Habitat Modification and its Influence on Prawn and Crab Fisheries

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Habitat Modification and its Influence on Prawn and Crab Fisheries

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Non Technical Summary

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OBJECTIVES:

1. To determine and correlate the distribution and relative abundance of prawns, crabs, and encrusting epibiota in the vicinity of prawn and crab grounds in relation to coastal discharge sites in Gulf St Vincent.

2. To measure and compare the outcome of controlled trawling on epifaunal composition of prawn/crab habitats & bryozoan dominated habitats.

3. To provide an understanding of the consequences of habitat modification on productivity of important commercial & recreational fisheries.

NON TECHNICAL SUMMARY:

Outcomes Achieved:

In conjunction with project 98/225 ‘Prawn fishery bycatch and discards: fates and consequences for a marine ecosystem’, this project will contribute significantly to the ecologicaly sustainable development of South Australian prawn fisheries. Together, the two projects provide a clear indication of the effects of prawn fishing on the ecosystem, and will allow industry and management to assess potential ways for reducing these effects. The results of this project will also be important for the industry to obtain export approval.

Experimental trawling in Gulf St Vincent indicated that epifaunal assemblages experienced substantial trawling mortality, which varied depending on sediment characteristics. Locations with strong currents and coarse sediments experienced minimal effects, whereas those with weak currents and fine sediments experienced larger effects. Overall, trawling caused a 36% reduction in the number of large epifaunal organisms. However, recruitment into trawled sites was higher than into untrawled sites, suggesting that recovery may be relatively rapid. Examination of infauna showed that they did not experience any effect, although there was some indication that at the location with fine sediments infaunal abundance was reduced.

Mathematical models of prawn population dynamics indicated that harvest rates were maximal when only a small proportion (2-3%) of the adult habitat was trawled. Adding stochastic variation to the model did not alter its behaviour, suggesting that yearly variation in environmental conditions and fishing strategies may have little effect on the long-term optimal harvest strategy and sustainability of the fishery. This conclusion only applies if such variation is random, and not caused by any long-term trends. According to the model, harvesting only 2+ prawns, which allows reproduction before animals enter the fishery, is a much better option than harvesting 1+ animals. If 1+ animals experience substantial mortality in the fishing process, the behaviour of the population changes and there are large declines in harvest.

Both juvenile prawns and blue crabs respond negatively to the Bolivar sewage effluent discharge, with abundances in intertidal nursery areas being lower at the outfall site than at 2 km either side of it. However, abundances decline again 4-5 km either side of the outfall, due to a change in habitat (from sand to seagrass). Given this localised effect, and the fact that the effluent discharge is probably causing the change in habitat, it appears as though there is little effect of the outfall on juvenile abundance of either species.

Habitat selection experiments using juvenile prawns showed that they preferred sand habitats to seagrass, and that selection did not change in response to predators. Juvenile blue crabs showed no habitat preferences, generally treating seagrass and sand habitats equally. Crabs changed their habitat preference in response to predators, although not in a consistent direction, and they responded to adult blue crabs and introduced green crabs in a similar way. However, while they buried in the presence of adult conspecifics, they did not do so in the presence of adult green crabs, which may make them more vulnerable to predation. Predation rates on both species were lower in seagrass than in sand, however close to patch edges predation was high. This suggests that fragmentation of seagrass habitats may have a negative influence, due to the increased amount of edge habitat.

Infauna did not appear to respond to habitat fragmentation, with similar assemblages and abundances in seagrass and sand patches in fragmented areas. Epifauna, however, showed reduced abundances and lower species richness in sand than seagrass. Generally, epifauna did not change in response to distance from the edge of a seagrass patch, but rather there was an abrupt change at the habitat boundary from the seagrass to the sand assemblage. Patch shape and orientation were important in determining the colonisation rate of epifauna in seagrass under certain circumstances. Species with directed movement (e.g. amphipods dispersing via currents, or fish retreating from intertidal areas at low tide) accumulate in higher numbers in patches perpendicular to their direction of movement.

Since the 1960's, there have been substantial changes in the benthic habitats of Gulf St Vincent. There have been extensive losses of deepwater seagrass and horse mussel assemblages in the southern parts of the gulf. The abundance of bryozoans and scallops in central areas has also decreased. Further north, there have been few changes. While the causes of these changes cannot be identified with certainty, there are two main factors likely to be responsible. The first is the increased turbidity due to sewage, urban & agricultural runoff and dust-storms, and the second is prawn trawling.

Keywords:
Effects of trawling, habitat fragmentation, habitat selection, western king prawn, blue swimmer crab, seagrass.

Acknowledgements:

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Background:

Gulf St Vincent supports important nearshore fisheries such as prawns ($3 million p.a.) and blue crabs ($2 million p.a.). With the city of Adelaide (population > 1 million) on its shore, Gulf St Vincent is also an important venue for recreational fishing, which approximately 300,000 South Australians engage in every year. This close proximity to a major city, however, means that the gulf is exposed to a number of anthropogenic influences that have resulted in substantial habitat change and degradation over the last several decades. These influences include fishing itself, especially prawn trawling, sewage and stormwater runoff from the city of Adelaide as well as smaller coastal towns, and agricultural runoff. As a result of the concerns about nutrient inputs into the gulf the SA government has recently spent $280 million upgrading Adelaide's sewage treatment plants to enable increased levels of wastewater re-use, and to decrease nutrient inputs into the gulf. There are still substantial anthropogenic nutrient inputs remaining, however, especially considering the arid nature of South Australia's environment, and the low nutrient status of its soils, which means that natural terrigenous inputs are very low.

The research described here was originally proposed because of the concern expressed by prawn, crab and recreational fishers over the level of habitat change in Gulf St Vincent, and how this might impact on their respective fisheries. Part of this concern came from low catches in the prawn fishery, despite a 2 year closure from 1991-1993. Since the commencement of this project, however, catches have almost doubled, and are now consistent with historical values. In addition, catch per unit effort is at a record high, being 109 kg/hr in the 2000/2001 season. Despite this improvement, some historically productive grounds now yield low catches of prawns. Also, crab fishers claim that the habitats utilised by blue crabs have changed over the last decade, with changes to the productivity of the commercial fishery. In particular, it has been suggested that the distribution and species composition of seagrasses in juvenile nursery areas has changed, resulting in spatial shifts in the distribution of juvenile blue crabs.

There is also increasing concern about the potential negative effects of trawling on both the environment and other commercial fisheries. Trawling has been likened to forest clear-cutting in its environmental effects, as not only does it destroy benthic species, but these species contribute much of the physical habitat in subtidal areas. By reducing the physical complexity of these habitats, trawling can thus potentially have serious negative effects on many other species that are not directly impacted by the trawl.

While there is strong anecdotal evidence for habitat change in Gulf St Vincent in recent decades, there have been no comprehensive surveys of benthic communities since that done in the 1960's by Shepherd and Sprigg (1976). Thus the extent of changes, and their potential implications for fisheries, were unknown. One of the suggested changes was the invasion of previous prawn habitats in the mid-northern section of the gulf by bryozoans, with subsequent decreases in the relatively unstructured habitats supposedly required by prawns. One suggested mechanism for this invasion was an increase in stormwater and/or sewage discharge into the gulf in recent years. It is also possible that the suggested increase in bryozoan cover could be due to a decrease in the amount of trawling activity in the gulf (from a peak of almost 21000 hours in 1978/79 to only ~2000 hours per annum in the 1990's. Thus this study aimed to rigorously quantify the changes in habitat that have occurred since the 1960's, to identify some of the possible causes of these changes, and to determine what consequences they have for the prawn and crab fisheries in particular.

This study thus has three major components to it:

1. An experimental trawling study was carried out to determine what impact trawling has on the benthic communities in Gulf St Vincent, how rapidly the initial stages of recovery occurred, and whether trawling had any subsequent negative impact on prawn and blue crab catches. Mathematical models were also used to examine the consequences of changing the proportion of the habitat trawled for long-term harvest rates.
2. The consequences of habitat change in shallow-water juvenile nursery areas of both prawns and blue crabs were assessed. This involved examining how abundances of these species varied as a function of distance from a sewage outfall. It has also been well documented that large areas of seagrass have been lost from the Adelaide coastline, and the potential consequences of this loss were examined by conducting habitat selection experiments on both juvenile prawns and blue crabs, and examining predation rates in response to distance from seagrass patches. The consequences of seagrass fragmentation for infaunal and epifaunal assemblages, the predominant source of prey for both juvenile prawns and blue crabs, were also assessed. Finally, I assessed whether the shape and orientation of seagrass patches was likely to have any effect on epifaunal assemblages.
3. The extent of habitat change in deeper-water areas of Gulf St Vincent since the 1960's was documented through a series of remote video surveys and construction of a habitat map which was compared to a similar map from over 30 years earlier.

Need:

This project seeks to address the need for information on the effects of anthropogenic disturbance on coastal habitats which are important for both commercial and recreational fisheries. Both the community as a whole, and the fishing industry in particular, seek to maintain healthy aquatic ecosystems for their aesthetic, recreational and commercial values. Ecologically sustainable development is a frequently expressed aim of modern fisheries management, but management objectives relating to this aim are rarely underpinned by high quality quantitative information. It is therefore difficult, if not impossible, to determine if fisheries are being conducted in an ecologically sustainable manner. So little is known of processes structuring sub-tidal ecosystems, especially those on soft sediments, that it is difficult to formulate coherent and meaningful policies governing activities in Australian aquatic habitats. More importantly, it is difficult to identify environmental performance indicators to assess the status of individual fisheries. In reality, the effects of harvesting on marine species, and on co-occurring biota, are poorly understood. This is particularly the case for inshore fisheries in which harvesting occurs in the euphotic zone and the potential for significant alteration of the food chain, mediated by fishing, is very real. There is a clear need to identify human-induced processes that may damage coastal ecosystems and that may affect the viability of nearshore fisheries.

Fishers in Gulf St Vincent claim that the productivity of fisheries is being affected by changes to the habitat. It is thus essential that these changes be properly quantified, and their consequences for fisheries determined.

This project is one of a suite of research projects aimed at evaluating the ecological consequences of fishing. Another major project on the fate of prawn discards directly complements this one. The linkages and common focus on coastal ecosystems will reinforce the outcomes and utility of the research.

Objectives:

1. To determine and correlate the distribution and relative abundance of prawns, crabs, and encrusting epibiota in the vicinity of prawn and crab grounds in relation to coastal discharge sites in Gulf St Vincent.
2. To measure and compare the outcome of controlled trawling on the epifaunal composition of prawn/crab habitats and bryozoan dominated habitats.
3. To provide an understanding of the consequences of habitat modification on the productivity of important commercial and recreational fisheries.

Chapter 1: The influence of prawn trawling on benthic assemblages in Gulf St Vincent, South Australia.

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Abstract

The effects of bottom trawling on the benthos are becoming of increasing concern worldwide, and a number of studies have been done to determine what the consequences of this widespread activity are. In this paper, I examine the effects of demersal otter trawling for prawns on the benthic fauna and flora of Gulf St Vincent, South Australia. Unlike most previous studies on soft substrates, I use a series of permanently marked quadrats to determine the consequences of experimental trawling for individual organisms, as well as the entire assemblage. The trawl sites are also located in areas that have not been fished for some 15-20 years, and thus the results are much more indicative of the damage originally caused when new trawl grounds are opened up than is generally the case. While there was a significant trawling by location effect for all multivariate analyses, and most individual taxa, I found that trawling did have an overall negative effect on the benthos. Epifauna at trawled sites decreased in abundance by 28% on average within 2 weeks of trawling, and by another 8% in the following 2-3 months (compared to control sites). Seasonal seagrasses were also less likely to colonise trawled sites than untrawled sites. Trawling did not have any detectable effect on the two commercially fished crustacean species present in the Gulf (western king prawns – *Melicertus latisulcatus*, and blue crabs – *Portunus pelagicus*). The persistence of established epifauna declined significantly in trawled areas compared to untrawled areas. In contrast to this, the recruitment rates of several taxa increased after trawling, presumably because of a reduction in competition. This indicates that recovery should occur relatively quickly, although it may still take many years for some species to reach their pre-trawling size structure.

Introduction

The consequences of bottom trawling for marine communities are coming under increasing scrutiny worldwide. As a result, there are an increasing number of studies that document the effects of trawling, or lack thereof, on infaunal and epifaunal abundance and community composition, benthic, pelagic and avian scavengers, sediment structure and turbidity, and structural characteristics of the benthos (for reviews see Messieh *et al*. 1991; Jones 1992; Dayton *et al*. 1995; Jennings & Kaiser 1998; Hall 1999; Turner *et al*. 1999). In many cases, however, it has proven difficult to detect an effect of trawling, especially on animal abundances, despite several reports likening the practise to forest clear-cutting (e.g. Watling & Norse 1998). There are two major reasons for this. Firstly, many studies are carried out in areas that have been repeatedly trawled over a number of years, and thus the community has probably already been modified, and vulnerable species removed. In many locations, unfished areas that could be used to experimentally determine the effects of trawling on virgin ground simply do not exist (e.g. Kaiser *et al*. 1998). Secondly, most studies have used remote sampling methods to determine changes in abundance (e.g. grab samples, remote video, trawl nets and benthic sledges – but see Van Dolah *et al*. 1987). While the advent of differential GPS systems has allowed sites to be relocated with a high degree of precision, it is still impossible to relocate individual animals before and after trawling with these methods. In combination with the high degree of spatial variability in organism abundance in many areas of the world's oceans, this means that only relatively large changes can be detected, and determining the fate of individual animals is difficult or impossible. A large study on Australia’s Great Barrier Reef has shown that a single pass of a trawl only removes about 10% of the epifauna, and that effects are only detectable in catches after several passes over the one spot (Poiner *et al*. 1998). Such intensive trawling tends to be rare in experimental studies, although not in commercial practise. For instance, in the North Sea 9% of the surface area of the seabed is trawled in excess of 5 times a year (Rijnsdorp *et al*. 1998).

The effects of trawling are likely to be mediated by the type of gear used, and its configuration, as well as the bottom habitat. Of the two main commercial trawl rigs used, beam trawling is generally considered to cause the greatest amount of damage (Hall 1999), although some otter trawl configurations can be just as destructive. With demersal otter trawling, the worst damage is caused by the otter boards, which scrape along the substrate at an angle, acting much like a bulldozer (e.g. Gibbs *et al*. 1980; Brylinsky *et al*. 1994; Auster *et al*. 1996). The footrope and net between the boards can be much less damaging depending on its configuration. Light gear tends to skip over the bottom, causing minimal damage (e.g. Gibbs *et al*. 1980), although if trawl shots are long the net may fill up and drag along the bottom. Heavier gear (weighing up to many tonnes), can, however, roll along the bottom and cause considerable damage (e.g. Jennings & Kaiser 1998; Freese *et al*. 1999).

Habitat type can also have a large influence on how much damage is caused by trawling. Auster (1998) presents a conceptual model that relates habitat complexity to effects, with more complex habitats sustaining greater levels of damage. Heavily disturbed areas are likely to be resilient to trawling, whereas more sheltered and stable areas are probably more vulnerable (Kaiser & Spencer 1996; Jennings & Kaiser 1998; Collie *et al*. 2000). In a meta-analysis of trawling studies, Collie *et al*. (2000) show that less stable habitats tend to recover faster, although they still take more than a year to converge back to the same state as untrawled control sites. It has also been suggested that fishing will lead to a decrease in habitat heterogeneity, primarily due to the removal of biotic elements of the habitat, and the smoothing of the substrate (e.g. Thrush *et al*. 1995; Engel & Kvitek 1998). This smoothing is often deliberate, to reduce subsequent damage to the trawl gear, as well as a byproduct of fishing, and could potentially result in semi-permanent changes to habitat quality which continue long after fishing ceases.

In this paper, I examine the effects of trawling for penaeid prawns (shrimp) in Gulf St Vincent, in southern Australia. Gulf St Vincent is one of two semi-enclosed inverse estuaries on Australia's southern coast in which extensive prawn trawling occurs, with the other (Spencer Gulf) having broadly similar habitat types (pers. obs.). I overcame the problem of small-scale spatial variation by using a series of permanent quadrats which allowed me to relocate specific areas, and follow the fate of individuals of the larger taxa. While the locations used were possibly trawled in the past, they have not been fished for 10-20 years, and thus have had considerable recovery time. This paper presents the effects on sessile epibenthic assemblages, both epifauna and seagrass, within one week of trawling and 2 ½ months later. Demographic rates of abundant taxa are examined to determine if trawling simply removes animals from the substrate, or if subsequent recruitment is also reduced through changes to the habitat. I also examine how catches of the two commercially important crustacean species present – the western king prawn (*Melicertus latisulcatus* (Kishinouye)), the target of the fishery, and the blue crab (*Portunus pelagicus* (Linnaeus)) respond to the initial trawling episode. The specific hypotheses are that trawling alters the structure of epifaunal assemblages by decreasing the abundance of some or all species groups, and that subsequent catches of commercial species also decline after trawling due to habitat alteration. The effects on infauna are examined in Chapter 2.

Methods

Site description:

Gulf St. Vincent is a large (~7150 km^2) relatively shallow (generally <30m) embayment on the southern coast of Australia (Shepherd & Sprigg 1976). As a result of minimal freshwater input, and high summer evaporation rates, it is an inverse estuary, with salinity increasing towards the head of the gulf. Water exchange with the open ocean is restricted by Kangaroo Island, located across the mouth, which also protects the area from high wave activity. Most of the gulf is depositional, with few areas of hard substrate, although calcrete commonly occurs less than 200 mm under the sediment surface, and may provide attachment points for some sessile species. The dominant fauna, however, are adapted to living in soft sediments. The mean grain size of sediments in the northern gulf, where this study was conducted, is about 0.25 mm, with calcium carbonate predominating (Waters 1976). Seagrasses occur extensively in shallow waters, covering an area of almost 2500 km^2 (Edyvane 1999). Most seagrass meadows occur from the intertidal to about 15m depth, although some species, notably in the genus *Halophila*, extend considerably deeper. The composition of the epibenthos in this region proved to be highly variable (pers. obs. - see also Fig. 1.2), and locating several similar sites in areas that had not been trawled for at least 10-20 years, but were considered by the fishermen to be trawlable, was not possible in the limited time available. The resulting variability in the composition of the epifaunal assemblage complicated interpretation of the results, and reduced the power of statistical tests, but provides greater ability to generalise over the gulf as a whole.

History of Fishing:

Bottom trawling for prawns commenced in Gulf St Vincent in 1968. Fishing pressure rapidly escalated, and reached a peak with 16 boats fishing for a total of 21,000 hours in 1978/79. Since then, effort has declined, and in recent years the fishery has been restricted to 10 boats fishing for about 2000 hours (30-40 nights) a year in total. Currently, the boats involved in this fishery are a maximum of 15.2 m long, and use a triple otter trawl with a maximum total headline length of 27.43 m. The gear is relatively light, with two 200 kg otter boards to spread the nets, and two 240 kg skids to separate them. The total spread of the nets when trawling is approximately 20 m.

Experimental design:

To examine the effects that trawling had on the benthic fauna in Gulf St Vincent, three locations in the northern gulf were selected for experimental trawling using a multiple before-after, control-impact (MBACI) design. These sites were located in approximately 20 m of water, the shallowest depth at which extensive commercial trawling occurs, and in areas which have not been recently trawled. Fishing effort in the gulf has been recorded in blocks of approximately 30 nm^2 since the fishery started. The block containing location 1 was trawled in 1997/98, but total trawling time in the previous 10 years was less than 1000 minutes, and discussions with the fishers indicated that this occurred further out to sea than the experimental location. The blocks containing locations 2 and 3 had not been trawled since 1985. Prior to this, more extensive trawling had occurred in these fishing blocks, but the area was closed to protect suspected spawning areas, and has not been used since re-opening due to substantial reductions in overall effort. Thus the locations used represented typical trawling ground that had not been trawled for at least 15 years. Casual inspection of *Pinna bicolor* (a large, long-lived, erect bivalve) showed no evidence of trawl damage, further supporting the contention that these areas had not been trawled recently. Such damage was readily obvious one year after trawling, although it is not known how much longer it remains so.

At each of the three study locations (see Figure 2.1), a series of three adjacent corridors were established using differential GPS (see Table 1.1. for a summary of the experimental design). Each corridor was 0.5 nm long, and 200 m wide. Two corridors were designated as trawl and control corridors to study trawl effects on the benthos, while the remaining corridor was used to compare catches in untrawled areas to catches in the trawl corridor subsequent to initial trawling. In both the trawl and control corridors, a series of ten 3m x 3m permanent quadrats were marked out by steel pegs driven below the sediment surface so that the net could pass freely over the top of them. Within each of these quadrats, nine 1m x 1m sub-quadrats were also marked out in a similar manner to facilitate comparisons between censuses. Each peg was tagged with a fluorescent streamer which projected above the sediment surface so that it could be relocated subsequent to trawling. Quadrats were randomly located (using random number tables) in an area of approximately 50 m × 20 m - about the maximum that could comfortably be covered by an encumbered diver in a single dive. These quadrats were set up in August 1999, when they were also photographed to quantify the abundance of epifauna. A digital video camera was used to photograph every ¼ m^2 , with the permanently located steel pegs ensuring precise matching between censuses. The numerical abundance of sponges, bryozoans, ascidians and the bivalve *Pinna bicolor* in each quadrat were later determined in the lab, and the fate of individual animals followed over time. The three former groups were not identified to a lower taxonomic level because of the large number of relatively rare species present, and the poor taxonomic knowledge of marine fauna in this region. Other sessile taxa, including soft corals, sea pens and hydroids were extremely rare (<1% each), and were not quantified. As it was not always possible to accurately distinguish and identify animals less than 2 cm in diameter because of poor visibility on some days, animals smaller than this were not included. The percent cover of seagrass was also quantified by placing a random grid of 25 points over every ¼ m^2 photograph. Infauna were sampled from areas adjacent to two of the quadrats in each corridor, and are discussed in Chapter 2.

The trawl corridors were trawled over a series of three nights by a commercial prawn trawler (the Jillian Sandra) from the fleet involved in the fishery in October 1999. A series of 10 adjacent passes were made over the entire corridor at a speed of 3.5 knots, which was then repeated. As the sweep of the nets was approximately 20 m, this resulted in the entire corridor being covered twice on average. Trawling was conducted in a fashion identical to commercial trawling, with the exception that each shot was only 10 minutes, compared to 1-2 hours in commercial trawling. The catch of prawns and blue crabs was quantified for each shot, but other components of the catch were discarded outside the study area.

Table 1.1: Summary of sampling design and experimental manipulations conducted.

Factor	Replication	Description
Location	2+1	Photographs taken in 2 corridors only
Corridor (treatment)		(0.5 x 200 m)
Quadrat	10	(3 x 3 m, 10 within v 20 x 50 m)
Subquadrat	9	(1 x 1 m – used for visual reference only)
Photographs	4/subquadrat	¼ m^2 – used to count fauna and for seagrass cover

Treatments (corridors):
T1 = 1st corridor – trawled October 1999 and November 1999.
T2 = 2nd corridor – not trawled
T3 = 3rd corridor – trawled November 1999 only.

Trawling pattern:
Each corridor – 10 adjacent trawls x 2.
October 1999 – T1 only
Novermber 1999 – T1 (excluding quadrats) + T3

Census Times:
August = before trawl
October = after trawl
January = after 4 months recovery

A week after trawling, in October 1999, locations 2 & 3 were photographed to determine what effect the trawl had on the benthic community. Poor weather prevented location 1 being censused at this time, and this location was not surveyed again until January 2000, when locations 2 & 3 were also re-censused to determine longer term effects of trawling. Three 10 min trawl shots were also conducted by the Jillian Sandra in each trawl corridor and the 3rd (untouched) control corridor on Nov 18, to determine if the previous trawling had any effects on subsequent catches of prawns or blue crabs. The marked quadrats were avoided on this occasion, and this was confirmed by the lack of disturbance to large guide stakes and marker bouys that were placed out during the first post-trawl census. The weight of prawns and number of blue crabs were recorded for each shot, and a subsample of approximately 200 prawns sexed and measured to obtain carapace length to the nearest mm using calipers.

Statistical Methods:

To determine the effects of trawling on the epifaunal assemblage present in Gulf St Vincent, a non-parametric multivariate ANOVA was used (NP-MANOVA, Anderson 2001) to test for differences between treatments (control vs trawl) and locations. NP-MANOVA uses random permutations of the original data to calculate P-values and is somewhat analogous to the more familiar ANOSIM (Clarke 1993), but allowing for tests of interactions between factors. This procedure was chosen because of the general inability of ecological data to adequately meet the assumptions of parametric MANOVA, although NP-MANOVA does have its own restrictions. As the current version cannot handle a repeated measures design, the change in abundance of the different epifaunal taxa had to be analysed for each census interval (August-October, October-January and August-January) separately. This procedure also avoided problems associated with location 1 being missing from the second census. Differences between samples were quantified using euclidean distances, as joint absences generally indicated no change rather than absence of the taxon (especially with only four taxa being analysed). Trawling was analysed as a fixed factor, while location was random, and a total of 4999 permutations of the residuals under a reduced model were performed (see Anderson 2001). Significant terms were further analysed using *a posteriori* pairwise comparisons conducted in a similar fashion to the complete analysis. Non-metric multidimensional scaling (MDS) was used to visualise differences between treatments and locations.

Individual taxa (including seagrass) were analysed using conventional univariate ANOVA with the same design (see Table 1.2). For seagrass, only % cover at locations 1 & 2 in the final (January) census was analysed. There was no seagrass present at the initial census, and data on % cover at location 1 was not available for the second census. Location 3 was not included in the analysis of seagrass, as seagrass was never observed to occur there. Catches of prawns and crabs in November were analysed using standard 2-way ANOVA, with individual prawn weights analysed with 3-way ANOVA (with sex as the third factor). Normal probability plots and Cochran's test for homogeneity of variances were used to test ANOVA assumptions, and indicated that analyses could not be improved by transforming the data.

To determine the potential mechanisms by which trawling alters the structure of epifaunal assemblages, both persistence and recruitment of the four main taxa were examined. Differences in persistence between sites were analysed using generalised linear models with a binomial distribution and logit link function, while for recruitment a Poisson distribution and log link function were used (McCullagh & Nelder 1989). It should be noted that persistence here refers to persistence within the quadrat, and animals that did not persist may have still been alive, but have left the quadrat either through the action of the trawl or of currents. Similarly recruitment does not equate to settlement, but includes existing animals that grew large enough to be censused, and more importantly adults that moved into the quadrats. Movement of adults appeared to be a relatively common occurrence for these so-called sessile organisms, and occurred because animals were either adapted to being rolled around by currents, or were only attached to pieces of shell etc which could be moved without damage to its attached fauna.

Results

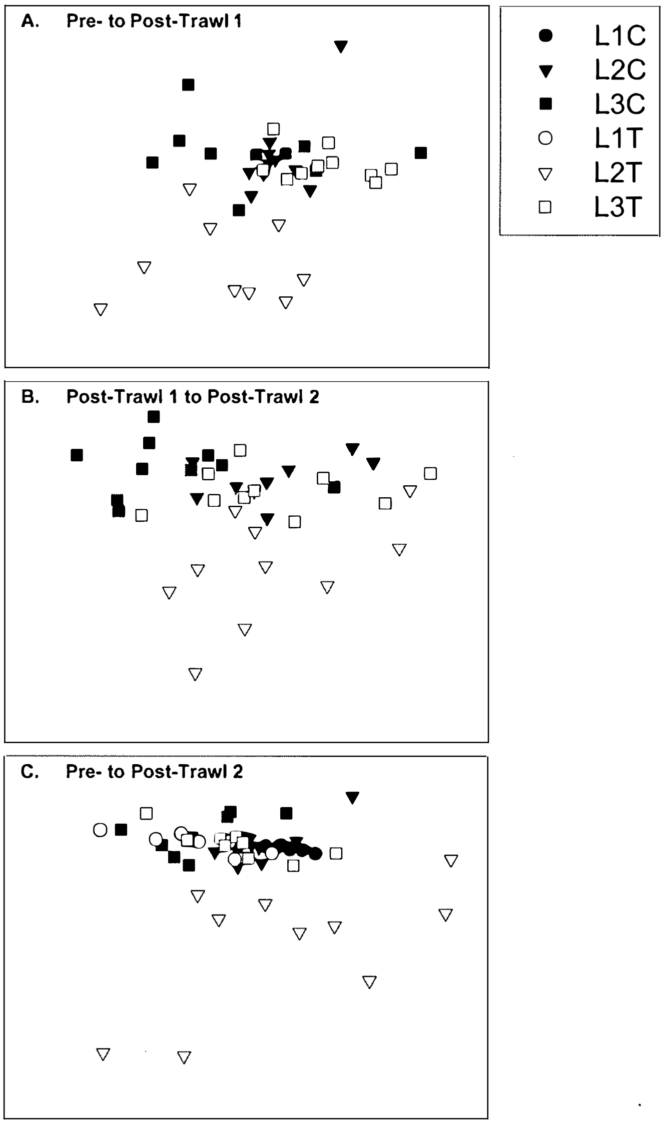
For all three time intervals, change in epifaunal composition was strongly influenced by the interaction between location and trawling (Table 1.2), indicating that the effects of trawling are location dependent. Changes in the control sites at locations 2 & 3 were very similar between the pre- and post-trawl censuses, indicated by the high overlap between the two groups of filled symbols in Fig. 1.1a, although location 3 was more variable. Pairwise comparisons showed the two control sites did not differ significantly (P = 0.74). The two trawl sites differed from each other (P < 0.002), and at each location the change at the trawl site differed to that at the control site (location 2: P < 0.002, location 3: P = 0.034). Univariate ANOVAs indicated that changes in the abundance of *Pinna* ($F_{1,36}$ = 22.8, P < 0.001), sponges ($F_{1,36}$ = 4.2, P = 0.048) and bryozoans ($F_{1,36}$ = 10.2, P = 0.003) were all significantly affected by the trawling by location interaction. *Pinna* and sponges decreased only at the trawl site at location 2, but not at the control sites or the location 3 trawl site (Figs 1.2a & 1.2b). Bryozoans declined at all four sites, irrespective of whether they had been trawled or not, with the decrease being greatest at location 2 trawl and least at location 2 control (Fig. 1.2c). Bryozoans at location 3 did not seem to be influenced by trawling. Ascidian abundance did not change with either trawling ($F_{1,1}$ = 1.3, P = 0.46) or location ($F_{1,1}$ = 0.4, P =0.63, Fig. 1.2d).

