMPROF (R-mode analysis), which had the great advantage of reducing the number of 47 prey taxa in the present study to a far more manageable number of prey guilds (12), thereby paralleling the benefits of using SIMPROF to identify predator guilds (see above).

The prey taxa within each prey guild, which were objectively identified by the use of cluster analysis with SIMPROF, showed a strong tendency to represent suites of prey with common distinctive ecological/functional characteristics. For example, all cephalopod and teleost prey, which are relatively large and mobile, are located in prey guild g, whereas prey guild b contained all of the very small planktonic crustaceans, represented by the Notostraca, Calanoida and Cladocera. Furthermore, the 'largest' of the prey guilds (l) comprised small benthic and epibenthic crustaceans and the errant and sedentary polychaetes, which are not particularly mobile and live on or within the substrate. Within prey guild f, the molluscs (mytiloids, mesogastropods, arcoids) and echinoderms (clypeasteroids) are relatively large and immobile, and cirripedes and leptostracans are amongst a multitude of taxa that live in or on structures created by mytiloids (e.g. Cinar et al., 2008; Galkin and Goroslavskaya, 2008). Prey guild c contained all of the insects, represented by either their larvae or adults. The larvae of the insects belonged in particular to the Tipulidae (Hourston et al., 2004), whose pupae possess plastron-bearing spiracular gills and are found in saltwater (Hinton, 1967), while the adults were represented by insects, such as those of the Formicidae, which alight on the water surface (Hourston et al., 2004). These results emphasise that, in the food web for the lower west coast of Australia, the members of each guild of demersal fish predators typically feed on prey that occupy a particular ecological niche. There are, however, a few cases where the basis for the distribution of taxa among guilds is not clear. For example, it is not evident why prosobranchs and cubomedusae are present together in prey guild h, and why opisthobranchs and phyrnophiurids occur together in prey guild j, in which they are the sole representatives. These pairings are likely to reflect some commonality in terms of ecology or function, but which, due to a paucity of data for these groups in south-western Australian waters, are not at present readily apparent.

The conventional food web shown in Fig. 7.13 emphasises that such webs are still very complex, even when, as in that figure, the data for the various predators and prey have been aggregated into guilds. Thus, the relationships between these guilds could be clearly identified in only a limited number of cases. In contrast, the relationships between predator and prey guilds, and their relative magnitudes, as shown by variations in shading, can readily be discerned in the 'shade plot' in Fig. 7.14, which matches the predator guilds against the prey guilds, in the hierarchical orders determined from the nMDS ordinations shown in Figs 7.9 and 7.11, respectively. Thus, the large predators at the apex of their trophic hierarchy can be seen to focus particularly on prey near the apex of the prey's hierarchy, which is towards the top left hand corner of the plot. In contrast, the smaller individuals of large species and the smaller species towards the base of the predator hierarchy concentrate on consuming prey towards the lower end of the prey hierarchy, which is situated towards the lower right hand of the shade plot.

The trends exhibited by the locations and colou shading in Fig. 7.14 emphasise that cephalopods, teleosts and other decapods (prey guild g) are consumed by all predator guilds. However, they also demonstrate that these larger, more mobile and/or hard-bodied prey are most important as a food source for large species, such as *Aptychotrema vincentiana, Glaucosoma hebraicum* and *Heterodontus portusjacksoni* and particularly their larger individuals, which belong to predator guilds B, D and E at the top of the predator hierarchy. It is also evident that the small crustaceans and polychaetes, which live in or on the benthos, belong to the other prey guild (l) that is consumed by all predator guilds. In contrast to the situation with prey guild g, however, the members of prey guild l are a far more important food source to predator guilds at the bottom of the trophic hierarchy and which include small species such as *Lesueurina platycephala, Atherinomorus ogilbyi, Pempheris klunzingeri, Lepidotrigla modesta* and *Ammotretis elongatus* and the small individuals of larger species such as *P. georgianus* (M, L, K, N and I). Although the larger individuals of the suite of sillaginids (predator guilds Q and P) lie in the middle of the predator guild hierarchy and feed on cephalopods, teleosts and decapods (prey guild g) and to a greater extent small benthic crustaceans and polychaetes (prey guild l), they are distinguished from other predator guilds by consuming a substantial collective volume of gastropods, small bivalves and brittle stars (prey guilds h, j and k). Thus, while two prey guilds are consumed by all predator guilds, the other prey guilds are typically ingested by at least three other predator guilds. The food resources are consequently spread among and within the demersal fish species on the lower west coast, thereby reducing the potential for inter- and intra-specific competition.

The production of a food web in the form of a shade plot, as shown in Fig. 7.14, will allow managers and scientists to be able readily to visualise the trophic relationships between the main commercial and recreational species and their prey and the magnitudes of those relationships. A graphical representation of this form is particularly effective (compared with a table) in assimilating the broad structure of predator-prey relationships and highlighting the major prey in the diets of the various predator groups. This in turn will allow the key trophic links in the ecosystem to be identified and thereby enable the effects of any perturbations in those relationships to be predicted. Conversely, the influence of anthropogenic and other activities on a given fish species can be predicted, when such activities are known clearly to have an effect on the abundances of the key prey of that species. This would be especially important in the case of fish species that were particularly selective in their choice of prey.

9. BENEFITS AND ADOPTION

Fisheries managers and scientists now have sound information on which particular suites of prey are important for Snapper and Silver Trevally in waters on the lower west coast of Australia, in which the former is an important commercial and recreational species and the latter is one of the fish species that is most frequently caught by recreational anglers. They also now know, however, that the diets of these two species change markedly with body size and that such changes thus need to be taken into account when using dietary data to help develop management plans for these species. It is also evident that, although several prey taxa are ingested by both species when they are abundant and co-occur, the relative contributions by each of those prey to the diets of the two fish species differ conspicuously and thus competition for food resources between Snapper and Silver Trevally is unlikely to be intense. Our data show that the dietary compositions of Snapper and Silver Trevally both vary conspicuously among different regions of Western Australia. While this indicates that, to a certain extent, both species can feed opportunistically, it also emphasises that separate food webs need to be constructed for each region.

The collation and inclusion of the dietary data for Snapper and Silver Trevally, alongside data collected over the last 20 years for 33 other demersal fish species on the lower west coast of Australia have allowed the construction of a modified form of food web. This web illustrates the inter-relationships between the predator and prey species and their magnitudes in a form that will allow managers and scientists to readily identify key trophic links in this ecosystem. This, in turn, will enable the effects of any perturbations in those relationships to be predicted. This first depiction of a demersal food web for the lower west coast of Australia will also provide a foundation for scientists seeking, in the future, to further quantify trophic interactions in this system using advanced ecosystem modelling techniques.

In broad terms, this study provides details of the trophic interactions of important demersal commercial and recreational fish species (and their prey) as well as those other fish species with which they potentially compete for resources. Commercial and recreational fishers, fishery and environmental managers and the general public will thus benefit from a better understanding of the inter-relationships of these demersal fish species and their prey. Such data will allow the likely implications of the declines in abundance of key demersal fish species (Wise et al., 2007) to be assessed and enable managers to develop appropriate plans for management of the demersal ecosystem.

The research workers involved on this project spent a morning with Dr Lindsay Joll (Director of Aquatic Management at the Department of Fisheries, Western Australia) and his colleagues in order to provide them with a detailed account of the results of the study and thus the opportunity to understand fully the implications of the results for management. Dr Joll considered that the simplified food web developed during this study was particularly useful because it presented the information in a clear and readily interpretable manner. Because managers will now be much better placed to understand the trophic environment and the relationships of the species they are managing, they can take this into account in their understanding of the role of these species in the ecosystem and the ramifications within fisheries management arrangements. During this study, reports of its progress were given at regular intervals at seminars convened by the Western Australian Marine Sciences Institute (WAMSI) and which were attended by staff of the Department of Fisheries, Western Australia. We plan to give an informal seminar to the members of the biodiversity group at the Department's research laboratories to provide them with information that may be relevant to the Department's current initiative to seek Marine Stewardship Council certification for Western Australia's commercial fisheries.