At the multivariate level, changes between the second and third censuses were similar to changes between the first two censuses, although pairwise comparisons indicated that the two control sites differed (p=0.004). Again the MDS plot shows that the location 2 trawl site differed most from the other sites (Fig. 1.1b). Univariate analyses indicated that the effect of prior trawling on *Pinna* ($F_{1,36}$ = 26.6, P < 0.001), sponges ($F_{1,36}$ = 7.4, P = 0.10) and bryozoans ($F_{1,36}$ = 10.2, P = 0.003) depended on location. Again, there were no differences in the response of ascidians due to either trawling ($F_{1,1}$ = 22.6, P = 0.13) or location ($F_{1,1}$ = 15.7, P =0.16). Sponges decrease at all but the location 2 trawl site (Fig. 1.2b), while bryozoan abundance continues to decrease at all sites (Fig. 1.2c).

Table 1.2: NP-MANOVA for changes in composition of the epifaunal assemblages due to trawling between censuses.

Source	**df**	**SS**	**F**	P
Pre- to post-trawl 1 (locations 2 + 3 only)				
Treatment	1	1096	1.21	0.46
Location	1	895	26.14	0.0002
Treat x Loc	1	903	26.38	0.0002
Residual	36	1232		
Post-trawl 1 to post-trawl 2 (locations 2 + 3 only)				
Treatment	1	1777	1.06	0.48
Location	1	1427	18.40	0.0002
Treat x Loc	1	1681	21.66	0.0002
Residual	36	2794		
Pre- to post-trawl 2				
Treatment	1	1274	1.15	0.39
Location	2	2014	18.58	0.0002
Treat x Loc	2	2213	20.41	0.0002
Residual	54	2927		

Figure 1.1. MDS plots showing the effect of trawling (open vs closed shapes) on change in community composition at different locations over three time periods. L1C – Location 1 control site, L1T – Location 1 trawl site etc.



Looking at the whole 5 month time period, pairwise comparisons show that changes in epifauna between the control and trawl sites are significantly different at both locations 1 & 2 ($P < 0.002$), but not at location 3 ($P = 0.44$). Changes were consistent at location 1 & 2 control sites ($P = 0.24$) but not at the location 3 control ($P = 0.023$). For the trawl sites, locations 1 & 3 responded similarly ($P = 0.53$), but both differed from location 2 ($P < 0.002$). The location 2 trawl site clearly differs from all other sites in the MDS plot and has a much higher degree of variability (Fig. 1.1c). All five other sites (control & trawl) show some overlap. Univariate ANOVAs show that trawling induced changes in the abundance of *Pinna* ($F_{2,54} = 28.9$, $P < 0.001$), ascidians ($F_{2,54} = 5.7$, $P = 0.005$) and bryozoans ($F_{2,54} = 5.8$, $P = 0.005$) are significantly affected by location. Sponges are affected by trawling irrespective of location ($F_{1,2} = 24.5$, $P = 0.038$) decreasing slightly at trawl sites, but remaining stable at control sites (Fig. 1.2b). *Pinna* show no overall change at control sites, while they decrease at the trawl site at location 2 (Fig. 1.2a). Bryozoans decrease at all sites except for the control at location 1 (Fig. 1.2c). Ascidian abundance declines at all sites, except location 2 trawl where it increases (Fig. 1.2d).

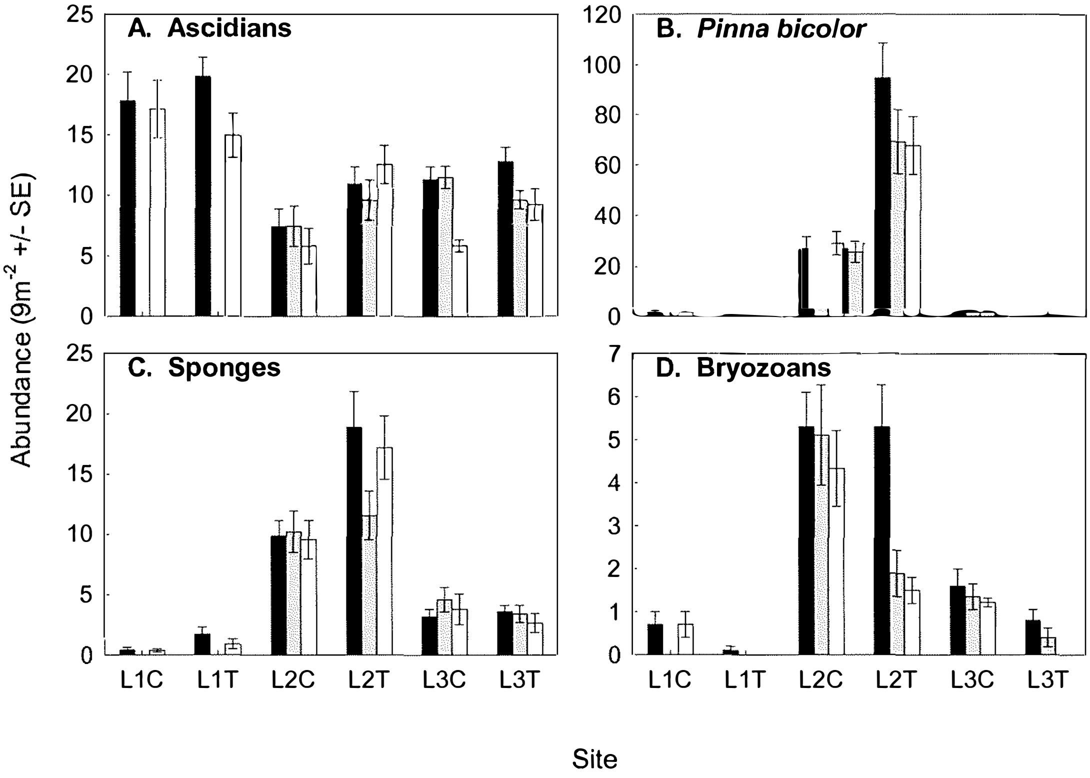


Figure 1.2. Changes in mean abundances in 9m^2 quadrats of major taxa over time. Black bar indicates census 1, grey census 2 and open census 3. L1C – Location 1 control site, L1T – Location 1 trawl site etc.

Over all three locations, and both treatments, there were 10 instances of individual taxa declining by more than 25% over the entire 5 month study period (see Fig. 1.2). Nine of these declines occurred at trawl sites, with only one being at a control site (ascidians at location 3). This is a significant bias towards decline at trawl sites (binomial test, $P = 0.011$), indicating that trawling does have an overall negative (although variable) impact on the abundances of epifaunal species. For the changes over the first two months (with only two locations), there were only five declines, all being at trawl sites ($P = 0.031$), so the negative effect of trawling is not always immediately obvious. There were only three instances of taxa increasing in abundance by greater than 25%, sponges at location 3 control over the first period, and ascidians and sponges at location 2 trawl over the second (recovery) period. No taxon increased by 25% at any site over the entire 5 months.

When individual demographic rates for the four main taxa were examined, the general trend was for persistence to decrease at trawl sites relative to control sites in the first (trawling) period, with few differences in the second (recovery) period. Conversely, recruitment was often higher at trawl sites over all periods, especially at location 2 (Figs 3-6). For period 1 (trawling), trawling decreased the persistence of all taxa (GLM: ascidians $F_{1,35} = 6.3$, $P = 0.017$; *Pinna* $F_{1,28} = 112.4$, $P < 0.001$; sponges $F_{1,37} = 14.6$, $P = 0.0005$;

bryozoans $F_{1,29}$ = 12.2, P = 0.0017) consistently at both locations (Figs 1.3a & 1.3b. Test for interaction between treatment and location P > 0.3 for all taxa).

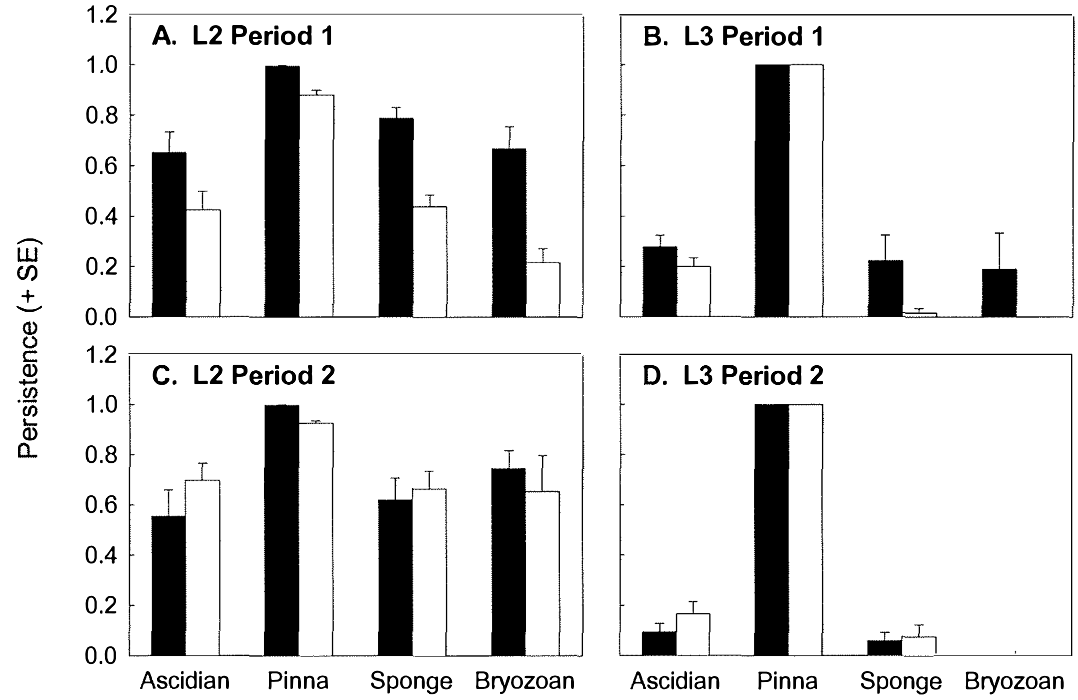
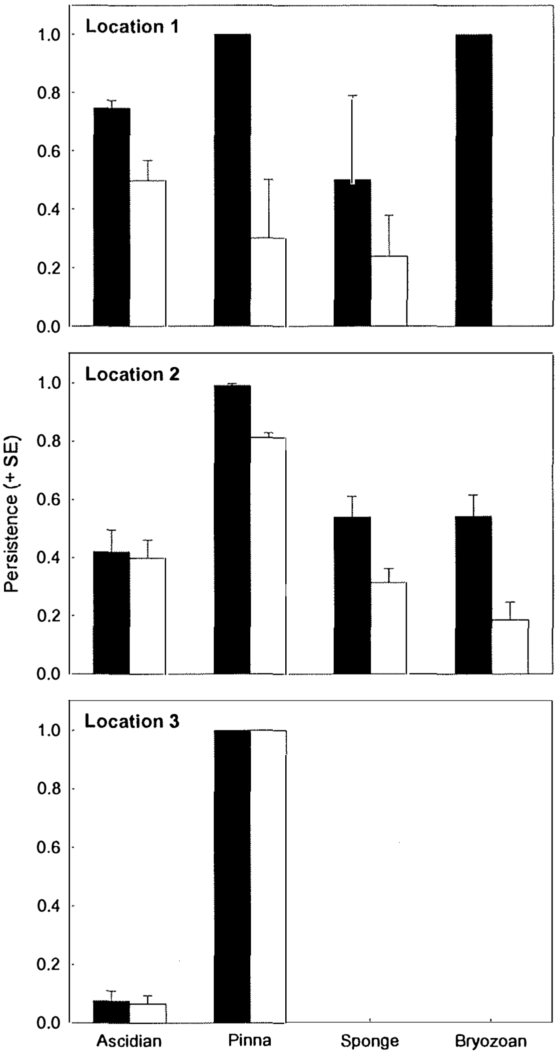


Figure 1.3. Effect of trawling on mean persistence of major taxa present in Gulf St Vincent. Black bars indicate control sites, and open bars trawled sites. L2 = Location 2, L3 = Location 3. Period 1 is when trawling occurred, period 2 is during recovery.

During period 2 (recovery) the only taxon to display an effect of trawling on persistence was *Pinna*, which continued to experience increased mortality at trawl sites (GLM: $F_{1,26}$ = 93.5, P < 0.001, Figs 1.3c & 1.3d), with all other taxa having the same persistence probability at both trawl and control sites (ascidians $F_{1,35}$ = 2.8, P = 0.11; sponges $F_{1,34}$ = 0.6, P = 0.43; bryozoans $F_{1,23}$ = 0.01, P = 0.92). Over the entire 5 months, *Pinna* ($F_{1,40}$ = 78.6, P = 0.001) and sponges ($F_{1,47}$ = 4.1, P = 0.05) had lower persistence in trawl than control sites, while ascidians had marginally lower persistence ($F_{1,57}$ = 3.7, P = 0.06). Bryozoans displayed an interaction between location and treatment ($F_{2,30}$ = 9.8, P = 0.005), with trawling decreasing persistence at locations 1 & 2, but not at location 3 where no bryozoans survived in either treatment (Fig. 1.4).

Figure 1.4. Effect of trawling on mean persistence over the entire 5 month study period for all three locations. Black bars indicate control sites, and open bars trawled sites.



Recruitment rates in period 1 (trawling) were greater in trawled than untrawled sites for *Pinna* only (GLM, $F_{1,38} = 36.4$, $P < 0.001$; sponges $F_{1,38} = 0.23$, $P = 0.64$; bryozoans $F_{1,38} = 0.8$, $P = 0.37$, Figs 1.5a & 1.5b). The effect of trawling on the recruitment of ascidians varied with location ($F_{1,36} = 9.6$, $P = 0.0038$), with a substantial increase at location 2, and a small decrease at location 3. During the second (recovery) period, recruitment of *Pinna* also increased in trawled relative to control sites ($F_{1,38} = 6.9$, $P = 0.012$), while again there was no effect for bryozoans ($F_{1,38} = 1.6$, $P = 0.21$; Figs 1.5c & 1.5d). For ascidians and sponges there was an interaction between treatment and location (ascidians $F_{1,36} = 8.3$, $P = 0.007$; sponges $F_{1,36} = 9.7$, $P = 0.004$), although prior trawling increased recruitment at both locations for ascidians, but only at location 2 for sponges, with a slight decrease at location 3. Over the full 5 months, recruitment of bryozoans was not affected by trawling ($F_{1,58} = 1.2$, $P = 0.28$), whereas that of *Pinna* increased ($F_{1,58} = 61.2$, $P < 0.001$, Fig. 1.6). Ascidians and sponges showed more complex behaviour, with results dependant on location (ascidians $F_{2,54} = 6.1$, $P = 0.004$; sponges $F_{2,54} = 7.0$, $P = 0.002$). Trawling decreased ascidian recruitment slightly at location 1, but increased it at locations 2 & 3 (Fig. 1.6). Sponges increased recruitment rates at locations 1 & 2 in response to trawling, but decreased at location 3 (Fig. 1.6).

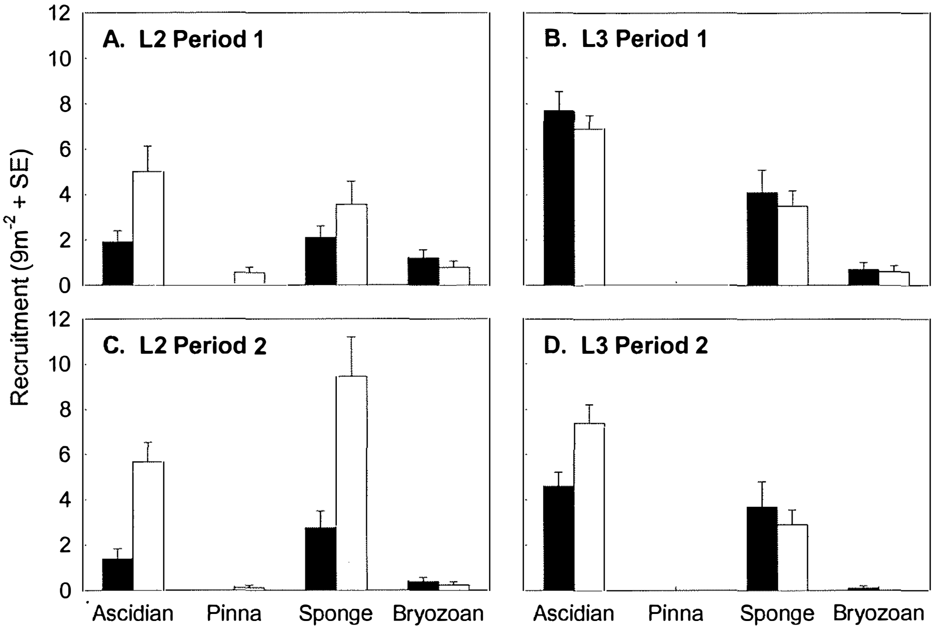


Figure 1.5. Effect of trawling on mean recruitment 9m^{-2} of major taxa present in Gulf St Vincent. Black bars indicate control sites, and open bars trawled sites. L2 = Location 2, L3 = Location 3. Period 1 is when trawling occurred, period 2 is during recovery.

There was a marginally significant effect of trawling on cover of the seagrass *Halophila ovalis* in January 2000 (2-way ANOVA, $F_{1,1}$ = 145.5, P = 0.053). Both trawl sites had substantially less seagrass than did the control sites (Fig. 1.7), although cover at the control sites was highly variable, with some quadrats having no seagrass, and others up to 18%. This difference represents an effect on colonisation, as no seagrass was present in October 1999.

Prawns showed no detectable response to trawling a month earlier. Catches in November did not vary as a function of whether a site had been trawled in October or not (2-way ANOVA, $F_{1,12}$ = 0.8, P = 0.38), although there was significant variation in catches among locations ($F_{1,12}$ = 22.2, $P < 0.0001$), indicating large-scale spatial variation in abundance. The mean size of animals also did not vary between trawled and untrawled sites (3-way ANOVA, $F_{1,2}$ = 0, P = 0.95), although there were significant effects of location and sex (and their interaction, $F_{1,2}$ = 0.7, $P < 0.0001$). There was, however, some indication of an effect on blue crabs, with catches at untrawled sites being marginally greater (27%), than at trawled sites in November (2-way ANOVA, $F_{1,12}$ = 3.9, P = 0.073).

Figure 1.6. Effect of trawling on mean recruitment 9m^{-2} over the entire 5 month study period for all three locations. Black bars indicate control sites, and open bars trawled sites.

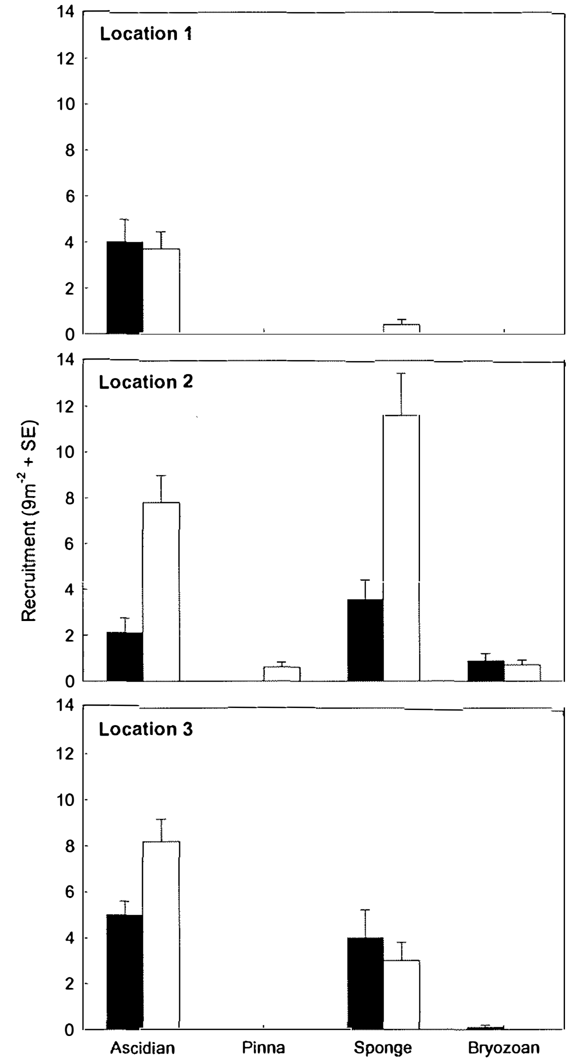
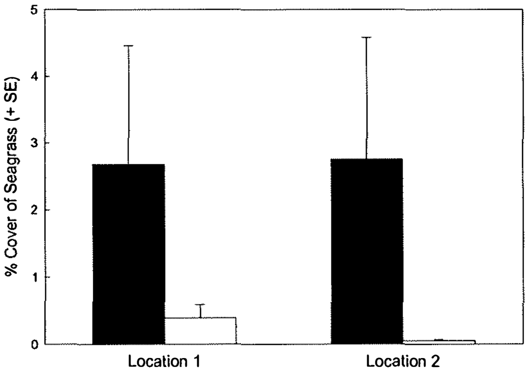


Figure 1.7. Response of the seagrass *Halophila ovalis* to trawling (abundance in January 2000). Black bars indicate control sites, open bars trawled sites.



Discussion

While the effects of trawling in this study were generally mediated by some unmeasured characteristics of the locations used, overall there was a decline in the abundance of epifauna at trawl sites compared to untrawled control sites. Of the four dominant taxa present (in six corridors), there were nine instances of a decline by more than 25% in the trawl corridors compared to only one such decline at the control corridors. The main negative effect of trawling was on the persistence of animals present at the start of the study (prior to any trawling), with recruitment rates of some taxa actually increasing at trawled corridors relative to control corridors, presumably because of an increase in free space. It seems likely that the natural disturbance regimes experienced by the different locations played a substantial role in determining this heterogeneous response. Location 2, with the most abundant epifauna, appeared to be a highly stable environment with a deep layer of fine sediment. Location 1 had coarser sediment, and less abundant epifauna, and appeared to experience an intermediate disturbance regime, while location 3 had very low epifaunal abundance and experienced very strong currents. At the later two locations, none of the epifauna appeared to be securely anchored to the bottom, but were instead attached to pieces of shell and simply resting on the sediment surface. Epifauna at location 2 were almost all attached to *Pinna*, which are capable of anchoring themselves in the sediment. Previous work has suggested that less stable habitats are less affected by trawling (e.g. Auster 1998; Kaiser *et al*. 1998; Jennings & Kaiser 1998), and also recover more quickly (Collie *et al*. 2000). Even in areas with no noticeable disturbance gradient, however, location differences in response to trawling have been found in a single experiment before (Lindegarth *et al*. 2000).

The level of damage reported here can probably be taken as the minimum effect that commercial trawling has on the benthos in areas of similar character that have not been trawled for some time. There are five main reasons for this. Firstly, the intensity of trawling was relatively low compared to what often occurs on the fishing grounds, where the same track is often repeatedly trawled (e.g. Rijnsdorp *et al*. 1998) which increases damage (e.g. Poiner *et al*. 1998). Secondly, not only is a given track likely to be trawled several times in close succession, but it may be trawled repeatedly over longer time-scales. Such long-term effects, and also indirect effects that may take some time to develop, are probably best examined by a rigorous comparison of trawl grounds (preferably newly opened) to nearby untrawled areas (e.g. Thrush *et al*. 1998; Frid *et al*. 1999). Given the low level of fishing effort in Gulf St Vincent, however, and the fact that prawn aggregations change location from year to year, it is likely that most trawled areas have time to undergo substantial recovery before repeat trawling. Thirdly, the trawl shots were of extremely short duration (10 min), and thus the cod end of the net contained little catch. Commercial shots in this fishery generally last for 1-2 hours, with several tonnes of catch accumulating in the cod end and being dragged along the bottom possibly causing extensive damage. Fourthly, the trawl doors did not appear to pass through any of the quadrats in this study. The doors are the most damaging component of the gear (e.g. Gibbs *et al*. 1980; Brylinsky *et al*. 1994; Auster *et al*. 1996), but affect only a small proportion of the substrate. Clear furrows about 0.5m wide, in which all epifauna had been bulldozed out of the way by the boards, were observed at all three trawl sites outside of the quadrats, so it is likely that if they had passed through the quadrats it would have been noticed. Finally, it has been assumed that the study locations have completely recovered from any previous trawling, but this may not be the case, even though some 15-20 years have passed. Thus we may be dealing with the shifting baseline syndrome (Pauly 1995, Carlton 1998). Due to the very imprecise nature of the existing logbook data on where trawling has occurred and the relatively low levels of effort in this fishery, it is also possible that none of the areas have ever been trawled. This is a problem for many studies of trawling, and highlights the need for accurate spatial data to be collected from day one of any new fishery.

If this experiment was repeated in the current trawl grounds it is unlikely that any effect would be detected. This is because most trawl damage occurs when an area is first trawled (Jones 1992; Jennings & Kaiser 1998), as vulnerable fauna are removed and only species capable of resisting trawl disturbance remain (e.g. Poiner *et al*. 1998). It is also possible that none of the current trawl grounds were ever like the study locations, although the fact that fishing stopped due to legislation reduces the probability of this. Since this study commenced, active commercial trawling has also resumed in the vicinity of location 2. Compared to many other fisheries, the trawl grounds occupy only a small portion of the available habitat in the gulf. Since a 2 year closure ended in 1993, the total area swept by the nets has ranged between 200-450 km^2 per year. Given that effort in this fishery is patchy, like other fisheries (e.g. Kaiser *et al*. 1996; Rijnsdorp *et al*. 1998), and that some areas are swept more than once, the total area disturbed each year may actually be substantially less than this. The total area of the gulf is about 7150 km^2, so less than 6% of the gulf is likely to be trawled in any one year.

The increase in heterogeneity of epifaunal abundance at location 2 after trawling is suprising given the general consensus that trawling decreases heterogeneity (Thrush *et al*. 1995; Engel & Kvitek 1998; Schwinghamer *et al*. 1998). Kaiser *et al*. (1998) did, however, find an increase in variation in community composition after beam trawling. Similarly, Ball *et al*. (2000) found increased variation in fished areas compared to nearby unfished areas around wrecks. In the current study, the increase in variation is likely to be due to the low intensity of the trawling regime. Thus, while the entire site was trawled twice on average, it is impossible to control the exact location of the net, so some areas are likely to have been trawled more, and some less. Some areas would also have had the cod end of the net dragged over them, which may cause more damage than the rest of the gear (with the exception of the otter boards), even when not loaded down with catch. There is also likely to be small-scale variation in vulnerability to trawling, due for example to changes in topography and sediment characteristics.