The studies on the diets of Snapper and Silver Trevally have been published (French et al., 2012) and the details of the innovative food web developed for demersal fish species on the lower west coast of Australia have been accepted for publication (French et al., in press). The approaches used for constructing this simplified food web have thus been subjected to peer group review and readily available to managers and scientists in Western Australia and elsewhere in Australia.

10. FURTHER DEVELOPMENT

The food web that has been developed, in the form of a shade plot, provides the key data required for the demersal component of an ecosystem model for the lower west coast of Australia. However, this food web does not extend to its base and thus does not identify the sources of energy flow that fuel this system. Future research of this demersal food web should therefore focus on using a variety of techniques, including stable isotope and fatty acid analyses, to fill this gap.

In view of the importance of estuaries, and the extent of the extreme anthropogenic influences to which they are now being subjected, it would be invaluable to develop the dietary data for the main fish species in such systems. These data could then be used to produce the type of food web that has been developed in the present study, which would therefore highlight the magnitudes of the relationships between the main predators and their prey, and thereby allow the prediction of effects of anthropogenic, climatic and other changes.

As pointed out in the previous section, the diets of Snapper and Silver Trevally and how they vary with body size region and season and details of the construction of the food web have been published and accepted for publication in an international journal, respectively. Consequently, the results and their implications are widely available. They have also been reported in this current final report and were discussed at length with Dr Joll (Director of Aquatic Management at the Department of Fisheries, Western Australia) and his colleagues so that they could make best use of this information. The results have already been reported at four separate seminars convened by WAMSI and attended by Fisheries Department staff and at an international conference in the United Kingdom. The results and implications have also been discussed with Dr Andrew Rowland, the CEO of RecFishWest. A copy of this report will be provided to WAFIC and will be followed up by discussions with its staff via Mr Richard Stevens.

The raw data will be deposited with the Department of Fisheries Western Australia and can thus be used by the Department for a variety of purposes related to management.

11. PLANNED OUTCOMES

The planned outcomes of this project have been achieved. Scientists thus now know how the diets of Snapper and Silver Trevally off the lower west coast of Australia change with body size and season, and with which species they are most likely to compete for food resources. Furthermore, the food web constructed during the study provides fishery managers and scientists with a sound understanding of the trophic interactions of demersal fishes in south-western Australia, thereby assisting in the implementation of ecosystem-based fishery management and providing the dietary data required for the future construction of reliable ecosystem models. In addition, commercial and recreational fishers, fishery and environmental managers and the general public now benefit from a better understanding of the inter-relationships of the demersal fish species and their prey. Such data will allow the likely implications of declines in the abundances of key demersal fish species to be assessed and enable managers to develop appropriate plants for management of the demersal ecosystem. The data on the diets of Snapper and Silver Trevally and on the food web are now published or in press in international journals and will thereby facilitate feedback from experts elsewhere in the world (see below).

French, B., Platell, M.E., Clarke, K.R., Potter, I.C., 2012. Ranking of length-class, seasonal and regional effects on dietary compositions of the co-occurring *Pagrus auratus* (Sparidae) and *Pseudocaranx georgianus* (Carangidae). Estuarine, Coastal and Shelf Science 115, 309-325.

French, B., Clarke, K.R., Platell, M.E., Potter, I.C., in press. An innovative statistical approach to constructing a readily comprehensible food web for a demersal fish community. Estuarine, Coastal and Shelf Science.

12. CONCLUSIONS

The following conclusions demonstrate that this study has achieved the three objectives of this project.

1. The diets of Snapper and Silver Trevally change markedly with body size, and sometimes season. Such changes thus need to be recognised by managers (Objective 1).