While substantial numbers of *Pinna* were removed by the trawl (a decline of just over 28% at location 2 compared to a 7% increase at the control site), most still remained after the trawl had passed. This is despite this species having a vertical orientation projecting some 20-30cm above the sediment surface, with only about 10cm below. In studying the effect of an otter trawl on erect sponges, Sainsbury *et al*. (1993) found that 90% were removed in a single pass. Presumably the hard-shelled *Pinna* are more robust than sponges (or the trawl gear used was less damaging). Closer inspection revealed that most remaining *Pinna* had been damaged, with the lip of the shell generally having been crushed, exposing the flesh of the animal. By the January census, about 2 ½ months after trawling, most of these had recovered, but it is likely that they did experience a cost of trawling, and that repeated damage would be beyond their abilities to repair. Most other sessile animals at location 2 were growing on the *Pinna*, although some of the bryozoans had grown to several times the size of the host. At the other two locations, most of the epifauna was attached to large pieces of shell (generally valves of scallops), and appeared to be capable of withstanding a degree of rolling along the bottom, as even at the control sites these sessile animals moved between censuses. This is especially true at location 3, where persistence was extremely low, and recruitment of ascidians very high. In this case, low persistence is probably due to animals being moved out of the permanent quadrats by currents, irrespective of trawling, whereas "recruitment" (which was usually of large animals), was probably often due to existing adults moving in. If *Pinna* can survive repeated trawling, then it may be possible to use growth checks in their shells as an index of trawling disturbance at a site, as has been done with other bivalves (Gaspar *et al*. 1994; Witbaard & Klein 1994).

An unusual aspect of this study is that the overall decline in abundance continued after the first post-trawl census, with an initial decline of 28% of all censused epifauna, and a further 8% decline in the next 2-3 months. Generally, those studies that included follow up censuses to assess longer-term effects and recovery only reported the later, with only comparisons of commercially fished areas to unfished areas including longer term effects. The level of damage found here is slightly higher than many other studies (e.g. 24% for Prena *et al*. 1999, and about 20% after two passes for Poiner *et al*. 1998), but less than the damage reported by Sainsbury (1988) for an erect sponge community (43-95%). The data on recruitment indicate that this continued decline is not a consequence of habitat degradation in trawled areas, but rather it is due to animals damaged by the trawl experiencing increased mortality rates. In fact, recruitment actually increased in trawled areas, suggesting that recovery may be swift, although very large colonies of bryozoans and adult *Pinna* may take longer to be replaced.

Epifaunal species are likely to provide habitat structure for other more mobile species (e.g. Bradstock & Gordon 1983; Sainsbury 1988; Turner *et al*. 1999). Thus their loss has greater consequences than might otherwise be the case. This is especially true given the largely sedimentary nature of Gulf St Vincent with little hard substrate, which means that most structure is biotic in nature. While no effect on commercially important crustaceans was detected in this relatively small scale manipulation, effects on fish were not tested because of the highly variable nature of their catches. At the larger scale of the fishery, there may, however, be consequences for the benthos that were not detected here.

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Chapter 2: Limited infaunal response to experimental trawling in previously untrawled areas.

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Abstract:

There is considerable argument about the effects of bottom trawling on the benthos. Many studies have been done on recently trawled grounds, where community composition has already been modified, and further effects are likely to be minimal. This study tests the effect of trawling on macroinfaunal assemblages in an area where little or no trawling had occurred in the previous 15 years. A spatially replicated Before-After, Control-Impact (BACI) design was used, with adjacent trawl and control corridors. Sampling was done in the same two small sites within each corridor before and after trawling to minimise confounding due to spatial variation. Despite this rigorous design, changes consistent with an effect of trawling were not detected. At only one of the three locations was a potential effect detected. These inconsistent results could be due to different disturbance regimes at each location, influencing the vulnerability of fauna to further disturbance. Given the high levels of variability in infaunal assemblages, however, the changes could also be due to asynchronous natural variation. The combination of high spatial and temporal variability, in association with light trawling gear, means that prawn trawling in South Australia does not have consistent effects on infauna.

Introduction

There is a consensus that dragging trawl gear across the sea floor is detrimental to marine biota and habitats (Jones, 1992; Engel and Kvitek, 1998; Hall, 1999). Watling and Norse (1998) suggested that, with the possible exception of agriculture, bottom trawling and dredging may be the most physically damaging and widespread of all human activities. Fishers have been complaining about the impact of bottom trawling since the 13th century (de Groot, 1984), blaming it for declines in commercial fish and shellfish stocks, of both target and non-target species. Trawling is believed to affect stock abundances directly by removing or killing individuals, and indirectly by affecting structures and organisms that serve as habitat and food (Sainsbury, 1988; Hall, 1999).

Despite these concerns, the intensity and extent of bottom trawling have continued to increase throughout the world, particularly over the last few decades (Hall, 1999). In heavily fished areas of the North Sea, every square meter of the sea floor is trawled on average seven times a year (Goñi, 1998). With improvements in technology, trawlers can now operate at depths down to

1200m (Judd, 1989), over rough ground, and near obstacles; areas that were de facto refuges from trawling until as recently as 10 years ago (Watling and Norse, 1998). The destructive potential of the gear used has also increased. The weight of the gear dragged along the sea floor is now as much as 13 tons when empty (Watling and Norse, 1998). ‘Tickler’ chains and chain matrices, used to improve catch rates, increase the amount of damage as much as ten-fold (Bridger, 1970).

A number of studies have investigated the impact of trawling on various components of the marine ecosystem, with mixed results. Demonstrating an impact of trawling on the benthos is not an easy task for a number of reasons. The severity of the damage caused varies, depending on the trawling regime, the trawl gear used (type, configuration and weight), the type of sediment and biota, and the natural disturbance regime (Jones, 1992; Kaiser and Spencer, 1996). In addition, the benthos is highly variable, both in time and space, which can confound sampling designs that attempt to detect effects of trawling (Lindegarth *et al.,* 2000). Quantifying the effects of trawling is also hindered by a lack of areas known to have not been recently trawled. The majority of research has been done in heavily fished areas such as the North Sea. The already-disturbed state of these areas is one explanation for why some studies have found that experimental trawls had no significant effect on the benthos (Bergman and Hup, 1992; Jennings and Kaiser, 1998; Kaiser, 1998).

The aim of this study was to investigate the effects of otter trawling for western king prawns (*Penaeus latisulcatus*) on the benthos in South Australia. Here, we concentrate on infauna, with the effects on epifauna discussed in Chapter 1. Previous studies (mostly on the effects of pollution) suggest that infaunal assemblages are good indicators of disturbance because of their sensitivity to habitat alterations, and importance to the structure and function of marine systems (Bilyard, 1987). Infauna are taxonomically and functionally diverse, and numerous other species, including those of commercial importance, depend directly or indirectly on them (Bilyard, 1987). The activities of infauna also affect important characteristics of the sediment, increasing the water and oxygen content, topographic detail, microbial activity and erosion resistance, decreasing compaction, and altering the grain size (Hall, 1994).

Trawling intensity in South Australia is relatively light. Less than 6% of the bottom has been trawled annually in recent years within Gulf St Vincent, where this study was conducted (Chapter 1). Despite this low intensity, trawling could still have important detrimental effects for this area. The waters off southern Australia are well known for their high levels of biological diversity and endemism (Lewis *et al.,* 1998). The gulfs are unusual in that they are ‘inverse estuaries’ where salinity (and water temperature) increase progressively towards the head of each gulf. These waters are important nursery areas for a number of commercially important fish and shellfish species, particularly in the extensive seagrass beds (Lewis *et al.,* 1998).

This study tests the hypothesis that bottom trawling affects macroinfaunal assemblages. We predicted that the structure of these assemblages (taxonomic composition and relative abundances) would diverge after trawling, from that of the same locations before trawling, and that of untrawled sites. The location and design of this experiment make it more sensitive and robust than most previous studies, as trawling in the vicinity of the study sites has been minimal for at least 10-15 years. The ability to detect effects in a naturally variable system was maximised by adopting a replicated, paired, control and impact experimental design, with sampling done both before and after trawling. Unlike most previous studies (particularly those using remote sampling gear), confounding of the before and after samples by spatial variability was minimised by sampling precisely the same small sites pre-and post-trawling.

Materials and Methods

Site selection

Three locations, 13-16 km apart, were chosen haphazardly in upper-central Gulf St Vincent (GSV), South Australia (Fig. 2.1). Bye (1976) describes the oceanography of GSV, and Shepherd and Sprigg (1976) give a large-scale description of the sediments and epibiota. The water depth was ~20 m at all locations. The distribution of trawling effort in GSV has been recorded in 30 nm^2 blocks since the fishery began in 1968. At the time of the study (1999), the block containing location 1 was last trawled during the 1997/98 season, but the trawling intensity had been very light since at least 1988/89 (< 1000 minutes total fishing time in 10 years in the entire block). The blocks containing locations 2 and 3 had not been trawled since 1985. Lack of trawling activity was due initially to a closure after collapse of the fishery in the early 1980s (Lewis *et al.,* 1998), and subsequently to a preference for the southern gulf area. The sediment at locations 1 and 3 was medium-coarse sand and shell fragments, while at 2, it was fine silt.

Each location included an east-west orientated ‘control’ corridor and an adjacent ‘impact’ (trawl) corridor, ~200 m wide by 0.5 nm (937 m) long. The close proximity of the control and trawl corridors within locations minimised any pre-trawl differences in the benthic assemblages due to spatial variation. Two 2 x 1 m sampling sites, within 10-20 m of each other, were chosen randomly near the centre of each corridor and marked out with steel pegs. Sampling therefore, was done at more than one spatial scale (sites were nested within corridors, and corridors within locations).

Experimental trawling

Trawling was done at night and under supervision by a locally chartered commercial triple otter prawn trawler (the “Jillian Sandra”) in October 1999. The combined sweep of the nets was ~20m. The two 102 x 213 cm otter boards weighed 200 kg each and the two skids 240 kg each (in air). The trawler made ten adjacent passes along each trawl corridor, which was then repeated to ensure complete coverage, so on average, the entire corridor was trawled twice. Bycatch was discarded when the vessel was outside of the study corridors. A DGPS was used for accurate navigation (± 10 m), and the vessel’s speed was 3.5 knots during trawling.

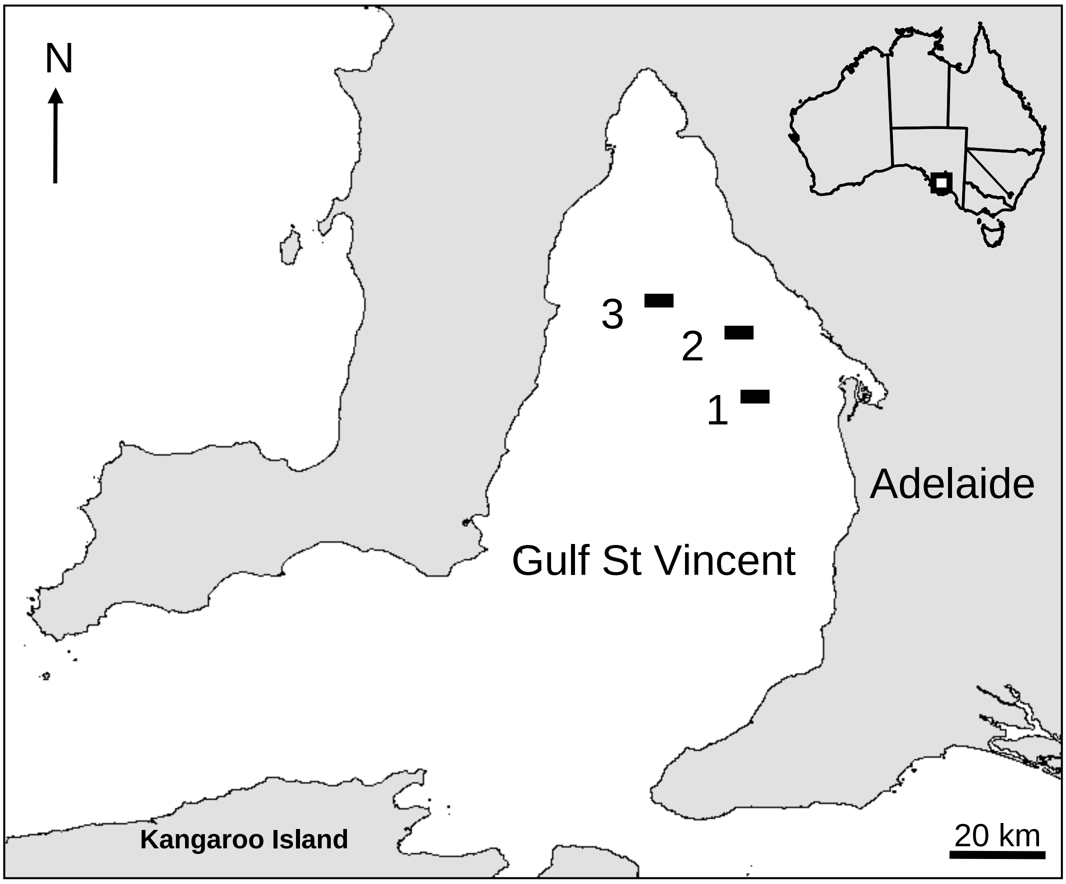

Figure 2.1. Map of Gulf St Vincent, South Australia, showing placement of the study locations.

Sampling

The before-trawl sampling was done two months prior to trawling. SCUBA divers collected samples of sediment to 150 mm deep using corers made of 40 mm internal diameter PVC piM. The relatively small size of the cores enabled more samples to be collected and processed in the time available, which improved the precision and power of the study. Small units are also more efficient when sampling aggregated organisms (as is the case for most infauna; Elliot, 1981). The samples were fixed in 10% formalin in seawater and buffered with borax immediately after collection. On the pre-trawl sampling trips, twelve replicate cores were collected from each site. Graphs of the standard error of the mean number of taxa and total abundance per core sampled for each site asymptoted before n = 10, indicating that statistical precision for these variables was optimised with ten replicates. Therefore, ten samples were collected at each site after trawling.

The post-trawl samples were collected at locations 2 and 3 within a week of trawling. However, bad weather prevented sampling at location 1 until the next scheduled cruise in January 2000. Tracks left by the trawler's otter boards and skids were evident within all trawl corridors. Between the otter board tracks, the footline and net had removed 28% of the epifauna (Chapter 1) and the topographic features of the sediment such as mounds created by burrowing animals. Epifauna in all trawled quadrats showed signs of damage, indicating that the trawl had passed directly over them at least once. Trawl board marks were also evident in the vicinity of some quadrats, but were not sampled.

The samples were washed through 2 mm and 1 mm-mesh sieves, with the fauna being picked out from the retained sediment under water. Most polychaetes were identified to family, with families that were common and containing a number of distinctly different gross morphologies (Spionidae, Syllidae, Ctenodrilidae) divided further into groups based on these differences. Other phyla were identified to suborder or higher, depending on taxonomic knowledge of the group for the study area. All infauna retained on the sieves were included in the analysis.

Statistical methods

The 'before-after, control-impact' (BACI) design is a factorial design in which the evidence for an impact appears as a significant Time (Before versus After the impact) by Treatment (Control versus Impact) interaction (Green, 1979). In light of the potential for 'background noise' to confound results, analyses were done at the phylum level as well as at the highest level of taxonomic resolution achieved (referred to subsequently as 'high resolution'). Polychaetes alone were also analysed at the family level, in case the use of phyla and other high level taxa obscured any patterns. Location 1 was analysed separately because the post-trawl samples were collected well after those from the other two locations, and the data were therefore temporally confounded. The analyses from location 1 should be interpreted with caution, as the data are not properly replicated (Hurlbert, 1984). The results from location 1 were used only to back up the results from the location 2 and 3 samples (referred to subsequently as 2+3).

Multivariate procedures

The non-parametric multivariate analysis of variance program, NP-MANOVA (Anderson, 2001), was used to test for differences among the infaunal assemblages between times and treatments (types and abundances of taxa in the replicate core samples). This program has been designed to test multivariate ecological hypotheses that require a complex multi-factorial experimental design such as BACI. The current version of NP-MANOVA has a constraint on the maximum number of factors (two), and thus the analysis had to be done in two steps. We used NP-MANOVA despite this shortcoming as traditional MANOVA does not give reliable results with most ecological data sets, and no other non-parametric alternative is capable of multi-factorial MANOVA (Anderson, 2001). The hypothesis predicts an interaction between Time and Trawling (trawled sites should vary through time differently to untrawled sites). Analyses were thus done with the factors Time (before vs after) and Trawling (trawled vs untrawled) by pooling sites and locations, for the standard test of an interaction between Time and Treatment ($n = 40$ for the 2+3 samples and $n = 20$ for the location 1 samples). Analyses were also done with the factors Time and Site ($n = 10$), making Time × Site the interaction of interest, to reveal any differences within and between locations and their responses to trawling.

The Bray-Curtis similarity measure was used in NP-MANOVA, because it is not affected by joint absences, and is one of the most reliable measures of ‘ecological distance’ (Clarke, 1993). The data were fourth-root transformed to prevent abundant taxa from influencing the Bray-Curtis similarity measure excessively (Clarke, 1993). Time and Trawling were treated as fixed factors, but Site was treated as random. Significance levels for all tests were calculated by conducting 4999 permutations of residuals under a reduced model (Anderson and Legendre, 1999). If the interaction between the two factors was significant, the source of the difference was found by using pair-wise *a posteriori* comparisons.

Non-metric multidimensional scaling (nMDS) ordinations provided a visual indication of the similarity of assemblages at each site, before and after trawling, based on the mean abundance per core for each taxon at each site (n = 10). Similarity is indicated by the distance between the positions assigned to the sites in the two-dimensional plots. The Bray-Curtis similarity measure was used to calculate the distances, after fourth-root transformation. Stress values associated with these plots indicate the magnitude of distortion between the original ordination and the 2-dimensional graphs. The values obtained (<= 0.13, Fig. 2.2) indicate they are adequate for interpretation (Clarke 1993), and 3-dimensional plots did not greatly improve their interpretability. The PRIMER program (Plymouth Routines in Multivariate Ecological Research; Clarke, 1993) was used for these ordinations. Ordinations were done for the 2+3 and location 1 data separately, and at both high and low (phylum) levels of taxonomic resolution.

Univariate procedures

The number of taxa and of individual animals per core are widely used indicators of disturbance, and are examined here. A diversity index was not used as they lack sensitivity (Warwick and Clarke, 1991) and different indices can give conflicting results (Hurlbert, 1971). The three most common phyla and high-resolution taxa were also analysed separately. Standard multi-factorial ANOVA was used to test for a significant Time × Trawling interaction in the number of taxa and total abundance at each site. The interaction between Time, Location and Trawling was also of interest for the 2+3 data, as it tests for differences in the effect of trawling between the two locations. When a significant interaction was found, Student-Newman-Keuls (SNK) tests were used to locate the source of the difference. The 2+3 data had four factors; Time (fixed and orthogonal), Trawling (fixed and orthogonal), Location (random and orthogonal), and Site (random and nested within both Trawling and Location). For the location 1 data, there were three factors, with the same structure as the 2+3 data, but without Location. Cochran’s Test was used to test for homogeneity of variance. Heterogeneous data were transformed using $\log_e(x+1)$. If transformation did not remove heteroscedasticity, the raw data were analysed. The traditional alpha value of 0.05 was used to define significance in all analyses including the heteroscedastic data, as ANOVA is robust to all but serious heterogeneity, and a more conservative alpha value increases the chance of Type-II errors, which are more detrimental in impact studies (Underwood, 1993). Post-hoc pooling of the Time × Location × Trawling interaction (for 2+3) and Time x Site interaction (for Location 1) with the Residual was done when $p > 0.25$ (Winer *et al.,* 1991) to improve the power of the test of the interaction (Time × Trawling) indicative of impacts.

Results

Multivariate analyses

We sampled a total of 1719 individuals, belonging to 67 high-resolution taxa and nine phyla (Appendix 1). Polychaetes accounted for 62% of individuals, crustaceans 20%, and nemerteans 10%. No consistent and unambiguous effects that could be ascribed to trawling were detected. Although there were significant Time × Site interactions at both taxonomic resolutions (Table 2.1a, b), pairwise tests did not reveal variation consistent with the predicted effects of trawling. For example, at high taxonomic resolution, temporal changes at location 2 were consistent with an effect of trawling, as only the trawled sites changed. At location 3, however, the opposite occurred, with only the control sites changing. When sites and locations were pooled within Trawling, the Time × Trawling interaction was not significant ($p = 0.80$), which again indicates no overall effect of trawling. Analyses on polychaetes alone at the family level gave similar results, and are not reported further.

The nMDS plots also do not indicate strong consistent effects of trawling (Fig. 2.2). If trawling had large effects, trawled and untrawled sites would show a greater separation after trawling (solid symbols) than before (open symbols). Instead, the plots reveal large spatial and temporal variation that does not match this pattern.

Table 2.1. Multivariate ANOVAs for effects of trawling, at high taxonomic resolution and at the phylum level, for locations 2 and 3, and separately for location 1.

Source	df	SS	F	P	SS	F	P
		(a) 2+3, high resolution			(b) 2+3, phylum level		
Time	1	6686	1.54	0.16	3120	1.72	0.23
Site	7	153426	8.74	0.0002	45565	7.60	0.0002
Time x Site	7	30351	1.73	0.0028	12692	2.12	0.0074
Residual	144	361082			123263		
		(c) 1, high resolution			(d) 1, phylum level		
Time	1	6197	1.77	0.11	648	1.46	0.32
Site	3	10132	1.18	0.24	837	0.28	0.94
Time x Site	3	10529	1.23	0.19	1334	0.44	0.87
Residual	72	206156			72564		

No effect of trawling was detected at location 1, as the Time × Site interaction was not significant for either phylum or high-resolution analyses (Table 1c, d). The first level effects of time and site were also not significant, indicating that little spatial or temporal variation occurred at this location. Repeating the analysis with sites pooled into treatments (i.e. testing the Time × Trawling interaction) did not make any difference to the results.

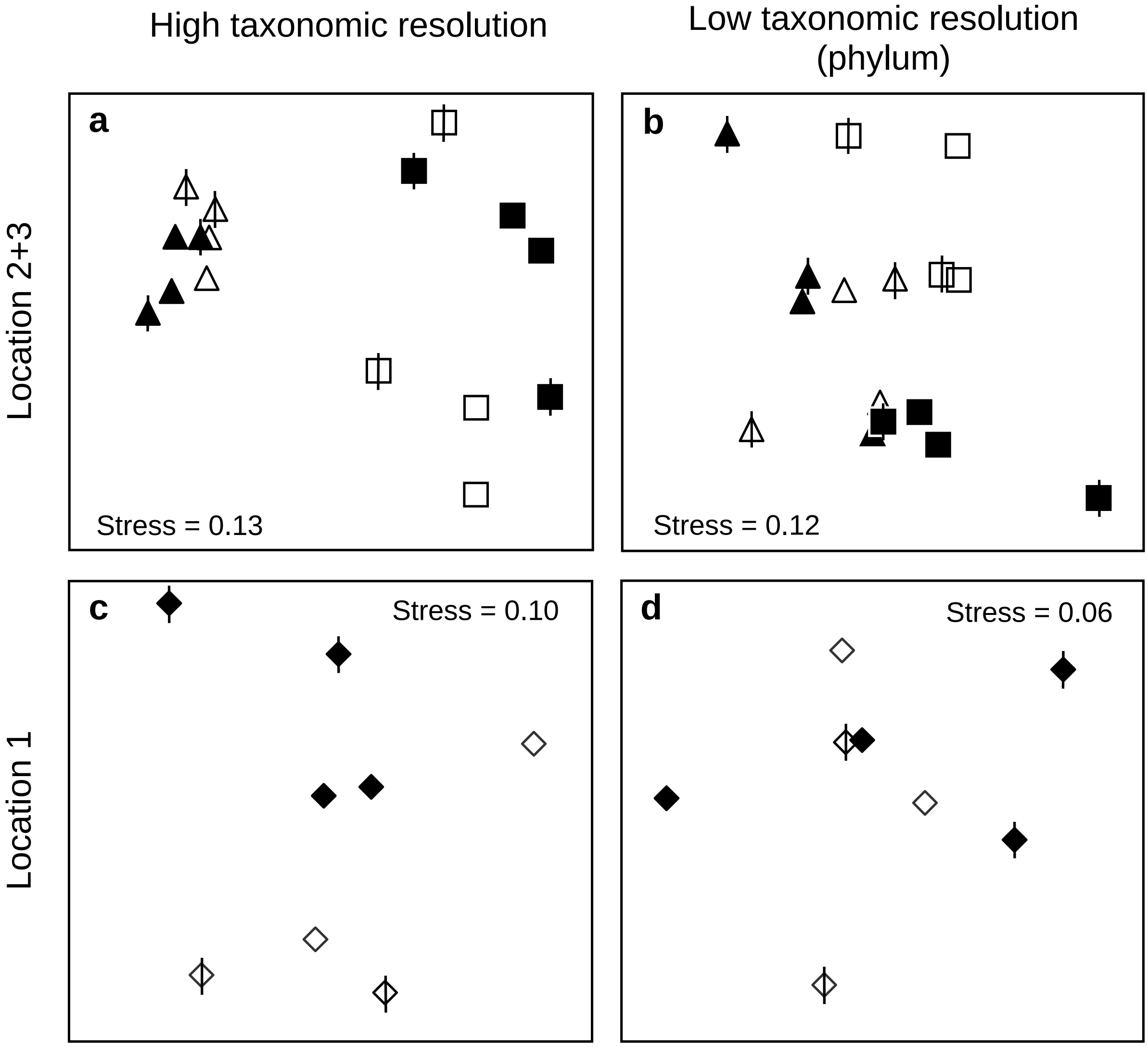

Figure 2.2. Non-metric multi-dimensional scaling (nMDS) ordinations, showing differences in the infaunal assemblages at the sites within locations 2 and 3, and location 1, before (open) and after (solid) trawling. Symbols with vertical lines refer to trawl sites.
▲ = Location 2, ■ = Location 3, ◆ = Location 1. *n* = 10

Univariate Analyses

Only three univariate variables exhibited changes indicative of an impact of trawling. Changes to total abundance for 2+3 mirrored the multivariate patterns discussed above. The Time × Trawling × Location interaction was significant (Table 2.2a), with total abundance decreasing at the trawled sites of Location 2 and the control sites of 3 (Fig. 2.3a, SNK tests).

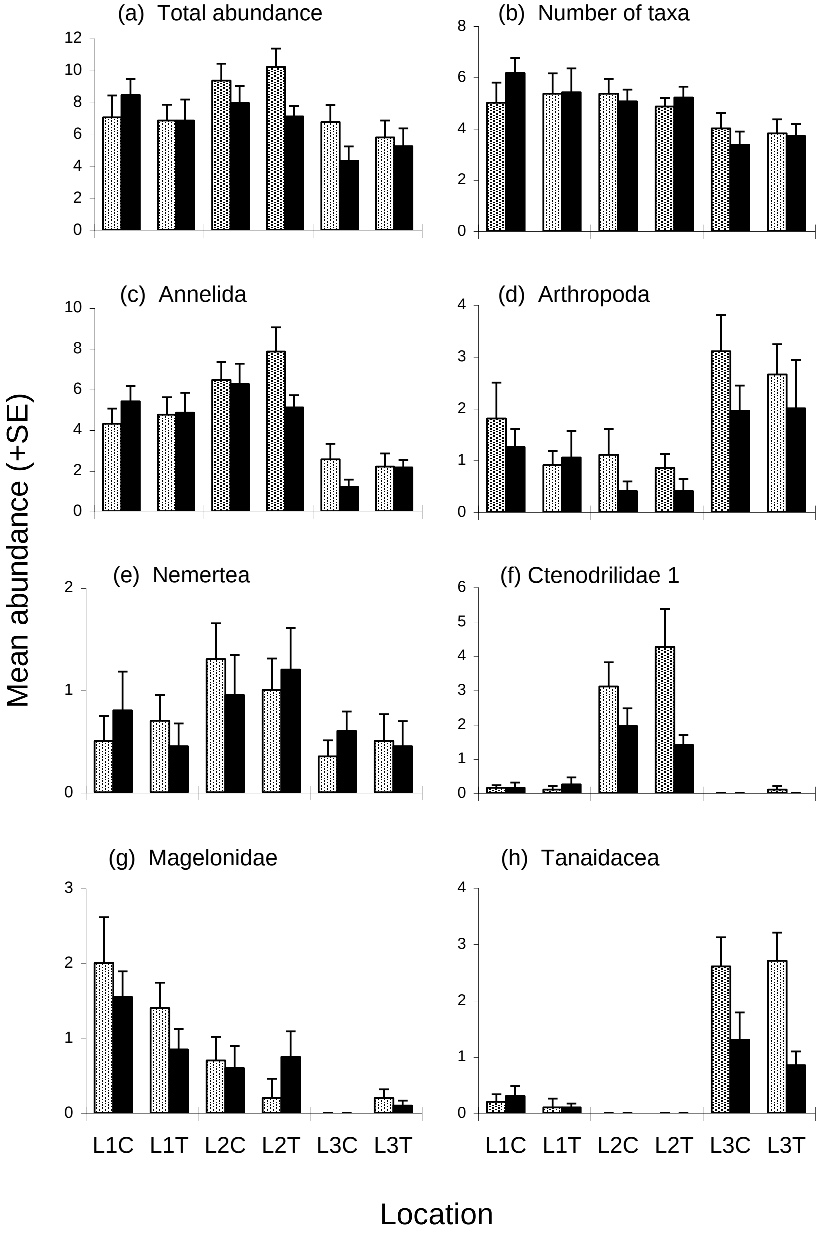

Figure 3.3. Changes in abundance over time (before versus after trawling), for total abundance, number of taxa, and the three most abundant phyla and high-resolution taxa. The two sites within each corridor have been combined to simplify interpretation of the graphs. Grey bars represent before trawling, black represents after trawling. *n* = 20. L1C = location 1 control, L1T = Location 1 trawl, etc.

Table 2.2. ANOVAs for effect of trawling on selected univariate variables (locations 2 & 3).

Source	*df*	*MS*	*F*	*p*	*MS*	*F*	*p*	*MS*	*F*	*p*	*MS*	*F*	*p*
		(a) Abundance			(b) Number of taxa^{p}			(c) Annelida			(d) Arthropoda^{p}		
Time	1	138.76	23.10	0.13	1.23	0.77	0.54	1.37	23706.7	0.0041	4.28	46.30	0.09
Location	1	387.51	188.45	0.0002	78.40	12.13	0.03	38.81	42.36	0.0029	16.07	26.83	0.01
Trawling	1	0.01	1.00	0.50	0.10	0.16	0.76	0.03	2.86	0.34	0.26	2.06	0.39
Site (Lo × Tr)	4	2.06	0.19	0.94	6.46	2.46	0.05	0.92	3.50	0.01	0.60	2.00	0.97
Ti × Lo	1	6.01	2.10	0.22	1.60	0.87	0.39	0.00	0.00	0.99	0.09	0.25	0.60
Ti × Tr	1	0.06	0.00	0.97	3.60	1.96	0.22	0.04	0.03	0.89	0.02	0.05	0.83
Ti × Si (Lo × Tr)	4	2.86	0.27	0.90	2.29	0.87	0.48	0.22	0.83	0.51	0.37	1.25	0.29
Lo × Tr	1	0.01	0.00	0.96	0.63	0.10	0.77	0.11	0.12	0.75	0.13	0.21	0.67
Ti × Lo × Tr	1	31.51	11.03	0.03	0.03	0.01	0.91	1.40	6.45	0.06	0.02	0.08	0.79
Residual	144	10.72			2.63			0.26			0.30		
		(e) Nemertea^{p}			(f) Ctenodrilidae sp 1			(g) Tanaidacea			(h) Magelonidae^{p}		
Time	1	0.01	0.05	0.86	42.03	1.11	0.48	14.40	1.00	0.50	0.01	1.00	0.50
Location	1	3.88	16.55	0.02	280.90	478.13	0.0000	112.23	40.62	0.0031	15.01	17.53	0.01
Trawling	1	0.01	1.46	0.44	1.23	1.96	0.39	0.90	1.00	0.50	0.31	5.44	0.26
Site (Lo × Tr)	4	0.23	1.05	0.38	0.59	0.22	0.93	2.76	2.53	0.04	0.86	1.55	0.19
Ti × Lo	1	0.15	0.31	0.60	38.03	78.00	0.0009	14.40	1152.00	0.0001	0.01	0.01	0.92
Ti × Tr	1	0.06	0.12	0.74	8.10	1.27	0.46	0.02	1.00	0.50	0.06	0.10	0.77
Ti × Si (Lo × Tr)	4	0.46	2.07	0.09	0.49	0.18	0.95	0.01	0.01	1.00	0.68	1.23	0.30
Lo × Tr	1	0.00	0.02	0.90	0.63	1.06	0.36	0.90	0.33	0.60	0.06	0.07	0.81
Ti × Lo × Tr	1	0.52	1.10	0.34	6.40	13.13	0.02	0.23	18.00	0.01	0.16	0.27	0.62
Residual	144	0.22			2.69			1.0931			0.55		

Post-hoc pooling of the interaction term Ti x Lo x Tr with the residual (when p>0.25 – indicated by ^{p}) enabled a more powerful test of the main interaction of interest, Ti × Tr (Winer et al, 1991). Results of Cochran's tests and transformations: a, b = homogeneous (p > 0.05) and untransformed; c, d, e = homogeneous after $\log_e(x + 1)$ transformation; f, g, h = heterogeneous and untransformable.

The number of taxa per core was also greater at location 2 than 3, but interactions indicative of an effect of trawling were not significant (Table 2.2b). Individual taxa exhibited asynchronous variation in abundance over time and space (Fig. 2.3c-h), but the Time × Treatment interactions indicative of trawling impacts were never significant (Table 2.2c-h). The polychaete Ctenodrilidae type 1 and crustacean Tanaidacea changed in a manner consistent with an effect of trawling at one location only (they were very rare at the other location), as indicated by significant Time × Location× Treatment interactions (Table 2.3f-g, SNK tests). Ctenodrilidae 1 were common but decreased over time at location 2, particularly at the trawl sites (Fig. 2.3f). Tanaidacea were common but decreased at location 3, decreasing slightly more at the trawl sites (Fig. 2.3h). For location 1, the Time × Treatment interaction was not significant for any of the univariate variables (p>0.17 in all cases). Post-hoc pooling of the Time × Location × Treatment (for 2+3) or Time × Site (for Location 1) with the residual enabled a more powerful test, but did not change the significance of any results.

In summary, there was considerable variation in abundances of taxa among locations (separated by 13 – 16 km) which at the scale of sites (10s of meters) was substantially reduced or not detectable (Table 2.2). This larger scale variation appeared, in general, to swamp any variation that could have been attributable trawling.

Discussion

The results do not support the hypothesis that trawling causes changes to infaunal assemblage structure as a general phenomenon. While the patterns of change at one location (2) and in two taxa supported the hypothesis, patterns at the other two locations and in other taxa did not. One possible reason for this is that different locations and taxa show differing susceptibilities to trawling, as has been found in other studies (e.g. Collie *et al.,* 1997, Engel and Kvitek, 1998, Kaiser, 1998, Kaiser and Spencer, 1996). Alternatively, the different patterns observed may be due to asynchronous, but natural, spatial and temporal variation. Thus, the changes at location 2 cannot be rigorously ascribed to trawling, as substantial changes also occurred at control sites, and so may have occurred by chance. Several other studies have failed to detect effects of trawling on infauna (e.g. Gibbs *et al.* 1980, Hall *et al*. 1993, Simboura *et al.* 1998), although none of these used a strictly controlled experimental trawling regime.

Given the high levels of natural variability inherent in marine assemblages (particularly infauna), it is important that studies on the effects of trawling are rigorously designed to avoid confounding. Inferences about trawling have been made by comparing existing trawled areas with areas believed to be untrawled or lightly trawled (e.g. Gibbs *et al.* 1980, Collie *et al.,* 1997, Engel and Kvitek, 1998, Simboura *et al.* 1998, Frid *et al.,* 1999), but these comparisons are spatially confounded as locations may vary naturally. Indeed, unless trawling has been excluded from an arbitrarily designated area by legislation, there is good reason to believe that trawled and untrawled areas will differ substantially. Trawling effort data, which is used to define the trawling regime, may also be unreliable as it has to be inferred from fishing logs or visual clues such as density of trawl tracks (Engel and Kvitek, 1998), and illegal trawling still occurs in ‘closed’ areas (Poiner *et al.,* 1998). Studies that sample before and after trawling but do not include control sites (e.g. Bergman and Hup, 1992), are temporally confounded. Assemblages change naturally over time, in response to factors such as recruitment events and natural disturbances. Lindegarth *et al.* (2000) compared different combinations of single control and trawl sites of a Multiple Before-After, Control-Impact experiment and found that some pairs showed changes indicative of an impact from trawling, but others did not. Even studies that are temporally replicated with multiple sampling times both before and after trawling (Before-After, Control-Impact Paired Series BACIPS, e.g. Tuck *et al.* 1998), but not replicated in space, are spatially confounded (Hurlbert, 1984; Thrush *et al.,* 1994). Thrush *et al.* (1994) found that spatial variation in infauna was greater and had more influence on results than temporal variation. They concluded that spatial variability confounds temporal patterns in time series data, such as that of BACIPS experiments.

The severity of the disturbance caused by trawling (and the ability to detect impacts of trawling) is influenced by the natural disturbance regime (Jennings and Kaiser, 1998). The infauna in stable sediments may be less tolerant to trawling because they are not adapted to high levels of disturbance (Kaiser and Spencer, 1996). The physical severity of the trawling disturbance will also vary with sediment type, as the gear penetrates deeper into soft muds than coarse or hard-packed sands (Hall, 1999). In areas with a naturally high disturbance regime, movement of the sediment can cause a dilution of the effects of disturbance (Hall, 1999). Kaiser and Spencer (1996) found lower numbers of species and individuals in trawled areas than in untrawled areas with stable sediments, but no significant difference in areas with coarse, mobile sediments. They found that the mobile sediments had an impoverished and highly variable infaunal community, and suggested that these factors may have prevented the detection of differences between trawled and untrawled areas. In our study, location 2 had very fine sediments compared to coarse sediments at locations 1 and 3, and this may account for the apparent effect of trawling at this location only. Lack of replication within this sediment type, however, means that this interpretation is tentative.

Most studies that fail to detect effects of trawling have been criticised on the grounds that they have been conducted in areas that have been trawled previously, or that they fail to adequately account for natural variation in organism abundance. In this study, however, we examine areas that have not been trawled for a relatively long period (15-20 years), and have carefully controlled for spatial variation. The lack of an effect is thus more likely to be due to the light trawl gear and low level of trawling used in the experiment, which is characteristic of the fishing grounds in this lightly trawled area. Poiner *et al.* (1998) in the Great Barrier Reef region found that a single pass with an otter trawl did not significantly affect the epifauna, and severe damage was only detected after repeated trawling of the same ground. Consistent with this finding, Tuck *et al.* (1998) found that repeated trawling in a Scottish sea loch caused clear long-term changes to topography and infaunal community structure. Damage would have been worse in areas subjected to the passage of the otter boards (e.g. Caddy 1973, Brylinsky *et al.* 1994, Gilkinson *et al.* 1997), although these tracks only cover a small proportion of the area affected by the trawl, and were not sampled in this study.

The amount of natural temporal and spatial variability in biological assemblages can exceed changes induced by anthropogenic disturbances. We suggest that, in South Australia, prawn trawling at its current level does not cause consistently significant changes to infaunal assemblages, due to a combination of high natural variability and relatively low-impact trawling gear, particularly in areas with high levels of natural disturbance. It is likely that the degree of adaptation to disturbance and the physical environment also affect the extent of disturbance caused by trawling. This result contrasts to that found for epifauna, which experienced an average 28% decline in abundance from the experimental trawling, and which slowly declined further in subsequent months (Chapter 1).

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Appendix 2.1. Identification and total abundances of taxa found over all sites and times sampled (from 240 cores).

Phylum	High-resolution	Total	Phylum	High-resolution	Total
Annelida	Ampharetidae	29	Annelida	Spionidae sp 4	5
	Arabellidae	12		Syllidae sp 1	47
	Caobangidae	1		Syllidae sp 2	17
	Capitellida	60		Syllidae sp 3	14
	Cirratulidae	13		Terebellida	41
	Ctenodrilidae sp 1	229	Arthropoda	Anthuridea	3
	Ctenodrilidae sp 2	4		Brachyura	4
	Dorvilleidae	7		Caprellidea	3
	Eunicidae	2		Caridea	2
	Flabelligeridae	72		Copepoda	31
	Glyceridae	4		Crustacea larvae	1
	Magelonidae	164		Cumacea	4
	Nephtyidae	103		Gammaridea	130
	Nereidae	1		Isopoda	9
	Opheliidae	5		Leptostraca	3
	Oweniidae	15		Mysidacea	2
	Paraonidae	9		Ostracoda	6
	Parergodrilidae	2		Pycnogonida	1
	Phyllodocidae	19		Tanaidacea	150
	Pilargidae	2	Chordata	Ascidiacea	13
	Poecilochaetidae	8	Cnidaria	Actiniaria	1
	Polychaeta sp 1	1	Echinodermata	Echinoidea	15
	Polychaeta sp 2	7		Holothuroidea	34
	Polychaeta sp 3	1		Ophiuroidea	13
	Polychaeta sp 4	2	Echiura	Echiura	3
	Polychaeta sp 5	1	Mollusca	Bivalvia	34
	Polychaeta sp 7	4		Gastropoda	2
	Polychaeta sp 8	3		Opisthobranchia	4
	Polynoidae	4		Polyplacophora	1
	Sabellidae	37	Nemertea	Nemertea sp 1	137
	Sigalionidae	11		Nemertea sp 2	29
	Spionidae sp 1	92		Nemertea sp 3	10
	Spionidae sp 2	10	Sipuncula	Sipuncula	13
	Spionidae sp 3	3			

Chapter 3: The influence of harvest refugia on penaeid prawn population dynamics and sustainable catch

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Abstract:

Harvest refuges have frequently been proposed as fishery management tools for species with sedentary adults and dispersive juveniles, but less often for species with a highly mobile adult phase. In this paper I use a population model to investigate the potential of using harvest refuges for managing species with both dispersive juveniles and mobile adults, using the penaeid prawn *Penaeus latisulcatus* as a model. Maximum harvest occurred when only a very small proportion of the habitat (2-3%) was fished very heavily ($F = 10$). When only a small percentage of the habitat was trawled, harvest increased as fishing mortality increased, but when trawling was more extensive, harvest peaked with a relatively low fishing mortality. This supports recent contentions that by themselves, marine reserves are insufficient to manage a fishery effectively, and that they need to be used in conjunction with effort restrictions. Sensitivity analyses indicated that adult, juvenile and larval mortality are all near thresholds that qualitatively change model behaviour, but provided their values remain below the threshold it is not important to know them accurately to determine the best harvest regime.

Introduction:

Increasing attention is being paid to the use of no catch areas as a precautionary tool for fishery management. Marine protected areas (MPAs) provide a spatial refuge for exploited stocks, in contrast to traditional management measures (e.g. closed seasons, effort restrictions) which provide a temporal refuge (Bohnsack et al. 1998), and are thus a fundamentally different way of management. However, a number of studies have shown that MPAs by themselves have severe limitations, and suggest that they need to be utilised in concert with more conventional effort restrictions (Holland and Brazee 1996; Allison et al. 1998). While protected areas have been a mainstay of terrestrial wildlife management, their use in marine systems is still relatively rare, although increasing, and often meets with fierce resistance from affected fishing industries (e.g. Brailovskaya 1998). It is now widely recognised that MPAs are probably one of the best ways of preserving exploited fish stocks under a wide range of scenarios where it is not possible to gain accurate estimates of the parameters (such as fishing and natural mortality) used in traditional fishery models, restrictions on effort are difficult to enforce, or there is a great deal of unpredictable variability in the dynamics of the exploited populations (e.g. Carr and Reed

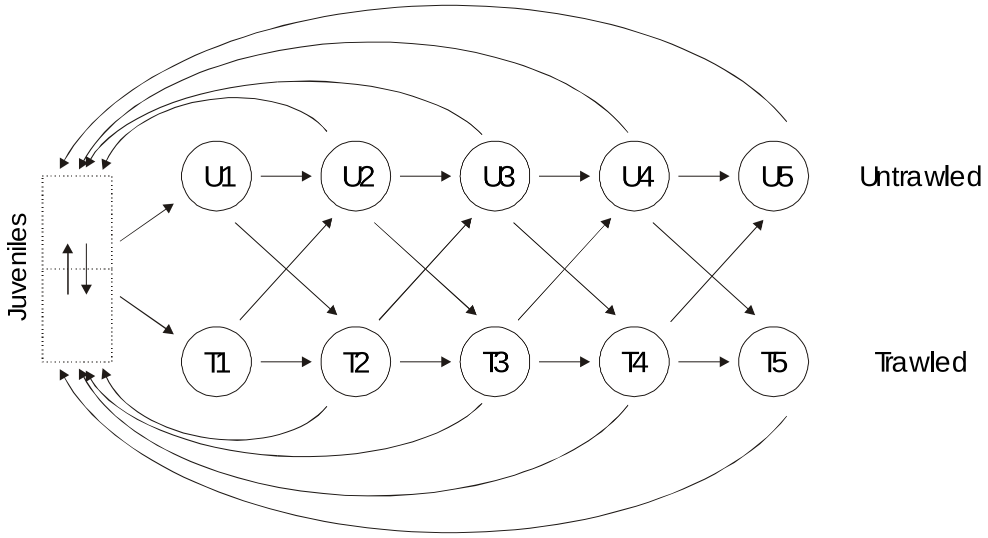
1992; Lauck et al*.* 1998; Sumaila 1998). In these cases, an MPA is often more easily enforced than other catch or effort restrictions, and provides a source from which over-exploited areas can be recolonised, improving the stock's sustainability (e.g. Buxton 1992; Mangel 1998).

Marine protected areas have been particularly emphasised for the management of relatively sedentary invertebrates, such as abalone and sea urchins (e.g. Dugan and Davis 1993). Many of these species rely on high density aggregations of adults for successful fertilisation of externally released eggs (Pennington 1985), and are thus vulnerable to even moderate reductions in population size. The use of MPAs to manage species with more mobile adults has received somewhat less attention, although the idea has been around for some time (e.g. Beverton and Holt 1957). For these species, the protection of spawning sites has been emphasised (e.g. Die and Watson 1992; Horwood et al. 1998), and the influence of protecting other areas of the habitat is not as well known. It is generally considered that because adults are likely to move out of protected areas over fairly short time-scales, MPAs will be of little use in preventing over-exploitation. However, some simulation studies indicate that providing intermittent protection to these mobile species can enhance abundance and possibly increase harvests (Polacheck 1990; Sumaila 1998; Maury and Gascuel 1999).

The major goal of this study is to investigate the potential of MPAs for the management of species with a moderately mobile adult life phase. The model used is that of the penaeid prawn *Penaeus latisulcatus* in Gulf St Vincent, South Australia. Fishing of this stock only occurs for 35-40 nights a year from ten boats, with effort concentrated in deeper regions of the Gulf (30-40 m), although most areas below a depth of 20 m are lightly fished. Fishing effort data are available for 121 fishing blocks (30 nm^2), and show that in the 1997-1998 fishing season only four blocks were fished sufficiently intensely that on average the entire area of the block was swept once (JE Tanner unpublished data). Effort restrictions mean that the fleet is only capable of trawling considerably less than 10% of the gulf in any one year, thus creating a de facto reserve, albeit one which can change location from year to year. While this seemingly results in a very low level of exploitation, the stock has only just recovered from collapse and a subsequent two year closure, with fishing recommencing in December 1993. Due to the low exploitation level, it should be possible to establish marine reserves as a habitat conservation measure with little effect on the fishery.

Penaeus latisulcatus in South Australia is at the southern limit of its range, and as a consequence has a much slower life-cycle than that of most exploited penaeid populations, making it more vulnerable to over-exploitation. Spawning occurs over the summer period, and is concentrated in December/January (King 1977). There is some evidence to suggest that populations of this species further north exhibit multiple spawnings in a season (Penn 1980), but whether this holds true for the study population is unknown. After spawning, juveniles undergo a planktonic phase which lasts for approximately four weeks, after which they settle into inshore nursery areas – predominantly intertidal and shallow subtidal mud flats between mangroves and seagrass beds (Kangas 1999). Juveniles spend slightly over a year in these nursery grounds, with most migrating to deeper water in about March of the following year, at which time they begin to recruit to the fishery. First spawning generally occurs at two years of age, and few individuals live past an age of five years. This contrasts to penaeid populations in tropical areas that have lifespans on the order of 12-18 months. Adults appear to be highly migratory within Gulf St Vincent and its approaches (an area of ~ 13 000 km^2), with a tendency to inhabit the northern portion during the summer spawning season and to move south over winter. There is, however, little exchange with other nearby populations (Kangas 1999).

A simple multi-habitat model of the population dynamics of *P. latisulcatus* is used to examine the consequences of varying the proportion of habitat trawled for long-term harvest rates. The model used differs from most previously published models in that both adults and juveniles disperse independently and at variable rates, juveniles occupy a different habitat to adults, and fishing mortality is spatially partitioned. This model also incorporates both a stock-recruitment relationship and density-dependent juvenile survival, both of which have important consequences for model output. The only difference between trawled and untrawled habitat in the model is the presence of fishing mortality in trawled areas. Importantly, it is assumed that both habitat types are equally suitable for adult prawns, and that trawling has no detrimental (or beneficial) environmental impacts. Preliminary data from experimental work indicates that light trawling has no effect on subsequent catches in the trawled area, suggesting that *P. latisulcatus* does not perceive a degradation in habitat quality from such trawling (Chapter 1). Exchange of adults between the two habitats occurs once a year, and juveniles can recruit to either habitat type irrespective of their origin. The model is used to determine the optimal proportion of the habitat to trawl, and to examine the consequences of changing fishing mortality. The assumptions of the model are tested via a sensitivity analysis to help determine what aspects of the life-history are most crucial in determining population dynamics.



$$\begin{array}{l|cccccccccc}
 & \multicolumn{5}{c}{\text{Untrawled}} & \multicolumn{5}{c}{\text{Trawled}} \\
 & 0 & 4.98 & 9.03 & 11.11 & 12.68 & 0 & 4.98 & 9.03 & 11.11 & 12.68 \\
 & S_U & 0 & 0 & 0 & 0 & S_{T\rightarrow U} & 0 & 0 & 0 & 0 \\
 & 0 & S_U & 0 & 0 & 0 & 0 & S_{T\rightarrow U} & 0 & 0 & 0 \\
\text{Untrawled} & 0 & 0 & S_U & 0 & 0 & 0 & 0 & S_{T\rightarrow U} & 0 & 0 \\
 & 0 & 0 & 0 & S_U & 0 & 0 & 0 & 0 & S_{T\rightarrow U} & 0 \\
 & 0 & 4.98 & 9.03 & 11.11 & 12.68 & 0 & 4.98 & 9.03 & 11.11 & 12.68 \\
 & S_{U\rightarrow T} & 0 & 0 & 0 & 0 & S_T & 0 & 0 & 0 & 0 \\
\text{Trawled} & 0 & S_{U\rightarrow T} & 0 & 0 & 0 & 0 & S_T & 0 & 0 & 0 \\
 & 0 & 0 & S_{U\rightarrow T} & 0 & 0 & 0 & 0 & S_T & 0 & 0 \\
 & 0 & 0 & 0 & S_{U\rightarrow T} & 0 & 0 & 0 & 0 & S_T & 0
\end{array}$$

Figure 3.1. Life-cycle graph and transition probability matrix for *Penaeus latisulcatus* existing in two habitats (trawled and untrawled). Adults progress through a series of age classes (1-5) in each habitat, and may also migrate between habitats at the end of each year. Individuals in age class 2 and greater (in either habitat) may reproduce at the beginning of the year, resulting in juveniles which occur in distinct nursery areas, and which recruit into either adult habitat at the end of the year. Fecundities (number of juvenile recruiting into age class 1) for individuals in each age class are given in the top row of each submatrix, while survival and migration probabilities are on the sub-diagonals. $P_{X\rightarrow Y}$ = Probability that an individual that migrates from habitat X to Y survives for the census interval (1 year). $S_{X\rightarrow Y}$ = Probability that an individual in habitat X migrates to habitat Y. $S_U = e^{-M}(1-P_{U\rightarrow T})$; $S_T = e^{-(M+F)}(1-P_{T\rightarrow U})$; $S_{U\rightarrow T} = e^{-(M+\frac{F}{2})}P_{U\rightarrow T}$; $S_{T\rightarrow U} = e^{-(M+\frac{F}{2})}P_{T\rightarrow U}$

Multi-habitat model

The model developed here is based on the age-structured Leslie matrix model (reviewed in Caswell 1989) with five one-year age classes. Two adult habitat types (or management zones), trawled and untrawled, are explicitly included in the model, while juveniles occupy a third nursery habitat in shallow untrawled waters (Fig. 3.1). To incorporate both adult habitats, the transition matrix is divided into four sub-matrices, with those in the top left and bottom right corners being Leslie matrices describing dynamics within untrawled and trawled habitats respectively, while the top right and bottom left sub-matrices describe migration between habitats. Because juveniles occur in a third distinct habitat, and occupy these nursery areas for approximately one year, it is assumed that they are completely mixed and recruit to adult habitats in proportion to habitat area, irrespective of whether they were derived from adults in the trawled or untrawled area (i.e. recruitment is uniform over the entire habitat). Reproduction is assumed to occur immediately post-census (on the 1st of January each year), and thus juveniles recruit straight into adult habitat as 1+ individuals just prior to the next census.

Adult movement between habitats in the model occurs at the end of the census interval. Because this is a highly mobile species, and the population being studied occurs within a single embayment (of ~ 13 000 km^2), the model assumes complete mixing of the adult population every year resulting in a uniform distribution across the habitat (i.e. all adults move, but not all change habitats in the process). Changing the frequency of movement (e.g. to a monthly basis) had only minimal effects on model output (JE Tanner unpublished data). Unless otherwise stated, natural mortality (M) in both habitats is 1.25 yr^{-1} (Morgan 1995), while prawns in the trawled habitat are also exposed to fishing mortality. In this case, natural mortality is constant for all age-classes. Catchability is also constant over all age classes which have recruited to the fishery, with recruitment to the fishery occurring at age 2+ unless otherwise stated. Further, it is assumed that F is uniform over the trawled area, and that all animals that die due to fishing are retained unless otherwise stated. The realised harvest is F/(M+F) of the animals in each age class that fail to survive. All mortality occurs after reproduction, and before migration, and can thus be considered an instantaneous process.

To calculate age-specific fecundities, the average carapace length of females in each age-class was determined from Morgan (1995). These average carapace lengths were then used to determine ovary weight according to the relationship (Penn 1980):

$$\text{(1)} \qquad \text{Ovary weight} = 6.95 \times 10^{-5} \times \text{Carapace length}^{\,2.916}$$

and then fecundities based on the value of 88 494 ova per gram of ovary (Penn 1980). The link between fecundity and recruitment was calculated using published stage duration times and mortalities. After spawning, several distinct phases are passed through before the juveniles settle into the nursery habitat. The egg phase at 29 ^{o}C lasts for 12.5 h, followed by a series of naupliar stages which last for 36.5 h, a protozoea of 2.96 days and a mysis of three days (Shokita 1984). However, Carrick (1996) studied the protozoeal and mysis stages at 18 ^{o}C (in Spencer Gulf, close to Gulf St Vincent) and found they lasted for eight and 12 days respectively (3-4 times as long as found by Shokita 1984). Thus the durations for the two earlier stages (egg and nauplius) were multiplied by 3.5 to correct for lower water temperatures and thus slower development times (becoming 1.8 and 5.3 days respectively). These development times are consistent with those for other species in the genus for which development at similarly low temperatures has been studied (Dall et al. 1990). Using data from Carrick (1996), protozoea have a mortality of 0.27 day^{-1}, and mysis 0.07 day^{-1}. Both eggs and the nauplius were arbitrarily assigned a mortality of 0.5 day^{-1}. The remaining 48 weeks of the first year of life were spent as juveniles in the nursery grounds where mortality was density dependent. Overall, survival of eggs to juveniles four weeks later was 0.0014.

Density-dependence in juvenile mortality was introduced to more accurately model population dynamics. As with many fished stocks, it was assumed that density-dependence occurs primarily in the juvenile stage of the lifecycle, as this is the stage with greatest abundance, and least amount of available habitat. Kangas (1999) estimated weekly juvenile mortality to be related to density according to the equation:

$$\text{Mortality} = 0.032 + 0.1 \times \text{density} \tag{2}$$

where density was the number of juveniles in 1 m^2. This relationship was incorporated into the recruitment calculations assuming that 150 km^2 of juvenile habitat was available (Kangas 1999), and that settlement density was constant throughout this area. The population size of the juvenile phase was calculated on a weekly basis using the above mortality rate for 48 weeks following the four week egg/larval period in between each annual iteration of adult population size.

The above model was simulated for 200 years starting with 100,000 individuals of age 1+ in the untrawled area to determine how harvest weight (in the final year) responded to changes in the percentage of the habitat trawled (PT - from 0-100% in 1% increments), and fishing mortality (F – from 0 to 10 in increments of 0.1). This starting population size produced equilibrium harvest rates consistent with current yearly harvests (~ 300 t yr^{-1}), and subsequent analyses starting with several different estimates of the current stock structure produced the same results (JE Tanner unpublished data). Two hundred years was more than sufficient for the model to equilibrate, which normally occurred in about fifty years. Results are presented in terms of yield by multiplying the number of harvested animals caught in each age class by age specific weights, and assuming equal numbers of males and females were caught. For females, weights used were 31, 66, 93, 110 and 120 g for age classes 1-5 respectively, while for males weights were 15, 32, 45, 53 and 58 g respectively. After determining the optimal fishing mortality and percentage of habitat to trawl (with optimal defined as that percentage which resulted in maximum yield in year 200 of the model simulations), I investigated how yield responded to changes in natural adult mortality, adult and juvenile mixing, the strength of juvenile density-dependence and target harvest age by altering these factors independently. The importance of density-dependence in the juvenile stage was also examined by setting recruitment to age 1+ constant at 1.4×10^9 animals year^{-1} - the number in this age class at equilibrium in the model with no fishing. This scenario assumes that harvesting the adult population does not result in a decrease in recruitment (i.e. there is no stock/recruit relationship). Reduced mixing between habitat types was simulated by requiring that a given percentage (from 0-100) of animals remain in their current (or parent's) habitat, while allowing the rest to mix randomly. Increased mixing was simulated in a similar fashion, except a given percentage of animals were forced to change habitats. Sensitivity analyses for changes in both adult and juvenile migration were conducted for two potential harvest strategies (F = 10, PT = 2% and F = 0.7, PT = 5%).