2. Although several prey taxa are ingested by Snapper and Silver Trevally, when these two predators are abundant and co-occur, the relative contributions by each of those prey taxa to the diets of the two fish species differ conspicuously. Thus competition for food resources between Snapper and Silver Trevally is unlikely to be intense when these species are found in the same environment (Objective 1).

3. The dietary compositions of Snapper and Silver Trevally both vary conspicuously among regions of Western Australia. This indicates that, to a certain extent, both species can feed opportunistically, and thus presumably accommodate changes in the composition of prey in their environment (Objective 2).

4. The development of a novel technique for exploring relationships between fish predators and their prey has facilitated the construction of a food web in which those relationships and their magnitudes can be readily visualised. This type of food web could be constructed for any ecosystem for which there are sufficient dietary data (Objective 3).

5. A food web of the key demersal fish species in south-western Australia, which includes both Snapper and Silver Trevally, and other commercially and recreationally important species such as Dhufish and Breaksea Cod, has been constructed and is available to scientists, managers and the public (Objective 3).

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APPENDIX 1: Intellectual property

The results of this study will be published so that they are available for use by fisheries scientists and fisheries and environmental managers but will have no direct commercialisation potential.

APPENDIX 2: Project staff

Murdoch University: Mr Ben French, Professor Ian Potter and Dr Margaret Platell.
Plymouth Marine Laboratories and Murdoch University: Dr Bob Clarke.

APPENDIX 3: Subsidiary data

Mean squares (MS), pseudo-*F* ratios, significance levels (*P*,%) and components of variation (COV) for a series of PERMANOVA tests, employing Bray-Curtis similarity matrices derived from the mean percentage volumetric contributions of the various dietary categories to the gut contents of the fish species as designated.

P. auratus on the lower west coast	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Length class	5	4333	3.3	0.01	25.6
Season	3	4805	3.7	0.01	23.6
Interaction					
Length class x season	10	2865	2.2	0.04	31.1
Residual	19	1303			36.1

P. auratus on the lower west and mid west coasts	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Length class	2	2565	1.8	6.6	17.7
Season	3	2826	2.0	2.4	16.8
Region	1	6384	4.5	0.1	31.9
Interactions					
Length class x season	6	2873	2.0	0.4	28.8
Length class x region	2	1256	1.1	38.7	6.2
Season x region	3	3723	2.6	0.5	33.8
Length class x season x region	1	857	0.6	66.8	17.0
Residual	16	1416			37.6

P. georgianus on the lower west coast	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Length class	5	4607	2.1	0.05	19.7
Season	3	3551	1.6	4.5	13.1
Interaction					
Length class x season	10	2679	1.2	12.1	14.5
Residual	35	2157			46.1

P. georgianus on the south coast	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Length class	4	1857	1.1	37.1	6.5
Season	3	9877	5.9	0.01	34.8
Interaction					
Length class x season	4	2715	1.6	6.2	23.7
Residual	17	1676			40.9

P. georgianus on the lower west and south coasts	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Length class	5	4922	2.5	0.02	16.0
Season	3	9265	4.6	0.01	18.9
Region	1	16879	8.4	0.01	19.8
Interactions					
Length class x season	11	2785	1.4	2.9	15.6
Length class x region	4	4124	2.1	0.4	19.7
Season x region	3	2636	1.3	18.2	12.4
Length class x season x region	3	3048	1.5	8.8	24.7
Residual	52	2000			44.7

Appendix 3 cont. on next page

P. auratus and *P. georgianus* on the lower west coast	Df	MS	Pseudo-*F*	*P*(%)	COV
Main effects					
Species	1	12426	6.6	0.01	21.2
Length class	5	3943	2.1	0.06	16.6
Season	3	4107	2.2	0.4	12.9
Interactions					
Species x length class	5	4156	2.2	0.02	23.8
Species x season	3	4951	2.6	0.02	24.1
Length class x season	13	2910	1.6	0.3	18.8
Species x length class x season	7	2722	1.5	3.7	22.6
Residual	56	1878			43.3