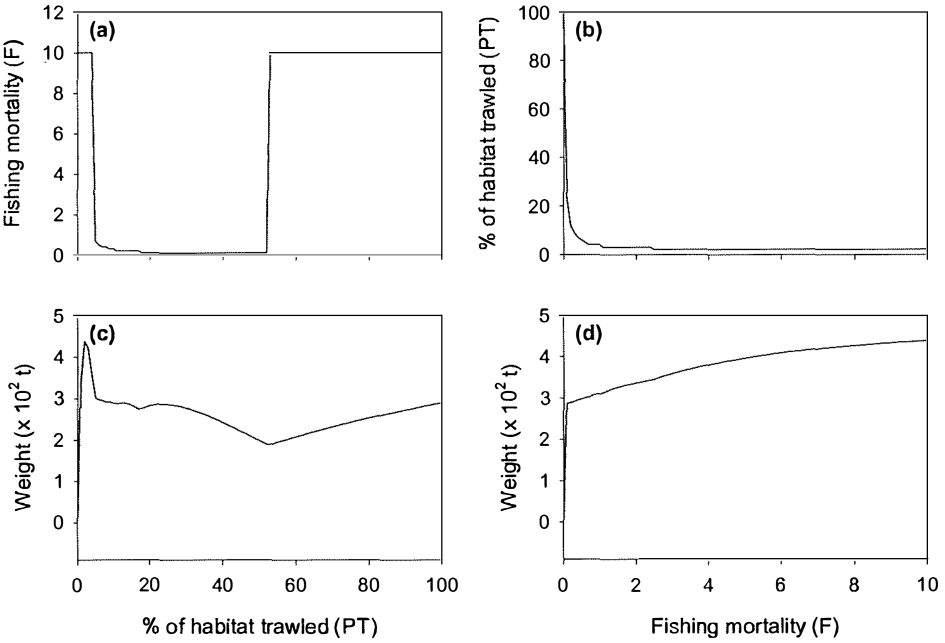


Figure 3.2. (a). Fishing mortality (F) for which maximum harvest is obtained when a given percentage of habitat is trawled (PT) and (b). PT to maximise catch at each F. (c). Weight of catch when optimising F for a given PT, and (d). weight of catch when optimising PT for a given F.

Results:

Under the situation described by the model, the obtainable harvest was greatest when only 2% of the habitat was trawled, but with an extremely high fishing mortality in the fished area (F ≥ 10, which was the cutoff in the model, Fig. 3.2c). Catches under this harvest regime would, however, be very dependent on knowing precisely how much of the habitat had been trawled, as only slight changes in this variable result in substantially lower catches (as indicated by the close spacing of the lines of equal harvest in the horizontal direction in Fig. 3.3). Harvests of ~70% of the maximum could be obtained by fishing a larger proportion of the habitat at a lower F (Fig. 3.2c), which has the advantage that harvest is not so dependent on precise estimates of the proportion of the habitat that has been trawled (isolines in Fig. 3.3 are widely spaced in the horizontal direction). For example, it only takes an increase in the trawled area to 5% of the habitat to bring the optimal F down to ~0.7 (Fig. 3.2a). Conversely, at very low F the majority of the habitat must be fished to maximise harvest, but it only requires a slight increase in F to greatly reduce the area fished (Fig. 3.2b). As would be expected, as the proportion of habitat trawled increases, the harvest depends more and more on a precise knowledge of F, and the extent of the area trawled becomes unimportant (Fig. 3.3). Interestingly, once harvest peaks for any given F or percentage of habitat trawled, it does not decrease monotonically. Instead, under very intensive harvesting regimes, it begins to increase again, although under the range of scenarios modelled it never reaches any more than about two-thirds the maximum obtainable (Figs 3.2, 3.3). The sudden increase in optimal F when just over 50% of the habitat is trawled (Fig. 3.2a) occurs because the reproductive value of any unharvested adults becomes less than their current value if harvested immediately (remembering that all animals have a chance to reproduce before being subjected to fishing). It must be kept in mind when considering these results that F only applies to the area actually swept by the nets (i.e. it equates to catchability). Under this definition, the actual F for the fishery is probably in the range of 2-3 (5-14% of animals escape capture), although no data on this are available.

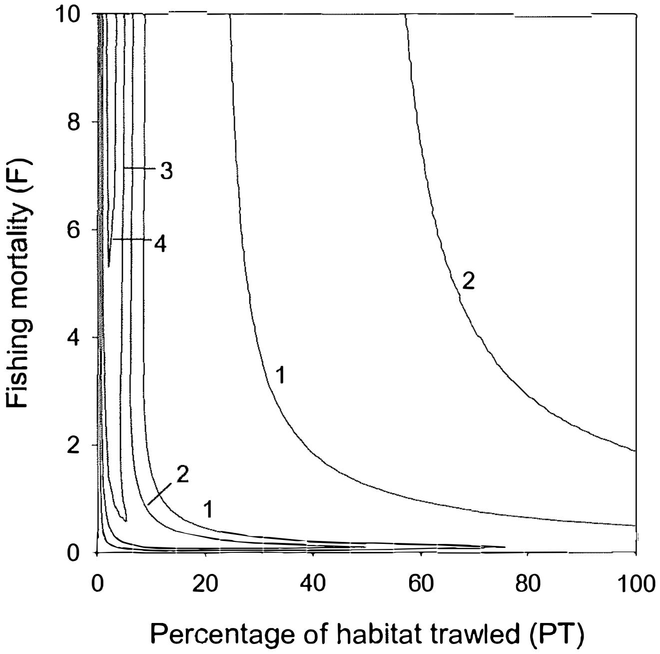


Figure 3.3. Influence of adjusting the proportion of habitat trawled and fishing mortality on relative harvest weight of *P. latisulcatus* when M = 1.25 yr^{-1}, and both juveniles and adults mix randomly between habitats. Isolines indicate parameter combinations with equal harvest (t x 10^2), with close spacing of isolines indicating that small changes in the parameter cause large changes in harvest.

A sensitivity analysis of natural mortality indicated that slight changes could dramatically alter the response of harvest to changes in the percentage of habitat trawled and F. The natural mortality rate used in the model (M = 1.25) is at the high end of the range of estimated mortality. Increasing this value further (to M = 1.3) resulted in a qualitative change in model behaviour, with harvest increasing monotonically with both fishing mortality and the proportion of the habitat harvested, although maximum harvest declined by almost 50% (Fig. 3.4a). This pattern suggests that as much of the habitat as possible should be trawled as heavily as possible to obtain the maximum harvest. Such heavy fishing is possible because harvest does not occur until after first reproduction, and high M means that despite first year reproductives having relatively low fecundity, as a group they provide a large proportion of new juveniles. Density-dependent mortality of juveniles further smooths out any differences in initial recruitment. Decreases in natural mortality, however, did not result in qualitative changes to model output, although they did result in harvest increasing to unrealistically high levels, suggesting that M does not drop much below 1.25 unless compensatory changes occur in other parts of the lifecycle (Fig. 3.4b). Providing the true M is no greater than 1.25, a precise knowledge of its value is not needed to determine the best harvest regime to use (although it is important in estimating the actual catch that will be obtained under that regime). Changing the survival rate of eggs and larvae (in the first four weeks), had identical consequences. Again, it only required a slight reduction in the number of larvae recruiting into the nursery habitat to result in harvest increasing monotonically with F and area trawled, while increasing recruitment increased harvest but did not alter the response to changes in the harvesting regime (JE Tanner unpublished data).

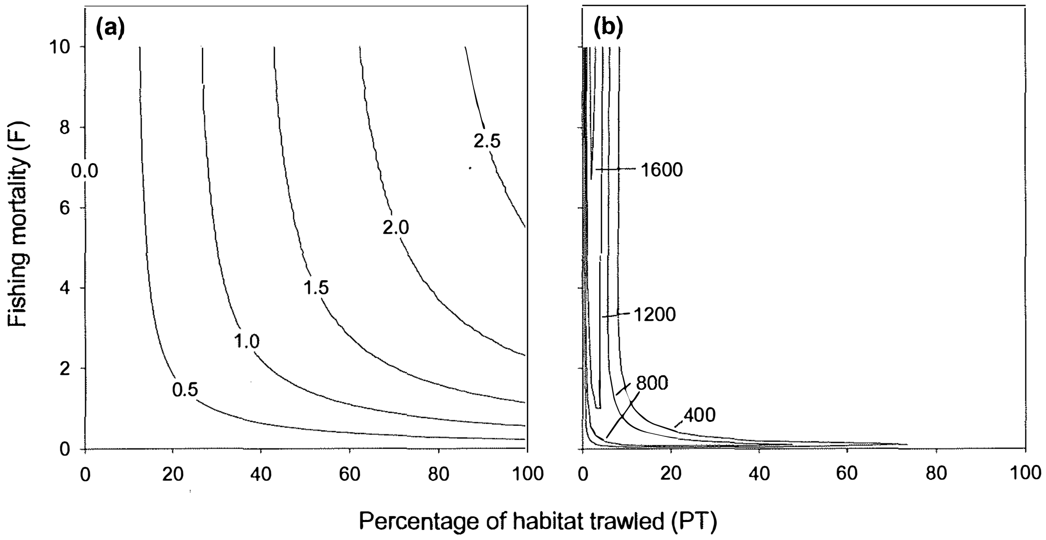


Figure 3.4. Influence of natural mortality on modelled harvest (t x 10^2) of *P. latisulcatus*. (a). M = 1.3, (b). M = 1.2. Harvest for M = 1.25 is given in Figure 3.3.

Small changes in movement patterns between habitats could sometimes result in dramatic changes in obtainable harvest, but at other times large changes in movement had little consequence for harvest (Fig. 3.5). If there is any tendency at all for adults to move between habitat types more often than expected by chance (i.e. if adult movement is > 0.5), then the harvest decreases substantially, although if there is almost complete swapping of habitats each year (movement close to 1) it does begin to increase again. While such complete swapping is biologically unrealistic (especially when only a small proportion of the habitat is trawled), it is impossible to determine the exact range of realistic scenarios, so all possibilities are presented for completeness. When adults tend to remain in the same habitat from year to year, and juveniles recruit to the same habitat as their parents (movement < 0.5 for both adults and juveniles), harvest remains at around the maximum unless there is very little exchange between the two habitats (i.e. unless there are actually two distinct populations). If, however, juveniles show a preference for recruiting to the opposite habitat to their parents, harvest again decreases substantially unless adults engage in perfectly random mixing. These patterns are consistent for a range of realistic harvest regimes (F = 10, PT = 2% and F = 0.7, PT = 5% are presented in Fig. 3.5, but similar patterns occurred for all PT < 10% when F was at its optimum).

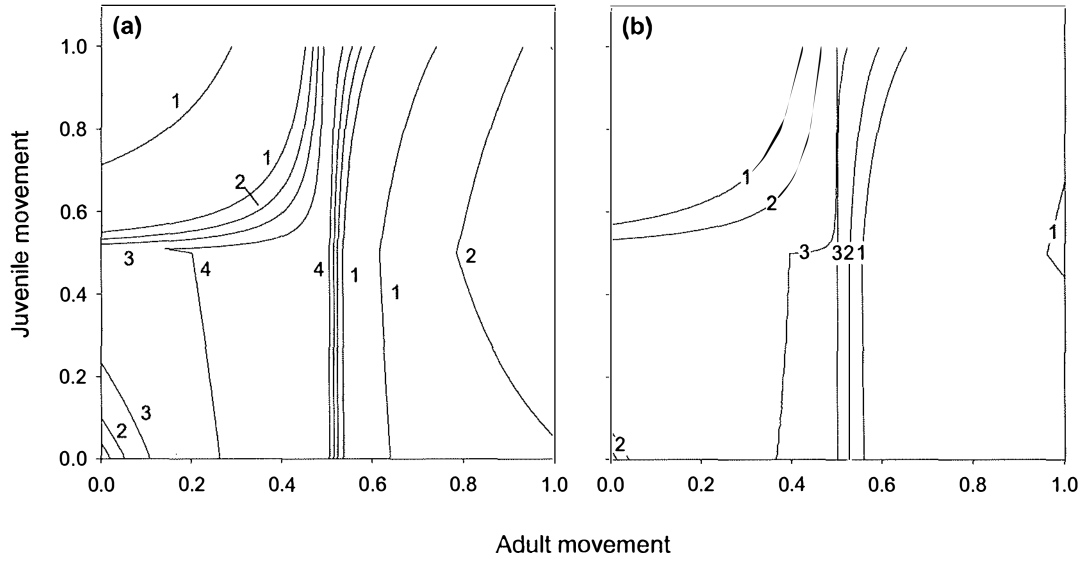


Figure 3.5. Sensitivity of harvest weight (t x 10^2) of *P. latisulcatus* to changes in assumptions about adult and juvenile mixing under two different harvesting strategies. A migration rate of 0 indicates that there is no exchange between habitat types, 0.5 indicates random mixing based on the proportion of habitat occupied by each type, while 1 indicates that all individuals migrate to the opposite habitat. (a). F = 10, PT = 2%; (b). F = 0.7, PT = 5%.

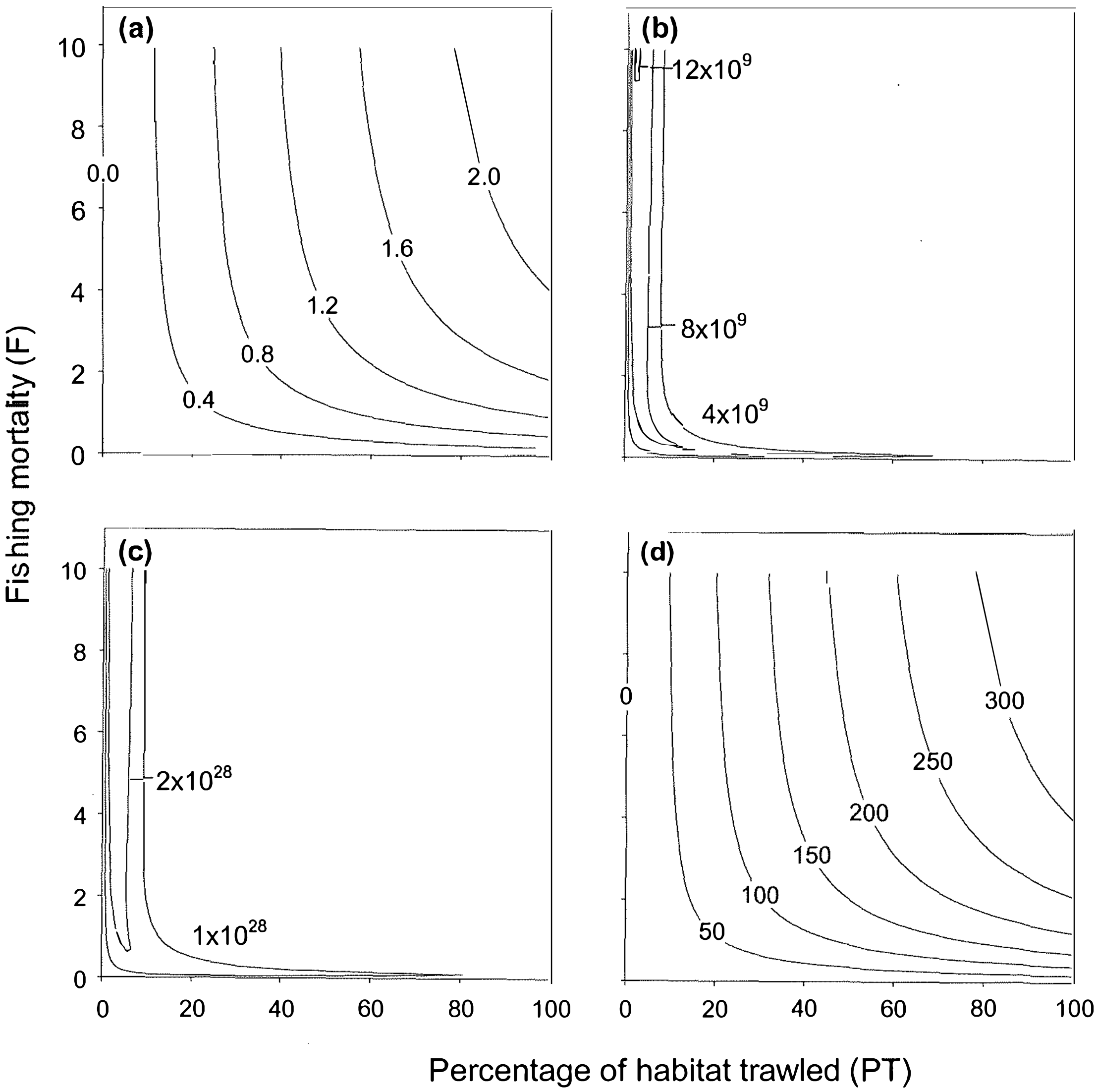


Figure 3.6. Influence of adjusting the strength of density-dependence in the juvenile phase on harvest weight (t x 10^2). For 125% strength (a), the density value in eqn. 2 is multiplied by 1.25, and for 75% strength (b) it is multiplied by 0.75. (c). No density dependence. (d). Constant recruitment to age 1+ (i.e. no stock-recruitment relationship). Figure 3 gives the situation when density-dependence is not modified.

The response of harvest to changes in the assumption about juvenile density-dependence was similar to the response to changes in natural mortality of adults. When density-dependence was made stronger, harvest increased monotonically with both fishing mortality and the proportion of the habitat trawled (Fig. 3.6a). Reducing the strength of density-dependence only resulted in a numerical response, however, with harvest increasing under a given fishing regime, but still reaching a peak when only a small proportion of the habitat was trawled (Fig. 3.6b). If density-dependence was removed from the model by setting juvenile mortality at 0.083 week^{-1}, population size and harvest grew exponentially (Fig. 3.6c). Assuming constant recruitment to age 1+ (i.e. assuming no density-dependence or stock-recruit relationship) had the same qualitative effect as increasing the strength of density-dependence, although harvest increased greatly (Fig. 3.6d). Again, most of these changes resulted in extremely unrealistic levels of harvest, indicating that the modified models contain incorrect assumptions, and that the original equation used to represent density-dependence is fairly realistic.

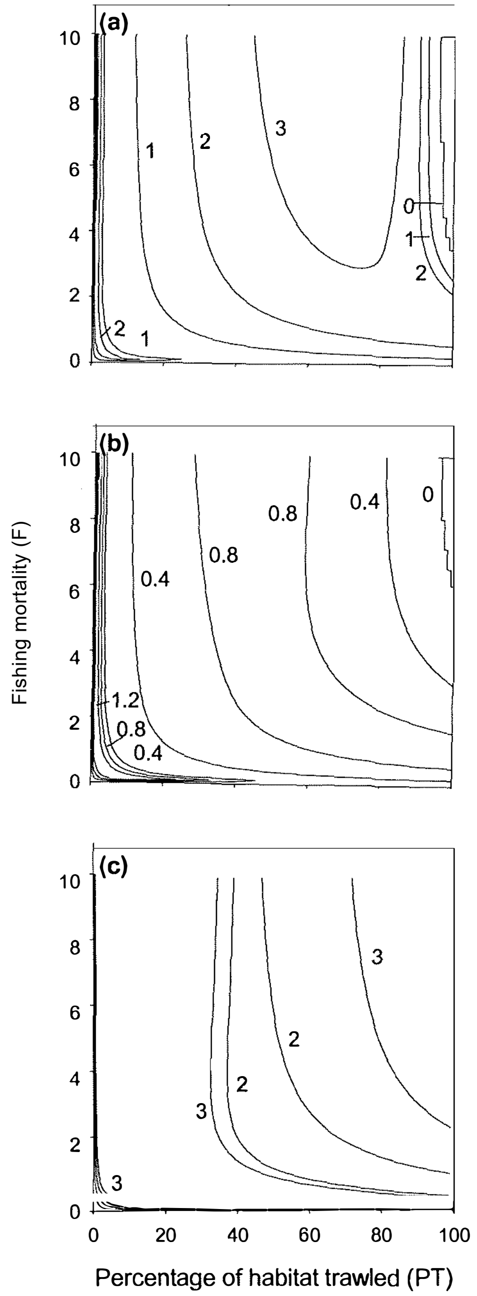


Figure 3.7. Effect of modifying age of entry into the fishery on relative harvest (t x 10^2) of *P. latisulcatus* when M = 1.25 yr^{-1}. (a). 1+ individuals are fished. (b). 2+ individuals are actively fished, but 1+ animals experience a fishing mortality of F/2, although they are not retained. (c). Entry into the fishery is delayed to age 3+. Figure 3 gives the situation for entry at age 2+.

Changing the target age for recruitment to the fishery showed that the optimum harvest strategy was to target the 2+ age class, as is currently the practise. Harvesting 1+ individuals resulted in harvest decreasing by about one third, although very intensive harvesting regimes could result in an increase in harvest back to almost the same level as when targeting 2+ individuals (Fig. 3.7a). However, if 2+ animals are targeted, but a substantial proportion of 1+ animals die in the process (either from damage sustained in escaping from the net, or from being caught and discarded), the harvest suffers. A fishing mortality of F/2 for the 1+ age group (but no actual retention of these in the catch) results in a 60% decrease in the harvest (which is more than from actively fishing the 1+ group, Fig. 3.7b). Switching to harvesting 3+ and older animals only, also resulted in declines in harvest, although the response to changes in the harvest regime was qualitatively similar to changes when harvesting 2+ individuals (Fig. 3.7b).

Discussion:

The model developed here indicates that restricting trawling to only part of the habitat of adult *Penaeus latisulcatus* can potentially result in greater catches than harvesting the entire habitat. The current fishing strategy, based on effort restrictions, is to fish a small proportion of the gulf fairly intensively. Although the catchability of prawns in this fishery is not known, it is likely to be high, and thus fishing mortality of the targeted age classes in the fished area (i.e. the area swept by the nets), is probably very high. Catch and effort records indicate that from 1993 to 1998, between 200 km^2 and 450 km^2 a year were trawled (assuming a trawl speed of 3 knots, with nets sweeping a swathe 20 m wide). This equates to between 1.5% and 3.5% of the gulf if no areas are trawled more than once. Thus the fishing strategy that has been adopted appears to be as close to optimal as it is possible to get with our current level of knowledge. Such low levels of fishing also mean that it should be possible to introduce marine reserves into Gulf St. Vincent as a conservation tool with little or no conflict with the fishing industry, provided fishers are consulted at an early stage.

Importantly, the incorporation of a stock-recruitment relationship into the model (through adult fecundity), produced qualitatively different behaviour to the scenario modelled with constant recruitment to age 1+ (i.e. to what is essentially a yield per recruit model). While yield per recruit models are likely to do a good job in situations where recruitment is controlled by factors extrinsic to the stock being modelled (e.g. environmental conditions, limited nursery areas, or large sources of recruits from outside the stock under consideration), if recruitment is determined largely by the total fecundity of the stock, then yield per recruit models may result in incorrect conclusions being drawn. Of course, the real situation for the current stock (and many others) is likely to lie somewhere in between, with a stock-recruit relationship obscured to some extent by environmental noise, and it is important to determine how this noise might influence population dynamics and harvest.

While maximum harvest under the assumptions of the model occurs when only ~2% of the habitat is fished, maintaining this harvest requires very precise knowledge of what proportion has been trawled, as indicated by the close spacing of the lines indicating constant harvest when PT changes at high F. As we do not have detailed knowledge on the habitat requirements of adult prawns (although we do know that they can be found over most of the gulf), determining this proportion precisely is not possible, making such a harvest regime very risky. It only requires a shift in strategy to trawling a slightly larger area (5-10%) with a lower fishing mortality (0.7-0.3) to make errors of a few percent in the proportion of habitat trawled considerably less important (i.e. at F = 10 there is a large change in harvest moving from trawling 1% of the habitat to 3% to 5%, whereas at F = 0.7, the change moving from 3% to 5% to 7% is less). Catches will only be 70% of maximum under such a regime, but because the model is less sensitive to errors in the estimates of F and PT there is less risk of overharvesting. While it is also difficult if not impossible to estimate F accurately, harvest under this later regime is also relatively insensitive to errors in F. Manipulating F is likely to be difficult, however, making it important to determine what areas are actually suitable habitat for this species. The high degree of sensitivity of the model to important parameters such as F and PT, and the inherent unknowability of their values, means that it is vital to carefully monitor the stock and adopt a precautionary approach to management.

As is the case with most fishery models, this model is very sensitive to the value of natural mortality. To be conservative (i.e. maintain stock size at the risk of reduced harvest), I have used the maximum mortality that has been estimated for this stock (M = 1.25), although other estimates range as low as M = 1 (Morgan 1995). Within this range, the general qualitative predictions of the model hold, although quantitative predictions vary greatly, and are therefore not reliable. In fact, when M drops to 1.2 harvest levels become unrealistically high due to a breakdown in density-dependent population regulation, and hence unrestricted population growth in the model. Similarly, the model was very sensitive to changes in recruitment to the nursery habitat, and in the strength of juvenile density-dependence, with both parameters being close to thresholds that qualitatively changed the behaviour of the model (for example, this study shows that stronger density-dependence leads to harvest increasing monotonically with fishing pressure, rather than reaching a peak at some intermediate level). Again both of these parameters were chosen to be conservative (i.e. to avoid overharvesting), so it is unlikely (but not impossible) that these thresholds are in fact exceeded in the real population. In particular, the equation for juvenile density-dependence assumes that all individuals in the trawl path were caught (Kangas 1999), and if this is not the case actual density-dependence will not be as strong, moving the population away from this threshold. Provided none of these thresholds were exceeded, the optimal harvest regime did not vary greatly (although catch did). This is in stark contrast to some other studies, where the optimal proportion of habitat to protect depended on the exact values of model parameters (e.g. Sladek Nowlis and Roberts 1998). That density-dependence only occurs in the juvenile phase is a standard assumption of fishery models (e.g. Hastings and Botsford 1999), although model sensitivity to this assumption is rarely tested.

Like several other simulation studies (e.g. Polacheck 1990; Sumaila 1998; Guenette and Pitcher 1999), the model developed here shows that removing a large proportion of the habitat from access by the fishery is a potentially viable way of managing the fishery. In this particular instance, such an action would be somewhat redundant, as current effort restrictions have the effect of creating a defacto restriction on the amount of habitat trawled anyway. The model also supports the contention that an MPA by itself would be unlikely to serve as a sufficient restriction on fishing (Holland and Brazee 1996; Allison et al. 1998). Unless the MPA covered 97-98% of the habitat, unrestricted effort in the open area could still easily result in substantial decreases in realised harvest (in this study harvest decreases at high F when > 3% of the habitat is trawled). Such a large area is needed because of the assumptions of complete mixing of both adults and juveniles, which mean that declines in stock size in the harvested area rapidly translate into declines in the unharvested area.

A particularly important point to note is that while restricting harvest to 2+ individuals is predicted to maximise harvest, if substantial numbers of 1+ individuals are killed in the process but not retained then this restriction is counterproductive. It thus becomes important to determine if 1+ animals which either pass through the net, or are caught but discarded, actually survive the event. As the gear used is relatively light, and the wings of the net are of a sufficiently large mesh size as to allow these smaller prawns to pass through, it is possible that these animals do have a high survival rate, with few being retained in the cod end. Those actually caught, however, are likely to experience high mortality rates even if returned to the water, as they will have been tumbled around in the cod-end for up to 2 h, and then subjected to considerable further damage when brought on deck. What is crucial to the maintenance of stock size (and thus yield) is the fact that high natural mortality rates in combination with harvesting only 2+ and older prawns (which have had a chance to reproduce), means the population is dominated by young unfished individuals. As a result, even very intensive fishing of older animals has little influence on the population's reproductive output, and subsequent recruitment to the fishery. In fact, the model indicates less than a 10% variation in the number of 1+ individuals present under the range of fishing regimes investigated (not shown).

The spatial arrangement of habitat patches is not considered in this study. Instead it is assumed that prawns are able to choose freely between habitat types when they migrate. If suitable patches of habitat are relatively ephemeral, or the areas trawled change on a regular basis, the spatial arrangement of patches may not matter. In a generalised simulation study, Fahrig (1992) showed that the temporal scale of habitat patchiness was much more influential in determining population size than was the spatial scale. It was only when habitat patches persisted for long periods of time that spatial scale became important. Even if habitat patches are permanent, the spatial arrangement of habitat may not be important if there is high connectivity between patches (Fahrig 1998). This is likely to be true for *P. latisulcatus*, which has a highly mobile adult phase in relation to the distribution of the population, as well as a dispersive juvenile phase. This suggests that under the assumption of a uniform habitat, it does not matter which areas are trawled and which are protected. It is probably more important, however, that the trawl areas don't change to a great extent on a yearly basis. Such yearly changes are possible under the current management regime, although fishers show a preference for fishing over previously trawled (and therefore clean) ground.

Most previous models looking at MPAs have assumed either that larvae disperse while adults are relatively sedentary (e.g. Botsford et al. 1993; Sladek Nowlis and Roberts 1998; Hastings and Botsford 1999), or that adults move and larvae recruit evenly across reserve and non-reserve areas (e.g. Polacheck 1990; Guenette and Pitcher 1999). Rarely are the consequences of varying both adult and juvenile dispersal abilities examined in a single model. The model used here suggests that for *Penaeus latisulcatus*, both adult and juvenile migration interact to determine stock size and harvest. Juvenile migration only becomes important when adults are relatively sedentary (i.e. tend not to swap habitats as often as would be expected under the random mixing assumption). In this case, if they recruit to the habitat not occupied by their parents (and then stay there), the usefulness of reserves breaks down and the stock rapidly collapses. There is a large area of parameter space where exchange of both adults and juveniles between the two habitats is limited (i.e. when the stock starts to behave like a metapopulation) that maintains high harvest rates. This is in accord with a study by Man et al. (1995) that shows reserves are particularly useful when a fished stock exists as a metapopulation.

It is particularly important to remember that this model does not include any environmental stochasticity. The addition of such stochasticity into population models almost always results in decreases in long-term modelled population size (but see Damman and Cain 1998; Tanner 2000), with consequent decreases in sustainable harvests. Lauck et al. (1998) demonstrate that as variation in the level of harvest increases, the probability of stock collapse can increase dramatically. In their model, even moderate levels of uncertainty caused collapse unless ~50% of the habitat was protected. Adding variation into demographic rates as well is likely to exacerbate the situation further, and will be examined in detail in a later paper.

Marine protected areas not only protect a stock from overexploitation, but may also increase the yield of certain fisheries (e.g. Russ and Alcala 1996). This study demonstrates that maximising long-term harvest requires protection of most of the habitat from exploitation, either directly by creation of a reserve or indirectly through effort controls. In the present situation, this occurs because there is a high level of exchange between harvested and protected areas, and because recruits derived from protected areas can colonise harvested areas. Maury and Gascuel (1999) show that such increases in yield occur chiefly in highly mobile species, as fish tend to be caught at older ages and thus larger sizes. Providing refuges for site-attached species can, however, decrease yield per recruit (which does not necessarily mean decreasing harvest if the reserve leads to increased recruitment e.g. if a source area is protected), as individuals in the protected area never become available to the fishery. The effect is still present in species that migrate between protected and unprotected areas on an annual basis. This is particularly true for moderately to heavily fished stocks, whereas if the stock is lightly fished an MPA is likely to have little positive affect and can substantially reduce yields (Holland and Brazee 1996). This is in line with the results presented here, where increases in fishing mortality resulted in maximum yield occurring when greater proportions of the habitat were protected. Conversely, at low levels of fishing effort, harvest decreased if large areas of the habitat were protected, albeit only slowly until well over 50% of the habitat was protected. Similarly, a number of field studies have shown that reserves can result in higher abundances of target species in nearby unprotected areas through spillover, and that this increase in abundance may even compensate for the decreased area available for harvest (e.g. Alcala and Russ 1990; Yamasaki and Kuwahara 1990). This is particularly true when juvenile habitats are protected, which is a much more common scenario than the protection of adult habitat.

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Chapter 4: Stability of optimal harvest regime under stochastic variation in prawn demographic rates and fishing strategies.

Jason E. Tanner

Abstract:

While mathematical models are frequently used to assist in the management of fisheries, models are a simplified version of reality, and it is important to determine if the simplifications made have any influence on the model outputs. I show that adding stochasticity to the parameters of a model describing a prawn fishery had little effect on the optimal harvest regime. In both the deterministic and stochastic models the optimal harvest regime involved fishing a small proportion of the habitat very intensively. In particular, random variation in the fishing strategy had almost no affect on long-tem harvest rates, although random variation in population parameters could increase the catch. Variation in natural mortality and fecundity influenced harvest rates under any particular fishing strategy more than variation in other parameters. It is likely that these results were obtained because density-dependent juvenile mortality damped out fluctuations in population size, and the targeting of age 2+ animals by the fishery meant that all animals had a chance to spawn before being exposed to harvesting.

Introduction

Marine protected areas (MPAs) are increasingly being advocated as an alternate means for managing overexploited fish stocks (e.g. Polacheck 1990; Dugan and Davis 1993; Bohnsack and Ault 1996; Guénette and Pitcher 1999). There is still a good deal of controversy over the efficacy of MPAs for fishery management, however, as there are few good empirical examples of their benefits, especially in temperate waters (but see for example Duggin and Davis 1993; Babcock et al. 1999; Edgar and Barrett 1999; Chiappone et al. 2000). Instead, much of the research effort into the benefits of MPAs has involved the use of mathematical models to determine the population level responses to closing a certain proportion of the habitat to fishing (e.g. Polacheck 1990; Hastings and Botsford 1999; Holland 2000; Mangel 2000; Lindholm et al. 2001). Models, however, are a simplified representation of the system being studied, and it can be difficult to determine whether their results are actually applicable to the real world. One of the main simplifications made in many models of fished species is that the parameter values used to describe the life-history of the organism, and the fishing strategy, are fixed and don't vary over time.

Adding temporal variability to a population model nearly always decreases population growth rates and population size relative to the equivalent deterministic model (e.g. Boyce 1977; Tuljapurkar 1989; Benton and Grant 1996; Nakaoka 1996), although there are situations when population size increases (e.g. Damman and Cain 1998, Tanner 2000). If fishery models also show this trend, then basing management decisions on deterministic models may be problematic, as they are likely to overestimate the harvest that can be taken, and may provide a false sense of security about the harvest regime employed. In fact, environmental variation has been implicated in the collapse of a number of fisheries around the world (Carr and Reed 1993; Ludwig et al. 1993; Hoffmann & Powell 1998). Indeed, it is well known that a good understanding of temporal heterogeneity is required if we are to properly understand ecological processes (Wiens 1977; Levin 1992; Oksanen et al. 1992). In a fisheries context, Lauck et al. (1998) modelled the effect of varying the proportion of the stock exposed to fishing, and found that unless a large proportion was protected the population size could decline dramatically as compared to the deterministic scenario. Even with minor variation in harvest rate, more than 50% of the area occupied by the stock had to be protected from harvesting to ensure that the stock size was maintained. Interestingly, when they examined how stochastic variation in carrying capacity influenced the stock, they found the effect to be much less. In a similar vein, Pfister and Bradbury (1996) modelled sea urchin stocks, and found that adding temporal variation to recruitment resulted in a 50% decline in stock size compared to the equivalent deterministic model. Conversely, other models have suggested that environmental variation may be unimportant (Braumann 1999).

Previously, I used a deterministic model of *Penaeus latisulcatus* population dynamics in Gulf St. Vincent, South Australia, to determine how harvest refugia altered prawn population dynamics and catch rates, and to determine the optimal harvesting strategy for the stock (Chapter 3). The model described the dynamics of adult prawns in each of two management areas (fished and unfished) using a Leslie matrix for each. Juveniles occupied a third, nursery, area for one year, and at the end of each year, movement between all three areas was allowed to occur. Under the assumptions of this model, maximum long-term harvest rates were obtained when only 2-3% of the adult habitat was fished every year, with a very high intensity. Under such a fishing strategy, the total catch was very sensitive to the proportion of the habitat fished, but not the fishing mortality. In this paper, I extend the model previously used to incorporate stochastic variation in the parameter values, to determine how important it is to consider natural variability when managing the fishery. The model used differs from most models examining the effects of harvest refugia in that it includes age structure, both adult and juvenile migration, density dependence in recruitment and a stock-recruitment relationship, as well as the spatially partitioned fishing strategy and temporal variation in model parameters.

Methods

To examine the potential effects of stochastic variation in demographic rates and fishing intensity on the optimal harvest regime for *Penaeus latisulcatus* in Gulf St. Vincent, South Australia, a multihabitat model of population dynamics was used. The model, described in more detail in Tanner (2001), was based on a Leslie matrix with two separate management zones (fished and unfished), and five age classes. The top left and bottom right submatrices describe population dynamics in the unfished and fished areas respectively, while the top right and bottom left submatrices describe patterns of movement between these areas (which occurs at the end of each 1 year time step in the model). Adults are completely redistributed between the management zones each year, and there is no requirement that the locations of these zones remain static from year to year. Importantly, there are no effects of fishing other than the direct mortality of harvested animals (Chapter 1). Juveniles occur in a third distinct habitat which is not fished, and recruit evenly into the adult habitats at the end of their first year of life. Juvenile mortality is density-dependent, but all other demographic rates are density-independent.

Stochastic variation was introduced into the model by multiplying the selected parameter by a random number drawn from a lognormal distribution with μ=0 and σ=0.2, 0.1 or 0.05. The resultant distribution is very similar to that produced from a normal distribution with μ equal to the original deterministic parameter value, and a σ of 20, 10 or 5% of that value (Fig. 4.1). The difference is that the left tail is slightly less drawn out (and never drops below 0), and the right tail is slightly longer. Parameters which were exposed to random variation were natural mortality (M), fecundity (both with each age class varying independently and together), adult and juvenile migration, juvenile survival, fishing mortality (F) and the percentage of the habitat fished.

In the last case, values greater than 100% were set to 100%, as it is impossible for more than 100% of the habitat to be fished. Simulations were also conducted in which every combination of two of the above variables was subject to stochastic variation to determine if there were any substantial interaction effects. For the pairwise combinations, the fecundity of all age classes varied together. All simulations in which two parameters were varied simultaneously were done with σ=0.1. Finally, to determine how variation in all parameters interacted to affect harvest, simulations were run in which all parameters varied in the pairwise tests were subject to random variation simultaneously. Separate series of simulations were run with σ=0.1, 0.2, 0.3, 0.4 & 0.5. Simulations in which more than one parameter was subject to random variation assumed independent variation in each. To determine if correlated variation in model parameters was important, a further series of simulations with σ=0.1 was run with fecundity, natural mortality and juvenile survival perfectly correlated, so that years of good survival were also good for reproduction and vice-versa.

For each scenario, harvest weight was calculated for a range of fishing strategies, with F ranging from 0 to 10 in steps of 0.1, and the percentage of the adult habitat trawled (PT) ranging from 0 to 100% in steps of 1%, as per the original deterministic model (Chapter 3). At each combination of F and PT, 1000 simulations of the population were run, each lasting 200 years. The mean harvest weight obtained in year 200 was then calculated, with the model output being this mean value for each combination of F and PT.

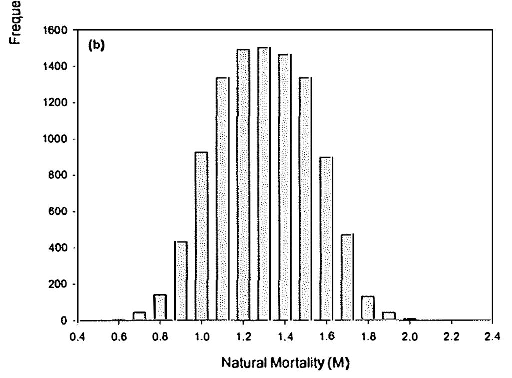

Figure 4.1. Comparison of mortality distribution obtained from (*a*) lognormal and (*b*) normal distributions, with μ=1.25 and σ=0.2.

Results

Overall, stochastic variation in a single parameter had very little effect on the optimal harvest regime for *P. latisulcatus*, with the same pattern of maximum harvest being obtained when only a small proportion of the habitat is fished at high intensity as for the deterministic model (Fig. 4.2). The greatest effects were caused by varying natural mortality, fecundity (either independently for each age class, or in concert) and juvenile survival. For each of these parameters, variation increased the mean harvest weight after 200 years when either F or PT were low, with greater variation leading to greater increases. Stochastic variation in these three parameters, especially M, also produced the greatest amount of noise in the mean harvest after 200 years. Interestingly, the model behaved similarly whether fecundity for each age class was varied independently or together. The secondary peak in production at high F and PT, however, is substantially reduced when either fecundity or juvenile survival are varied stochastically (Fig. 4.2c, d, e). For all other parameters, there was very little change in realised harvest when stochastic variation was introduced, and also very little noise in mean harvest rates. The results of the deterministic model (Chapter 3 - Fig. 3.3) are not reproduced here for comparison, as they are essentially identical to the results obtained when F or juvenile migration were varied (Fig. 4.2b, h). As would be expected, increasing the amount of variation in any parameter caused an increase in the model response (Figs 4.2a & 4.3).

When two parameters were exposed to stochastic variation simultaneously, similar results were obtained (Fig. 4.4). Combinations in which either fecundity or natural mortality were varied showed the greatest deviation from the deterministic case, with harvest rates increasing, but no changes in the optimal harvest regime. Varying natural mortality had a slightly greater effect than varying fecundity, although the greatest increase in harvest rates occurred when both fecundity and juvenile survival, or fecundity and natural mortality (M) were varied. Under all of the scenarios modelled, the secondary peak in harvest when fishing was intensive and occurred over a large proportion of the habitat, was present. For those single parameters in which stochastic variation produced a large response in the model outputs, simultaneously varying another parameter further increased this response (compare Fig. 4.4a, b to Fig. 4.3b).

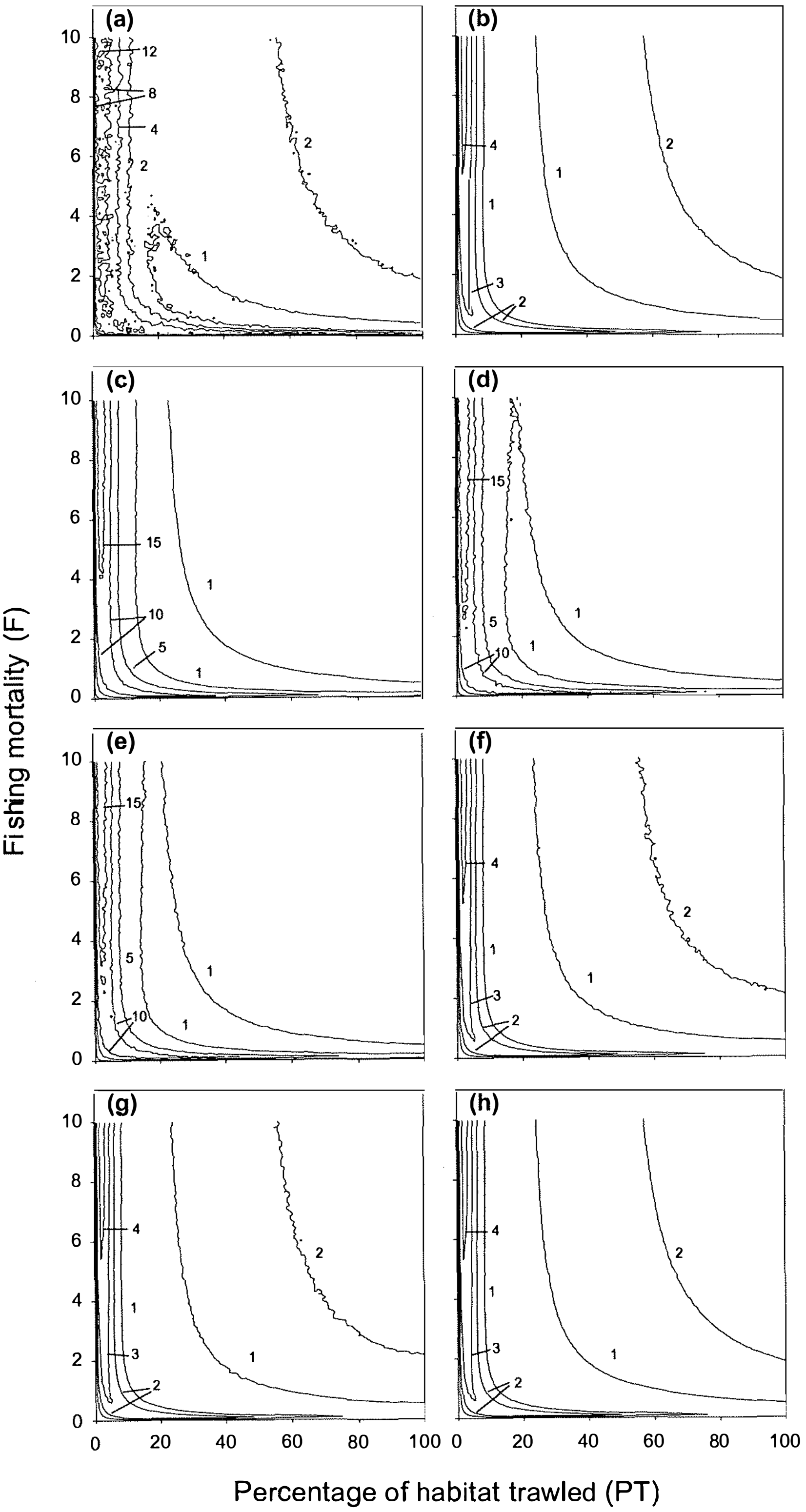

Figure 4.2. Influence of stochastic variation (σ=0.2) in a single parameter. (*a*) natural mortality - M. (*b*) Fishing mortality - F. (*c*) Fecundity - independent variation for each age class. (*d*) Fecundity - perfectly correlated variation for each age class. (*e*) Juvenile survival. (*f*) Percentage of habitat trawled - PT. (*g*) Adult migration. (*h*) Juvenile migration. The deterministic result is not shown but is identical to that for fishing mortality and juvenile migration. Isolines show parameter combinations with equal harvest weight (×10^2 t).

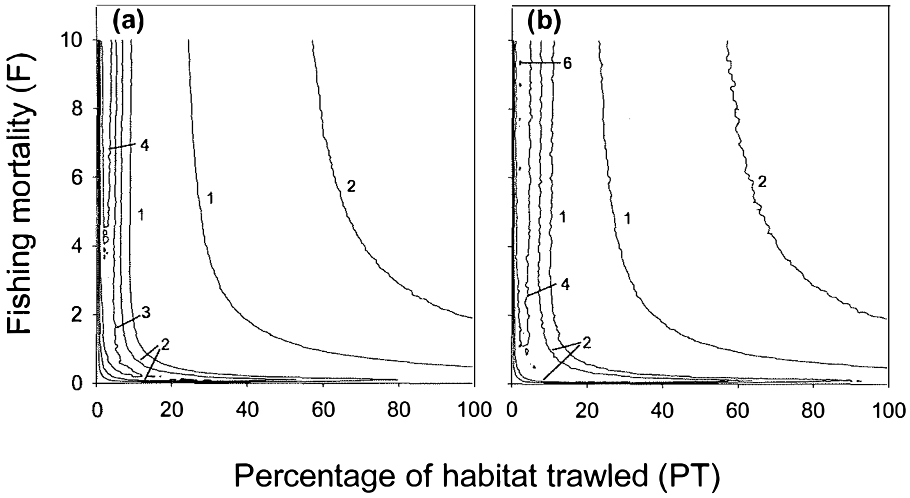

Figure 4.3. Influence of different levels of stochastic variation in natural mortality - M. (*a*) σ=0.05. (*b*) σ=0.1. Fig. 4.2a gives the case for σ=0.2. Isolines show parameter combinations with equal harvest weight (×10^2 t).

When all parameters were varied simultaneously, but only over a small range (σ=0.1), the response in the model output was still similar to that produced when only natural mortality was varied (Fig. 4.5a), although again this response was accentuated. Increasing the range of variation experienced by the model parameters (by setting σ=0.2) resulted in harvest increasing by an order of magnitude (Fig. 4.5b). Further increases in σ resulted in another order of magnitude increase in harvest, although such large amounts of random variation caused the model output to be very noisy, and so the results are not presented. The same pattern of maximum harvest occurring at high F when only a small percentage of the habitat was trawled persisted, however, no matter how much variation was incorporated into the model. Also, in no simulation did the population go extinct. There was a further increase in harvest rates, but no change in the pattern with varying F & PT, when environmental variation was assumed to cause correlated changes in fecundity, natural mortality and juvenile survivorship (i.e. when there were good years with high survival and fecundity and bad years with low survival and fecundity) (Fig. 4.6). Under this scenario, peak harvest doubled compared to the situation with independent variation in these three parameters, although for most combinations of F & PT there was little change.

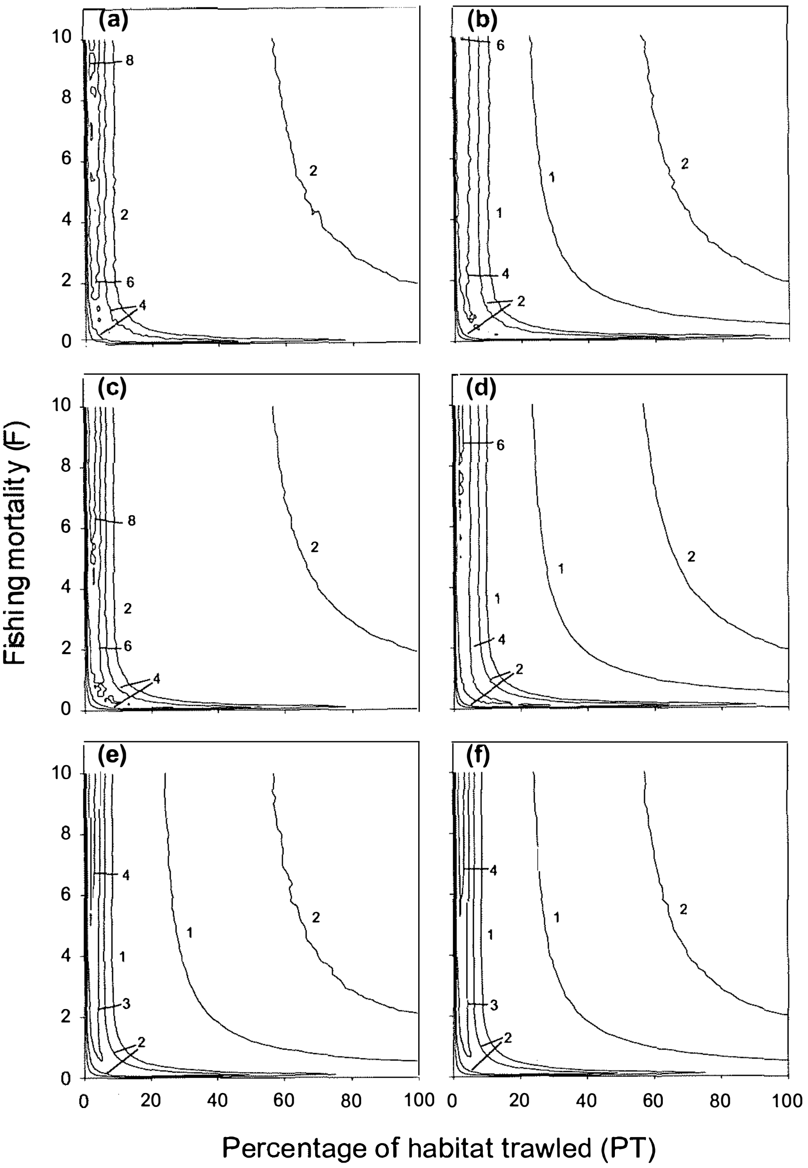

Figure 4.4. Influence of stochastic variation in selected pairs of model parameters (σ=0.1). (*a*) Natural mortality and Fecundity. (*b*) Natural and Fishing mortality. (*c*) Fecundity and Juvenile survival. (*d*) Fishing mortality and fecundity. (*e*) Percentage of habitat trawled and Adult migration. (*f*) Fishing mortality and Percentage of habitat trawled. Isolines show parameter combinations with equal harvest weight (×10^2 t).

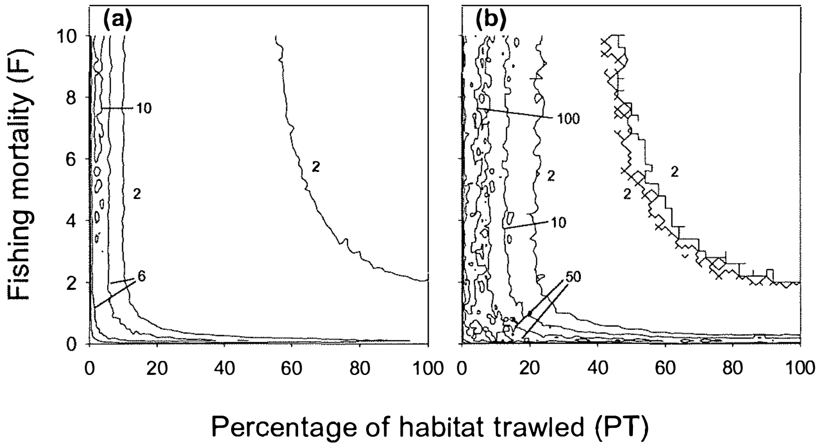

Figure 4.5. Influence of independent stochastic variation in all model parameters. (*a*) σ=0.1. (*b*) σ=0.2. Isolines show parameter combinations with equal harvest weight (×10^2 t).

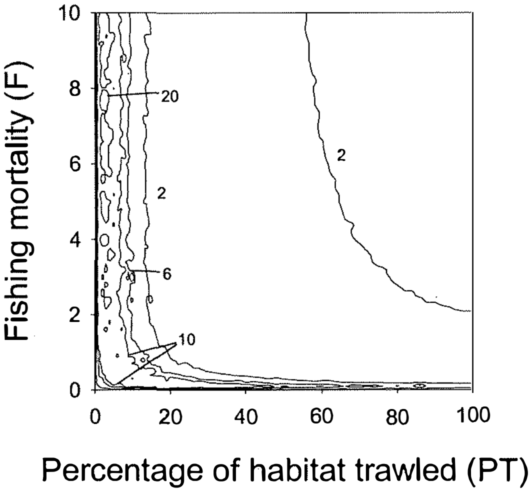

Figure 4.6. Influence of perfectly correlated variation in natural mortality, juvenile survival and fecundity (σ=0.1), with other parameters varying independently. Isolines show parameter combinations with equal harvest weight (×10^2 t).

Discussion

Somewhat surprisingly, the addition of stochastic variation to the model of prawn population dynamics did not alter the optimal harvest regime for the modelled stock. Instead, when environmental variation is present in the model, harvest is greatest when a small proportion of the habitat is fished very intensively, as suggested by the original deterministic model (Tanner 2001). This result is counter to a number of other studies, which have suggested that variation in either the environment and/or the harvesting regime could make fished stocks more prone to collapse and thus requires more conservative fishing strategies (i.e. reduced catches. e.g. Bradbury and Pfister 1996; Lauck et al. 1998; but see Braumann 1999). It is interesting that in the model presented here, even large fluctuations in the fishing pressure (either in fishing mortality - F, or the proportion of the habitat trawled - PT) from year to year have almost no effect on mean harvest, whereas Lauck et al. (1998) predicted that even small variations in the proportion of the stock caught from year-to-year would result in a large increase in the probability that the stock would fall below the target biomass.

In the previous paper (Chapter 3), I showed that harvest and population size were very sensitive to changes in a number of model parameters. Indeed, even slight deterministic changes in some parameters such as natural mortality and juvenile density-dependence could result in qualitatively different behaviour by the model. The present paper indicates that so long as these changes are only temporary, and the long-term mean value of the parameter remains constant, the model is not sensitive to changes in parameter values. Thus environmental variation that essentially occurs as white noise is not important in managing the fishery, but any variation that can produce long-term trends in life-history parameters for *P. latisulcatus* may have important implications. For example, a persistent long-term increase in M could dramatically alter the population dynamics of the stock and its response to fishing (Chapter 3).

In predicting that environmental variation is not important in determining the best harvesting strategy for the fishery, it is assumed that effort does not increase in response to declining catch rates in bad years to maintain actual harvest. Fishing also does not increase in good years to take advantage of the extra production. Instead, the same fishing mortality and percentage of area trawled is maintained (although with stochastic variation). If fishing strategies do change in response to variation in catch, then it is possible that the stock would react differently to what the model predicts. Maintaining constant fishing effort in the face of fluctuating catches will not always allow the long-term harvest to remain steady, however. In an example of a sea-urchin stock exposed to random variation in recruitment, Bradbury and Pfister (1996) show that environmental variation can drive the stock size down substantially under all but the very lightest fishing pressure. Similarly, when Lauck et al. (1998) modelled random variation in F, they found substantial decreases in stock size unless a large proportion of the habitat was protected from fishing.

There are several features of the population studied that are likely to contribute to the results found here. Firstly, the stock is contained within a single large embayment, with distinct density-dependence operating in the juvenile phase of the life-cycle, and relatively strong coupling between juvenile and adult stocks. These features mean that much of the random variation in the model is damped out and does not propagate through to the final harvest. Also, fishing targets prawns in the 2+ and older age groups, which have already had a chance to reproduce. In combination with the relatively high natural mortality rates, this means that the reduction in the stock's reproductive output due to fishing is fairly low, accounting for the lack of an effect of variation in fishing mortality or area trawled. Allowing all animals to spawn at least once before becoming vulnerable to the fishery has previously been suggested as a way of preventing stock collapse in the event of exceeding the target fishing mortality (Myers and Mertz 1998), and it appears that this is the most important feature of the fishery that allows it to remain resilient to changes in model parameters (see also Chapter 3).

The method by which stochastic variation was entered into the model might also account for the results found. There was no autocorrelation between years, meaning that the model did not allow runs of good or bad years beyond what would occur by chance. Thus there was no allowance for coupling to long-term environmental cycles such as might occur due to El Nino for example (e.g. Hoffmann and Powell 1998). When multiple parameters were varied, they were also generally varied independently, whereas a good year for survival of adults say is also likely to be a good year for reproduction and survival of juveniles. However, when independent and correlated variation in fecundities of each age class was examined, there was little difference between the model outputs. The single set of simulations in which survival and fecundity were correlated also suggests that such correlated variation would increase harvest rates, but not alter the optimal fishing strategy.

The modelled population may also be protected from problems related to variation in the parameters because high harvests only occur when a very small proportion of the habitat is fished. One of the major conclusions of Lauck et al. (1998) was that protecting a large part of the habitat allowed the target stock size to be maintained despite variation in catch rates, whereas this could not be done when little or no habitat was protected. In fact, one of the major conceptual arguments for marine reserves in a fisheries management context is that they will reduce year-to-year variation in catches related to variation in environmental conditions or harvest rates (e.g. Guénette et al. 1998; Hall 1998; Hastings and Botsford 1999; Sladek Nowlis and Roberts 1999).

While the higher fishing mortality rates allowed in the model (up to F=10) may seem extremely unrealistic, it must be remembered that this F only applies to those areas actually in the path of the trawl, and while the effectiveness of the gear is not known, it is likely to be high. Also, because total mortality is partitioned between fishing and natural causes proportionally, a high F can represent intense fishing early in the year before many animals have had the opportunity to die of natural causes.

In conclusion, the model used here suggests that environmental variation is not an important consideration for the management of the *P. latisulcatus* stock in Gulf St. Vincent, unless it takes a substantially different form to that modelled. While variation could lead to long-term increases in average harvests, under none of the scenarios examined did it alter the optimal harvest regime, or noticeably decrease harvest rates for a broad range of fishing strategies. The likely reason for this result is that animals only enter the fishery after their first spawning, and in combination with high natural mortality rates, this means that the fishery has relatively little impact on reproductive output of the stock. Density-dependent juvenile survival also helps to dampen out fluctuations. This conclusion could alter substantially, however, if environmental variation is autocorrelated, with long runs of either good or bad years.

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Chapter 5:The effect of effluent discharge on marine macrofauna in Gulf St Vincent, South Australia.

Rachel J. Marsh

Abstract

In Adelaide, the Bolivar Wastewater Treatment Plant, which treats the majority of wastewater within South Australia, discharges approximately 100 ML/day of secondary-treated effluent into the intertidal region of eastern Gulf St Vincent. Macrofaunal assemblages surrounding the Bolivar Outfall varied substantially along the resulting pollution gradient. While the abundance of some species did not vary, the abundance of both *Melicertus latisulcatus* Kishinouye (western king prawn) and *Portunus pelagicus* (Linnaeus) (blue swimmer crab) progressively increased up to 2 km from the outfall. A decline in water quality adjacent to the outfall is likely to explain these changes. At peripheral sites (4-5 km away) species diversity increased and the abundance of *M. latisulcatus* decreased, possibly due to a change in habitat from sand to seagrass. Temporal variation in the response of macrofaunal assemblages to sewage discharge is evident, with a storm prior to sampling on one occasion masking the effects of pollution and habitat changes. Failure to detect consistent changes in the size frequency distribution of *M. latisulcatus* and *P. pelagicus* along the pollution gradient, or in growth of *M. latisulcatus* in a nutrient enrichment experiment, suggests that nutrients do not interfere with the growth of these species. The results of this study suggest that the disposal of effluent into Gulf St Vincent is only having a localised effect on the faunal assemblages surrounding the discharge point. Furthermore this study reiterates the importance of investigating pollution effects over several spatial and temporal scales.

Introduction

Environmental pollution and its effects on aquatic ecosystems continues to be a problem of growing worldwide concern (Goldberg 1995; McIntyre 1995; Koop and Hutchings 1996). Of particular importance is organic enrichment from wastewater discharge into the oceans (McIntyre 1992; Yap 1992; Edyvane 1999), which has been recognised as one of the principal causes of faunal change in near-shore benthic environments (Pearson and Rosenberg 1978). Despite these concerns, not only does effluent disposal continue unabated, but the quantity of sewage being discharged into the oceans is steadily increasing (McIntyre 1992; Otway 1995). The primary driving force behind disposal of sewage into the oceans is continual population growth and increasing urbanisation along the coasts (McIntyre 1992; Otway 1995; Yapp 1986; Edyvane 1999). Furthermore, alternative methods of effluent disposal are not considered due to the cost effectiveness of ocean-disposal and the oceans supposed large assimilative capacity (the ability to absorb a given quantity of material without producing an unacceptable impact) (Otway 1995).

It is well documented that sewage effluent, which may be treated to one of a number of levels prior to discharge, leads to structural changes in faunal assemblages (Pearson and Rosenberg 1978; Vanes *et al.* 1980; Rygg 1985; Austen *et al.* 1989; Smith and Simpson 1992). While a range of ecological responses have been attributed to sewage discharge, Pearson and Rosenberg (1978) synthesised the available literature to produce a general model of organic enrichment effects. A consistent pattern of faunal change along a gradient of organic enrichment was found, whereby the effects are more pronounced in the vicinity of the outfall and decrease progressively with distance from the point of discharge. At points of high organic input, a few opportunistic species will become abundant and dominate the community, while less tolerant species will become increasingly rare or disappear. With increasing distance from the most organically-enriched area, however, a rapid decline in the abundance of opportunistic species is observed and the total number of species increases. A majority of subsequent studies have investigated components of the model produced by Pearson and Rosenberg (1978) and have supported the general trends outlined (Dorsey and Synnot 1980; Dorsey 1982; Spies 1984; Rygg 1985; Smith and Simpson 1992; Growns *et al*. 1998; Inglis and Kross 2000).

While some species do not respond to the input of pollution, or are minimally affected, others are dramatically influenced either positively or negatively. Positive indicators of pollution are those species that increase in abundance and dominate with increases in nutrients; they are often small bodied, poor competitors, and include many infaunal species with high tolerance to nutrient additions (e.g. capitellid polychaetes, some spionid polychaetes, gastropod molluscs and corophiid ampipods) (Dorsey and Synnot 1980; Vanes *et al.* 1980; Dorsey 1982; Rygg 1985; Inglis and Kross 2000). Other positive indicators of pollution include some algae such as *Ulva* (Connolly 1989) that are fast growing in nutrient rich waters (Fujita 1985), and other species that can form characteristic blooms as a result of eutrophication (Brooker and Walsby 1981; McIntyre 1992; Hardy *et al*. 1993). Negative indicators of pollution (or positive non-pollution indicators) frequently occur in less polluted areas and eventually disappear when their environment becomes polluted

(Pearson and Rosenberg 1978; Vanes *et al*. 1980; Rygg 1985; Keough and Quinn 1991). Negative indicators of pollution include macrofaunal species such as crustaceans and some fish (Lui and Morton 1998; Smith and Suthers 1999). Extensive seagrass degradation has also been closely linked to elevated nutrient levels (Neverauskas 1987; Shepherd *et al.* 1989; Walker and McComb 1992; Short and Wyllie-Echeverria 1996). Seagrasses, which are particularly sensitive to organic enrichment, are lost due to the direct effects of effluent input and indirect effects brought about by increased turbidity, algal and epiphyte growth, all of which attenuate light and consequently photosynthetic activity (Shepherd *et al.* 1989; Walker and McComb 1992; Short and Wyllie-Echeverria 1996).

Sewage is discharged into the oceans via deep ocean outfalls, rivers or direct discharges into the intertidal or shallow sub-tidal regions. The input of sewage into intertidal regions is of particular importance due to the threat it places on the vast diversity of animals inhabiting these areas. The intertidal or littoral zone makes up a very small fraction of the continental shelf, and despite exposure to highly variable conditions, is an extremely important area for many species which utilise is as a nursery ground. An example of this can be found in Gulf St Vincent, where *Melicertus latisulcatus* Kishinouye (western king prawn) and *Portunus pelagicus* Linnaeus (blue swimmer crab) utilise the intertidal throughout juvenile stages of their life cycle (Kangus and Jackson 1998; Kangus 1999; Kumar *et al*. 2000). However, the ever increasing input of sewage, often to these important nursery grounds, can impinge directly or indirectly upon their survival (Engel and Thayer 1998).

Despite extensive literature documenting the effects of organic enrichment, a few studies have failed to detect significant changes in organism abundance in intertidal areas as a result of its impact (Smith 1994; Lardicci *et al*. 1999). This failure is primarily due to the highly variable nature of the intertidal, both spatially and temporally, which confounds attempts to reliably detect the effects of sewage (Pearson and Rosenberg 1978; Vanes *et al*. 1980; Peckol and Searles 1984; Livingston 1987; Austen *et al*. 1989; Ferraro *et al*. 1991; Keough and Quinn 1991; Anderlini and Wear 1992; Morrisey *et al*. 1992; Smith 1994; Chapman and Underwood 1998; Hewitt *et al*. 2001). For example, a survey of the macrofauna inhabiting kelp (*Ecklonia radiata*) holdfasts in Jervis Bay, New South Wales, failed to detect differences in species composition between those sites close to a sewage outfall and those further away. It was concluded that natural environmental factors were more influential than the input of effluent, due to the highly variable community structure both spatially and temporally (Smith 1994).

Difficulty in assessing the impact of sewage can also be due to a lack of baseline information from outfall sites prior to the commencement of effluent disposal. To overcome this dilemma, most researchers compare environmental variables around a discharge area to one or a few supposably pristine sites located many kilometres away (Gray *et al.* 1992; Lye *et al.* 1997; Lui and Morton 1998; Smith and Suthers 1999). Despite the acceptance and subsequent utilisation of this experimental design, few studies have determined how far from the point of effluent disposal organisms and/or habitats are influenced. Furthermore, there is a limited amount of information regarding factors which may affect this response. In a study performed by Anderlini and Wear (1992), benthic macrofaunal communities affected by the discharge of sewage were found to occur within 500 m of the outfall. Consequently, the effect of effluent into this area is relatively localised. Substantial spatial and temporal variability in the intertidal, combined with the tendency of researchers to investigate the effects of pollution by only comparing sites experiencing heavy organic enrichment to pristine control locations, both confound attempts to reliably detect the effects of pollution. The investigation of several sites along a pollution gradient, however, minimises the effects of natural variation, and contributes additional information on the effects of pollution.

Misinterpretation of the effects of nutrient enrichment in a number of studies is also caused by the examination of the response to pollution by a single (indicator) species. The use of a single species to assess possible perturbations in environments is widely accepted (Phillips and Segar 1986) and used (Gray *et al*. 1992; Lui and Morton 1998; Smith and Suthers 1999). Criteria by which indicator species are chosen, however, often fail to include their ecological significance, representativeness of other species, and suitability as an indicator of the current status of ecological processes or predicability of the future health of the system, all of which are necessary for determining appropriate indicator species for establishing pollution effects (Underwood and Peterson 1988). While there are benefits to utilising indicator species, their use can provide a misleading view of the total habitat response. Quantification of multiple variables, including indicator species, provides a better indication of the consequences of pollution in marine ecosystems. Furthermore, there is a tendency to assume that changes between sites are due to changing pollution levels, which are often not quantified. Although knowledge of the actual level of pollution is not essential for detecting its effects, it will greatly improve the ability to predict effects of similar impacts in different areas or habitats (Keough and Quinn 1991), and will provide additional evidence for explaining differences among sites.

In light of the intrinsic problems and frequent employment of simplistic experimental designs, this study investigates temporal and spatial variation in the distribution of marine macrofauna surrounding the Bolivar Wastewater Treatment Outfall (Adelaide, South Australia). The abundance of *M. latisulcatus* and *P. pelagicus* within the area is of particular interest due to their commercial importance and utilisation of the intertidal as a nursery ground. The extent to which changes in water quality can explain the abundance and distribution of marine macrofauna will also be examined. As well as looking at the effects on assemblage structure and distribution of individual species, one of the potential mechanisms (growth) by which pollution could be affecting fauna will be examined. To do this the size frequency distribution of both *M. latisulcatus* and *P. pelagicus* along a pollution gradient will be established, in addition to growth rates of *M. latisulcatus* in a range of nutrient enriched treatments.

Materials and Methods

Study site

To examine the influence of effluent discharge on the distribution of marine macrofauna, a number of sites were surveyed around the Bolivar Wastewater Treatment Outfall, where secondary treated sewage is discharged daily into Gulf St Vincent, approximately 28 km north of Adelaide (Fig.5.1). Average volume of sewage entering the Bolivar Treatment Plant is approximately 135 ML/day (D. Tintor pers. comm. 2001), however, due to the re-use of a quantity of this water by the Virginia Market Gardens, not all of this is discharged into Gulf St Vincent. The sewage that does enter Gulf St Vincent is discharged via Fork Creek directly into the intertidal zone, which is characteristically a low energy area where mangroves line the coast. The soft bottom environment surrounding the outfall was once inhabited by extensive *Heterozostera* and *Posidonia* beds, however, loss of these seagrass species since Bolivar began operating in 1967 has occurred (Shepherd *et al.* 1989). A significant dieback of mangroves next to the Bolivar Outfall has also been attributed to nutrient enrichment in the area (Edyvane 1999). The region is presently dominated by extensive, intertidal sand flats, up to 1.5 km wide.

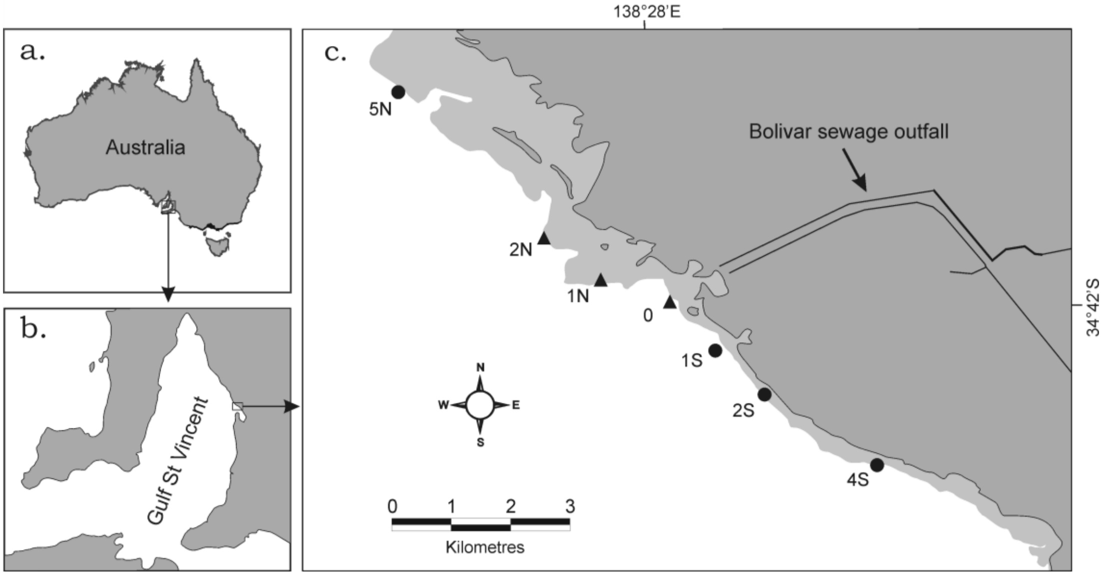

Figure 5.1. Map of (a) Australia, (b) Gulf St Vincent and (c) location of sampling sites surrounding the Bolivar Outfall. σ = sites for Temporal and Spatial Faunal Sampling, λ = sites for Spatial Faunal Sampling.

Spatial variation in fauna around Bolivar

Spatial variability in the macrofaunal assemblage with distance from effluent discharge was investigated. Sites were located at the outfall in addition to 1, 2 and 5 km north and 1, 2, and 4 km south of the outfall (Fig.5.1). The original sampling site 5 km south of the outfall was not used in the experimental design, as it is situated within Barker Inlet itself, rather than Gulf St Vincent, subsequently a site located 4 km south of the outfall was used as a control site. A water-jet net (Fig. 5.2) (Kangas and Jackson 1998), was used to sample larger macrofauna, and was specifically designed to sample juvenile *M. latisulcatus* during daylight when the prawns are buried in sediment. The water-jet net was constructed of galvanised steel tubing (25 mm in diameter) and consisted of a frame measuring 1.0 m (width) × 0.95 m (length) × 0.35 m (height) (Fig. 5.2a). A central T-bar had holes (3 mm in diameter) drilled every 50 mm, through which water was pumped by a Finsbury centrifugal pump (500 L min^{-1}) driven by a 5.5-hp Honda engine (Kangas and Jackson 1998). Two millimetre nylon netting covered the entire frame with a 2.5 m long tail which was tied off at the cod-end (Fig.5.2b). As the net is towed behind the boat and water is pumped through the central T-bar, the water jets penetrate the substrate to a depth of 50 mm. Animals buried within the sediment or in close proximity to the sediment are disturbed and lifted, and subsequently collect in the tail of the water-jet net. Species collected predominantly include a variety of small fish and crustaceans. Jet-netting is a highly effective means of sampling *M.latisulcatus*, as it ensures a higher degree of accuracy in catch compared to methods such as beam trawling (Kangas and Jackson 1998). Samples were collected on three days during a five day period. A survey of juvenile *M. latisulcatus* utilising the water-jet net found insignificant day to day changes in abundance over a similar time period, indicating sampling over a five day period is adequate (Kangas 1999). The original sampling period (March 26th to 30th) occurred immediately after a major storm, which could potentially have influenced the results, so sampling was repeated in May (7th to 11th) following a period of calm weather. Mean daily volume of effluent was recorded as 95.2 and 98.4 ML during the times of sampling in March and May, respectively (D. Tintor pers.comm 2001).

Figure 5.2. Water-jet net design showing (a) the galvanised frame without netting and (b) with net attached.

Trawls were approximately 100 m long (determined using a Global Positioning System receiver (GPS)), and were made within 20 m of the mangroves, parallel to the shore, at high tide. The net was retrieved after each trawl (three trawls at each site), and the contents emptied into 20 L buckets and later sorted on shore. The samples were then fixed in 10% formaldehyde, identified to species level where possible, and counted. Habitat type with regard to sand/seagrass cover was visually estimated at each site. To establish if effluent discharge influenced the growth of commercially important species, the size of all juvenile *M. latisulcatus* and *P. pelagicus* were measured.

Weight (to the nearest 0.0001 g) was measured and recorded using a Mettler AE200 balance, while carapace length/width (to the nearest 0.1 mm) was determined using an ocular micrometer and vernier callipers for larger animals.

To identify temporal and spatial variation in the macrofaunal assemblage, a non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2001a; b) was performed, with time being treated as random, and distance fixed. The data were transformed (fourth root) to reduce the influence of abundant taxa. Differences between samples were quantified using Bray-Curtis similarities, as this measure does not give any weight to joint absences. Probability values were calculated using 4999 permutations of the residuals under a reduced model (Anderson 2001a; b). Where macrofaunal assemblages were found to be significantly different among distances (<0.05), pair-wise *a-posteriori* comparisons between sites were performed. The low replication at each site (*n* = 3), caused by logistical problems, meant that there were only 10 possible permutations for each pair-wise test. The minimum *P*-value obtainable was thus 0.1, which was taken as the value for a significant difference. Temporal and spatial variation was represented graphically using non-metric multidimentionsal scaling (MDS), with Bray-Curtis similarity measure. To determine how individual species varied with time and distance from the outfall Generalised Additive Models (GAM, Hastie and Tibshirani 1990; Yee and Mitchell 1991) were used. GAM is a statistical method analogous to regression that is ideal for distinguishing major features that influence large scale spatial trends. GAM fits non-linear smooth curves to data and thus the shape of the curve is data driven rather than being limited by the assumptions of models (Yee and Mitchell 1991). Models were produced for each species separately in Splus (Math-Soft Inc. Seattle) assuming a Poisson distribution (for count data). Generalised Linear Modelling (GLM) was adopted if the non-linear component for distance was found to be insignificant (*P*>0.05) (McCullagh and Nelder 1989; Dobson 1990).

To compare mean carapace length and weight of *M. latisulcatus* and *P. pelagicus* at different distances from the outfall, non-parametric Kruskal-Wallis tests were performed in SPSS (SPSS inc, Chicago). Size frequency distributions of *M. latisulcatus* and *P. pelagicus* were also compared among sites using Chi-square tests. If a significant change in size frequency occurred between sites, pair-wise Chi-square tests were performed to establish how size frequency distribution differed among sites.

Temporal variation in fauna around Bolivar

The influence of temporal variation on the response of the macrofaunal assemblage to effluent discharge was further investigated with the incorporation of results from a preliminary study. Sites were situated at the outfall, in addition to those located 1 and 2 km north of the outfall (Fig. 5.1). Samples were collected following calm conditions on February 26th and August 2nd, 2001, with a water-jet net. Sewage discharged the night prior to sampling was quantified as 96 and 125 ML in February and August, respectively (D. Tintor pers. comm. 2001). To identify both temporal and spatial variation in the macrofaunal assemblage, a NPMANOVA was performed which included the data from the corresponding sites from the study investigating spatial variation in fauna around the Bolivar Outfall. Where macrofaunal assemblages were found to be significantly different among distances ($\alpha = 0.05$), pair-wise *a-posteriori* comparisons were made between sites, at different times. Non-metric MDS was used to graphically present the data. To determine how individual species varied with time and distance from the outfall GLM was again used. GAM was not used in this situation as a minimum of four study sites is required for its application.

Water quality

To assess how water quality varied with distance from the Bolivar Outfall, samples were collected during each trawl, at the time of macrofaunal collections during March and May, 2001. Samples were collected in labelled, 250 ml glass jars during each trawl, and placed directly on ice. Once on shore the samples were covered in aluminium foil and stored at 2-5^{o}C until analysis. Ammonia, nitrite, phosphate and dissolved oxygen concentration in addition to pH, were measured using a Hanna Instruments C203 photometer. A NPMANOVA was used to determine if any spatial or temporal variation in water quality existed. Euclidean distances were used in the analysis due to the nature of the data. Pair-wise *a-posteriori* comparisons between sites were performed for both sampling times. Non-metric MDS was used to graphically represent spatial and temporal variation between sites, however this did not prove to be useful.

Relationship between macrofaunal abundances and water quality

To establish the extent to which water quality could explain patterns seen in the abundance and distribution of macrofauna over both time periods, a canonical correlation analysis was performed in SPSS. Canonical correlation analysis is an analytical technique that can be used to describe the relationship between a set of environmental variables (such as water quality) and a set of species abundances (McGarigal *et al*. 2000). The analysis was also performed on data from the five sites located within 2 km either side of the outfall, for each sampling period together, and separately (hereafter referred to as the restricted data set). These additional analyses were performed due to the substantial change in faunal composition between those sites within 2 km of the outfall, and those located beyond this distance. Due to the nature of this analysis, species that only occurred once were removed. During March in the restricted data set the number of variables exceeded the number of samples, therefore species were removed from the analysis in order of least abundance (the species removed, however, had no more than four individuals).

Effects of nutrient enrichment on Melicertus latisulcatus *growth*

To examine the effect of nutrient enrichment on the growth of juvenile *M. latisulcatus*, growth rates in a range of nutrient enriched treatments were observed. A series of 27 tanks were set up in controlled environment rooms. Each round tank was 59 cm in diameter, 43 cm deep, and filled to a depth of approximately 35 cm (total volume ~ 95 L). The controlled environment rooms were maintained at 26°C. Juvenile *M. latisulcatus* were collected off Outer Harbour with a 1.5 m beam-trawl at night, and held in a 500 L outdoor holding tank with flow through seawater until needed. Nine nutrient treatments were established consisting of three levels (none, low and high) each of ammonia and phosphate (Table 5.1). The nutrient concentrations used, corresponded to ammonia and phosphate concentrations found in the vicinity of the Bolivar Outfall in late March, 2001. Phosphate and ammonia levels were manipulated using mono-potassium phosphate (KH_2PO_4) and ammonium chloride (NH_4Cl), respectively.

Table 5.1. Nutrient concentrations used in *Melicertus latisulcatus* growth experiments.

Treatment	Concentration of Ammonia (mg/L^{-1})	Concentration of Phosphate (mg/L^{-1})
1	0	0
2	0	0.6
3	0	1.2
4	0.85	0
5	0.85	0.6
6	0.85	1.2
7	2.2	0
8	2.2	0.6
9	2.2	1.2

Seven juvenile *M. latisulcatus* were randomly allocated to individual tanks. To identify individual prawns within respective tanks, they were tagged prior to the start of the experiment. Fluorescent elastomer internal tagging (Dewey and Zigler 1996; Godin *et al.* 1996; Willis and Babcock 1998; Jerry *et al*. 2001) was used in which four colours were administered (fluorescent green, yellow, pink and orange) in one of two positions (intramusculatory into either the ventral side of the sixth tail segment or dorsally into the second abdominal segment). At the start, and on completion of the experiment, the weight and carapace length of each prawn was recorded. Weight was measured using a Mettler AE200 balance, while carapace length was determined with the use of an ocular micrometer. The experiment ran for 29 days, beginning on 5th July, and ending on 2nd August, 2001. Water changes of 20 L were made every two days. Approximately 1 g of chopped marinara mix was provided to every tank daily, with food remaining the next day being removed to avoid a build up of excess nutrients. Each treatment was replicated three times, with treatments randomly allocated to tanks.

To determine whether or not ammonia and/or phosphate concentration had an effect on juvenile *M. latisulcatus* growth, an analysis of covariance (ANCOVA) was performed in SPSS. Prawn growth (weight and carapace length) during the experiment was treated as the dependent variable, while ammonia and phosphate concentration were fixed, independent variables. Initial prawn size (weight or carapace length) was the covariate. To determine if there was a tank effect, tank was also included in the analysis as a random factor. To ensure the assumptions of ANCOVA were met, a Levene's test (for homogeneity) and Q-Q plots (for normality) were performed. Data were transformed (square root) when necessary to meet the assumptions of ANCOVA.

Results

Spatial variation in fauna around Bolivar

Following the collection of macrofauna around the Bolivar Outfall using a water-jet net, a total of 7025 individuals were identified, comprising 20 species from three orders (Table 5.2); the three most abundant species were *M. latisulcatus*, *P. pelagicus* and *Favonigobius lateralis* (Macleay). A significant interaction between distance from the Bolivar Outfall and month of sampling was found (Table 5.3) indicating that the effect of the outfall varied over time. The grouping of data between sites is evident in the MDS plot (Fig. 5.3), the stress value was low (0.1) suggesting that the relationship between sites is well portrayed in two dimensions. Particularly obvious is the separation of the peripheral sites (5 km north and 4 km south of the outfall) from those in close proximity to effluent disposal. The samples from the outfall site (0) are scattered, and some appear most similar to distant sites, indicating their variable nature (Fig. 5.3). Pair-wise *a posteriori* comparisons among sites during March and May indicated that the majority of sites were significantly different from each other, particularly for those samples taken during May following a period of calm weather (Table 5.4).

The macrofaunal assemblage was significantly different in the majority of pair-wise *a posteriori* comparisons made between north and south sites at the same distance from the outfall (Table 5.4), indicating that the response to effluent is different depending on direction. North and South differences can also be seen when assessing the abundance of *M. latisulcatus* and *P. pelagicus* (Fig. 5.4), with the effect of effluent more pronounced in the south, during May.

The response of different species to distance from the effluent outfall varied. Although abundances of the majority of species including *F. lateralis, Kastratherina esox* (Klunzinger) and *Ozius truncatus* Milne Edwards fluctuated substantially between sites, no apparent trend with distance from the outfall was observed. In contrast, other species such as *M. latisulcatus* (GAM, $F_{4,37}$, $P<0.001$) and *P. pelagicus* (GAM, $F_{4,37}$, $P = 0.0016$), displayed clear trends, generally increasing in abundance with distance from the outfall until a point is reached (~4 km South, ~5 km North) where abundances dramatically drop to approximately those found at the outfall. This response to distance, however, is far more pronounced in May than in March (Fig. 5.4). Species richness differed significantly between sites, and was found to increase with distance from the Bolivar Outfall (GLM, $F_{1,40}$, $P = 0.0046$) (Fig. 5.5).

Table 5.2. Total number individuals of each of the macrofaunal species collected in the area surrounding the Bolivar Outfall, for both spatial and temporal studies of pollution effects.

Species	Order/Class	Family	SFS	TFS
Idiosepius notoides Berry, 1821	Cephalopoda	Idiosepiidae	1	1
	Decapoda	Alpheidae	4	1
Philyra laevis Bell, 1855	Decapoda	Leucosiidae	53	15
Ozius truncatus Milne Edwards, 1834	Decapoda	Menippidae	24	23
Palaemon marcrodachytus Rathbun, 1902	Decapoda	Palaemonidae	89	8
Melicertus latisulcatus Kishinouye, 1896	Decapoda	Penaeidae	4228	2940
Carcinus maenas (Linnaeus, 1758)	Decapoda	Portunidae	15	11
Portunus pelagicus (Linnaeus, 1766)	Decapoda	Portunidae	576	166
Atherinosoma elongata (Klunzinger, 1879)	Osteichthyes	Atherinidae	22	1
Kestratherina esox (Klunzinger, 1872)	Osteichthyes	Atherinidae	39	39
Favonigobius lateralis (Macleay, 1881)	Osteichthyes	Gobiidae	1903	1594
Arenigobius bifrenatus (Kner, 1865)	Osteichthyes	Gobiidae	1	13
Platycephalus laevigatus Cuvier, 1829	Osteichthyes	Platycephalidae	6	6
Platycephalus bussensis Cuvier, 1829	Osteichthyes	Platycephalidae	6	7
Gymnapistes marmoratus (Cuvier, 1829)	Osteichthyes	Scorpaenidae	8	3
Sillaginodes punctata (Cuvier, 1829)	Osteichthyes	Sillaginidae	7	6
Vanacampus phillipi (Lucas, 1891)	Osteichthyes	Syngnathidae	3	4
Pelates octolineatus (Jenyns, 1842)	Osteichthyes	Terapontidae	34	1
Contusus brevicaudus Hardy, 1981	Osteichthyes	Tetraodontidae	4	7
Contusus richei (Freminville, 1813)	Osteichthyes	Tetraodontidae	2	4

SFS = Spatial Faunal Sampling, TFS = Temporal Faunal Sampling.

Table 5.3. NPMANOVA results of the effect of distance from the Bolivar Outfall on the macrofaunal assemblage during March and May, 2001.

Source	df	SS	*F*	*P*
Distance	6	13040	2.49	0.0054
Month	1	2163	6.01	0.0004
Distance × Month	6	5231	2.42	0.0004
Residual	28	10080		
Total	41	30514		

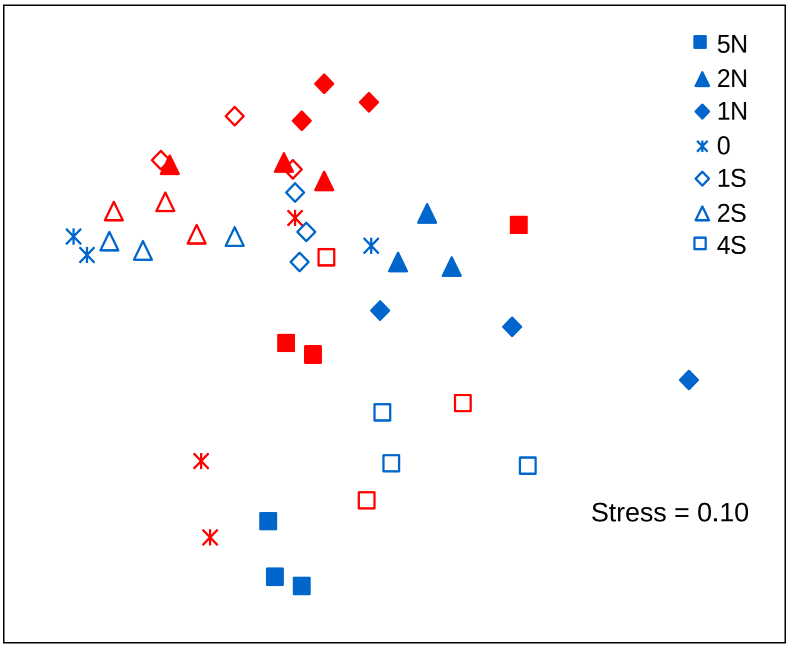

Figure 5.3. Two dimensional MDS plot of macrofaunal assemblage at a range of sites with distance from the Bolivar Outfall, in March and May, 2001. Blue symbols represent those samples collected in March and red symbols represent those samples collected in May.

Table 5.4. Results of pair-wise *a posteriori* tests comparing macrofaunal assemblages between sites during (a) March and (b) May.

a)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 55.32						
1N	**<0.001** 145.99	**<0.001** 94.46					
0	**<0.001** 54.92	0.18 3.39	**<0.001** 94.06				
1S	**<0.001** 54.09	0.28 2.55	**<0.001** 93.22	0.34 2.15			
2S	**<0.001** 80.06	**<0.001** 28.53	**<0.001** 119.20	**<0.001** 28.12	**<0.001** 27.29		
4S	**<0.001** 50.70	0.12 4.17	**<0.001** 94.84	0.15 3.77	0.23 2.93	**<0.001** 28.91	

b)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 58.58						
1N	**<0.001** 132.69	**<0.001** 92.51					
0	**<0.001** 59.54	**<0.001** 19.37	**<0.001** 93.47				
1S	**<0.001** 53.15	**<0.001** 12.97	**<0.001** 87.08	**0.003** 13.93			
2S	**<0.001** 70.23	**<0.001** 30.05	**<0.001** 104.16	**<0.001** 31.01	**<0.001** 24.62		
4S	**<0.001** 74.67	**<0.001** 34.50	**<0.001** 108.61	**<0.001** 35.46	**<0.001** 29.06	**<0.001** 46.15	

Top number = *P* value, bottom value = ©^{2} value, bold numbers indicate a significant relationship between sites (<= 0.05).

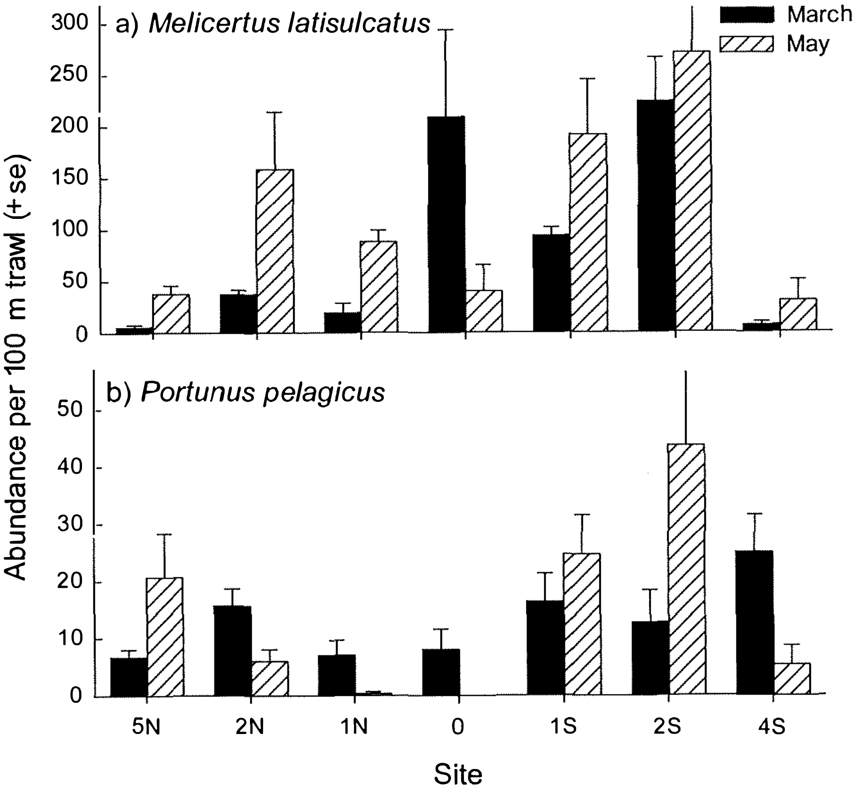

Figure 5.4. Abundance (mean + se) of juvenile (a) *Melicertus latisulcatus* and (b) *Portunus pelagicus* at seven sites surrounding the Bolivar Outfall during March and May, 2001.

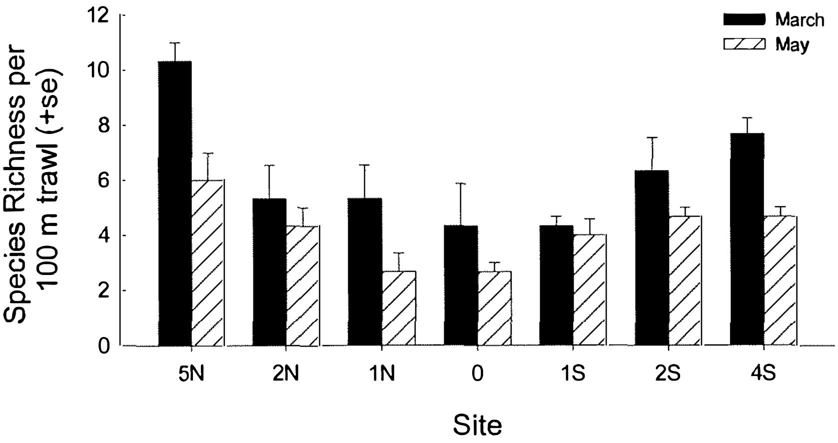

Figure 5.5. Species richness (mean + se) at seven sites surrounding the Bolivar Outfall in March and May, 2001.

Visual observations of habitat type surrounding the Bolivar Wastewater Treatment Plant revealed that seagrass cover changed substantially with distance from the input of sewage. Within 2 km of the outfall a minimal amount of seagrass was observed, however at sites located further away (i.e. 5 km North and 4 km South), percentage seagrass cover substantially increased, indicating a change in habitat at sites located further away from the effluent disposal.

The mean size of *M. latisulcatus* and *P. pelagicus* varied significantly between sites (Table 5.5). Despite these significant differences, however, no specific trend with distance from the Bolivar Outfall was found. Size frequency distributions for each species were also significantly different among sites (Table 5.6). Pair-wise *a posteriori* comparisons between the size of those species studied and sampling sites, indicated that in the majority of cases their size varied between sites (Table 5.7). Despite these spatially significant differences in size frequency distributions, however, graphical representation of data shows that there were no consistent effects of distance (Figs 5.6 and 5.7).

Table 5.5 Results of Kruskal-Wallis tests, investigating the influence of distance from Bolivar Outfall on the mean carapace length and weight of *Melicertus latisulcatus* and *Portunus pelagicus* during March and May.

Source	df	χ^2	*P*
Melicertus latisulcatus W, March	6	94.86	<0.001
M. latisulcatus W, May	6	83.60	<0.001
M. latisulcatus CL, March	6	73.62	<0.001
M. latisulcatus CL, May	6	103.77	<0.001
Portunus pelagicus W, March	6	121.35	<0.001
P. pelagicus W, May	5	96.44	<0.001
P. pelagicus CL, March	6	126.42	<0.001
P. pelagicus CL, May	5	96.30	<0.001

W = weight (g), CL = carapace length (mm)

Table 5.6. Results of Chi-square tests investigating the effect of distance from the Bolivar Outfall on the size frequency distribution of *Melicertus latisulcatus* and *Portunus pelagicus.*

Source	df	χ^2	*P*
Penaeus latisulcatus CL	18	201.97	<0.001
M. latisulcatus W	12	178.94	<0.001
Portunus pelagicus CL	18	410.55	<0.001
P. pelagicus W	12	191.30	<0.001

W = weight (g), CL = carapace length (mm).

Table 5.7. Results of pair-wise *a posteriori* Chi-square tests comparing juvenile *Melicertus latisulcatus* (a) weight and (b) carapace length, and *Portunus pelagicus* (c) weight and (d) carapace length between sites during March and May. Months of sampling pooled.

a)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 55.32						
1N	**<0.001** 145.99	**<0.001** 94.46					
0	**<0.001** 54.92	0.18 3.39	**<0.001** 94.06				
1S	**<0.001** 54.09	0.28 2.55	**<0.001** 93.22	0.34 2.15			
2S	**<0.001** 80.06	**<0.001** 28.53	**<0.001** 119.20	**<0.001** 28.12	**<0.001** 27.29		
4S	**<0.001** 50.70	0.12 4.17	**<0.001** 94.84	0.15 3.77	0.23 2.93	**<0.001** 28.91	

b)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 58.58						
1N	**<0.001** 132.69	**<0.001** 92.51					
0	**<0.001** 59.54	**<0.001** 19.37	**<0.001** 93.47				
1S	**<0.001** 53.15	**<0.001** 12.97	**<0.001** 87.08	**0.003** 13.93			
2S	**<0.001** 70.23	**<0.001** 30.05	**<0.001** 104.16	**<0.001** 31.01	**<0.001** 24.62		
4S	**<0.001** 74.67	**<0.001** 34.50	**<0.001** 108.61	**<0.001** 35.46	**<0.001** 29.06	**<0.001** 46.15	

c)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 12.54						
1N	**<0.001** 27.65	**<0.001** 9.06					
0	0.26 2.68	**<0.001** 11.07	**<0.001** 24.69				
1S	**<0.001** 20.44	**<0.001** 55.99	**<0.001** 91.41	0.067 5.41			
2S	**<0.001** 22.47	**<0.001** 68.01	**<0.001** 109.65	0.36 2.02	0.49 1.42		
4S	**<0.001** 20.21	**<0.001** 6.09	**<0.001** 25.67	**<0.001** 9.32	**<0.001** 53.38	**<0.001** 65.09	

Table 5.7. continued.

d)

Site	5N	2N	1N	0	1S	2S	4S
2N	**<0.001** 85.51						
1N	**<0.001** 124.21	**<0.001** 105.99					
0	**<0.001** 64.34	**<0.001** 46.11	**<0.001** 84.82				
1S	**<0.001** 100.98	**<0.001** 82.76	**<0.001** 121.47	**<0.001** 65.59			
2S	**<0.001** 110.82	**<0.001** 92.59	**<0.001** 131.30	**<0.001** 71.42	**<0.001** 108.07		
4S	**<0.001** 184.02	**<0.001** 165.80	**<0.001** 181.28	**<0.001** 144.63	**<0.001** 204.51	**<0.001** 191.11	

Top number = *P* value, bottom value = χ^2 value, bold numbers indicate a significant relationship between sites ($\alpha = 0.05$)

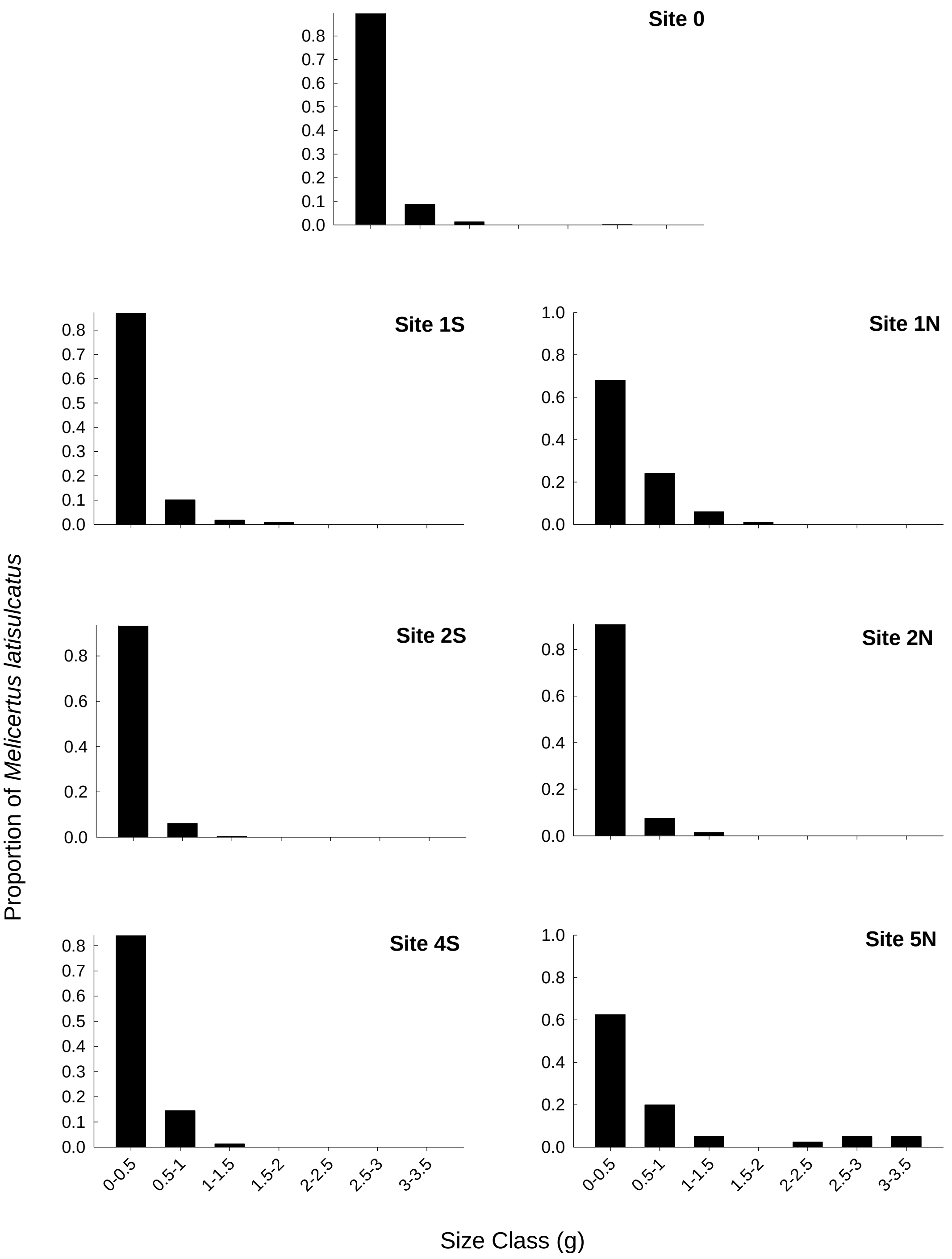

Figure 5.6. Weight frequency distributions of juvenile *Melicertus latisulcatus* around the Bolivar Outfall.

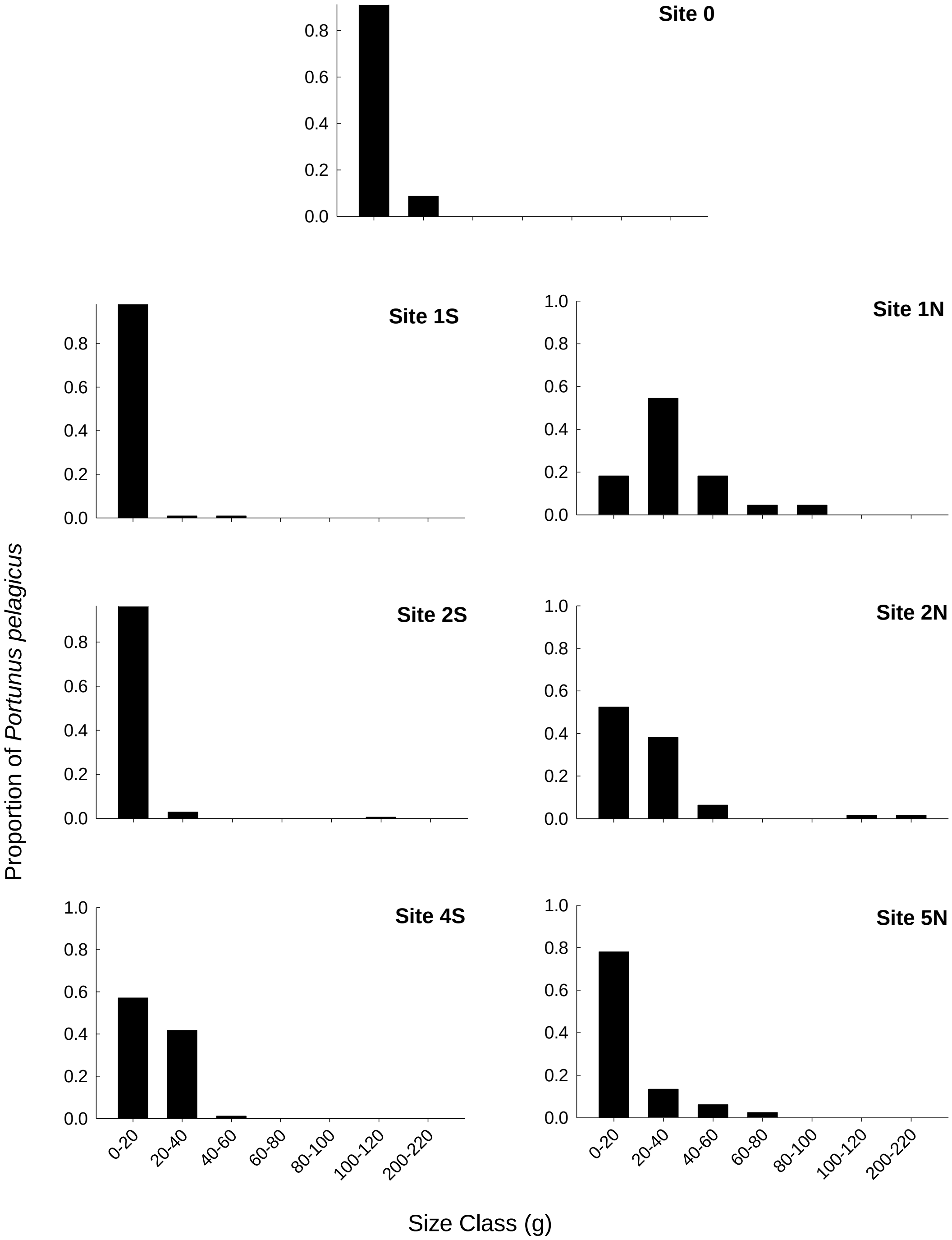

Figure 5.7. Weight frequency distributions of juvenile *Portunus pelagicus* around the Bolivar Outfall.

Temporal variation in fauna around Bolivar

In the investigation of temporal variation in the response of macrofaunal assemblages to effluent discharge, a significant interaction between distance from the outfall and month of sampling was found (Table 5.8). The difference between sites is evident in MDS plot (Fig. 5.8), the low stress value (0.08), indicating that the relationship between sites is well portrayed in two dimensions. Pair-wise *a posteriori* comparisons indicated that all sites were significantly different, except during March, following a major storm when there were no differences between sites (Table 5.9). The response of individual species varied. While most species responded to distance with no apparent trend, other species, such as *M. latisulcatus* (GLM, $F_{2,30}$, $P = 0.0055$) and *P. pelagicus* (GLM, $F_{2,30}$, $P<0.001$) generally increased in abundance with increasing distance from the Bolivar Outfall (Fig. 5.9). During March, however the typical response of these two species differed. While abundances of *P. pelagicus* showed a similar trend with distance from the outfall, a substantial increase in abundance existed over all sites. Abundance of *M. latisulcatus*, however was higher at the outfall compared to other sites.

Table 5.8. NPMANOVA results of the effect of distance from Bolivar Outfall (0, 1 and 2 km North) on macrofaunal assemblage during February, March, May and August.

Source	df	SS	*F*	*P*
Distance	2	6735	2.69	0.0106
Month	3	6563	4.24	0.0002
Distance × Month	6	7504	2.42	0.0002
Residual	24	12386		
Total	35	33188		

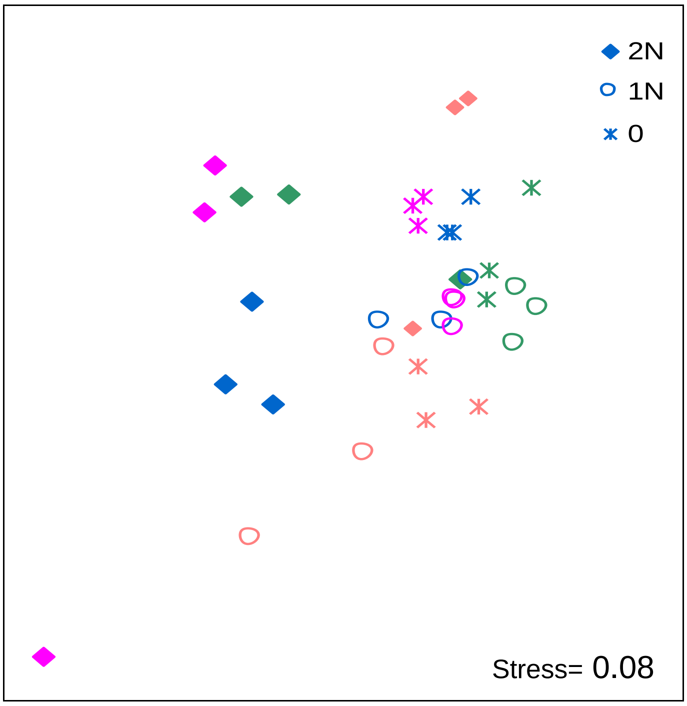

Figure 5.8. Two dimensional MDS plot of macrofaunal assemblage adjacent to the Bolivar Outfall, and 1 and 2 km north of the outfall, in February, March, May and August, 2001. Months of sampling pooled.

Table 5.9. Results of pair-wise *a posteriori* tests comparing the macrofaunal assemblages between sites during (a) February, (b) March, (c) May and (d) August.

Month	Site	t	*P*
a) February	0, 1N	1.32	0.1
	0, 2N	2.22	0.1
	1N, 2N	1.70	0.1
b) March	0, 1N	1.38	0.3
	0, 2N	1.23	0.3
	1N, 2N	0.70	0.7
c) May	0, 1N	2.03	0.1
	0, 2N	2.19	0.1
	1N, 2N	1.87	0.1
d) August	0, 1N	2.21	0.1
	0, 2N	2.56	0.1
	1N, 2N	2.57	0.1

Value for a significant difference *P* = 0.1.

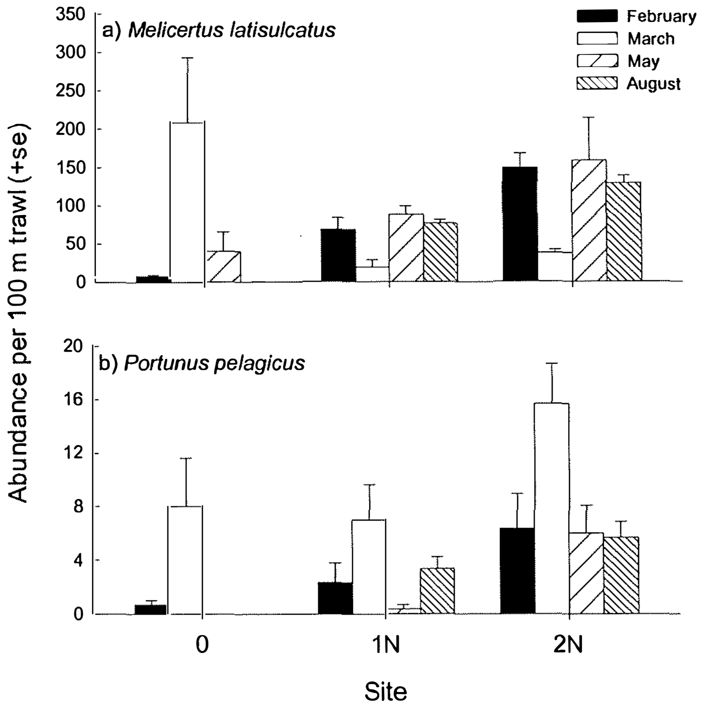

Figure 5.9. Temporal variation in abundance (mean + se) of juvenile (a) *Melicertus latisulcatus* and (b) *Portunus pelagicus* at three sites surrounding the Bolivar Outfall, in February, March, May and August, 2001.

In conjunction with macrofaunal samples taken in the study investigating spatial variation in fauna around Bolivar, water quality was assessed. A significant interaction between distance from the Bolivar Outfall and month of sampling for water quality was discovered, indicating that water quality at various distances from the outfall varied temporally (Table 5.10). Concentrations of ammonia, phosphate and nitrite were elevated at the outfall and decreased with distance from the outfall. Dissolved oxygen and pH displayed the opposite trend, being lower at the outfall and increasing with distance from the outfall (Fig. 5.10). These trends, however, substantially change with time and are certainly more pronounced during March than May.

Table 5.10. NPMANOVA results of the effect of distance from Bolivar on water quality during March and May, 2001.

Source	df	SS	*F*	*P*
Distance	6	1.80	3.79	0.0084
Month	1	0.64	19.94	0.0002
Distance × Month	6	0.47	2.46	0.0056
Residual	28	0.90		
Total	41	3.81		

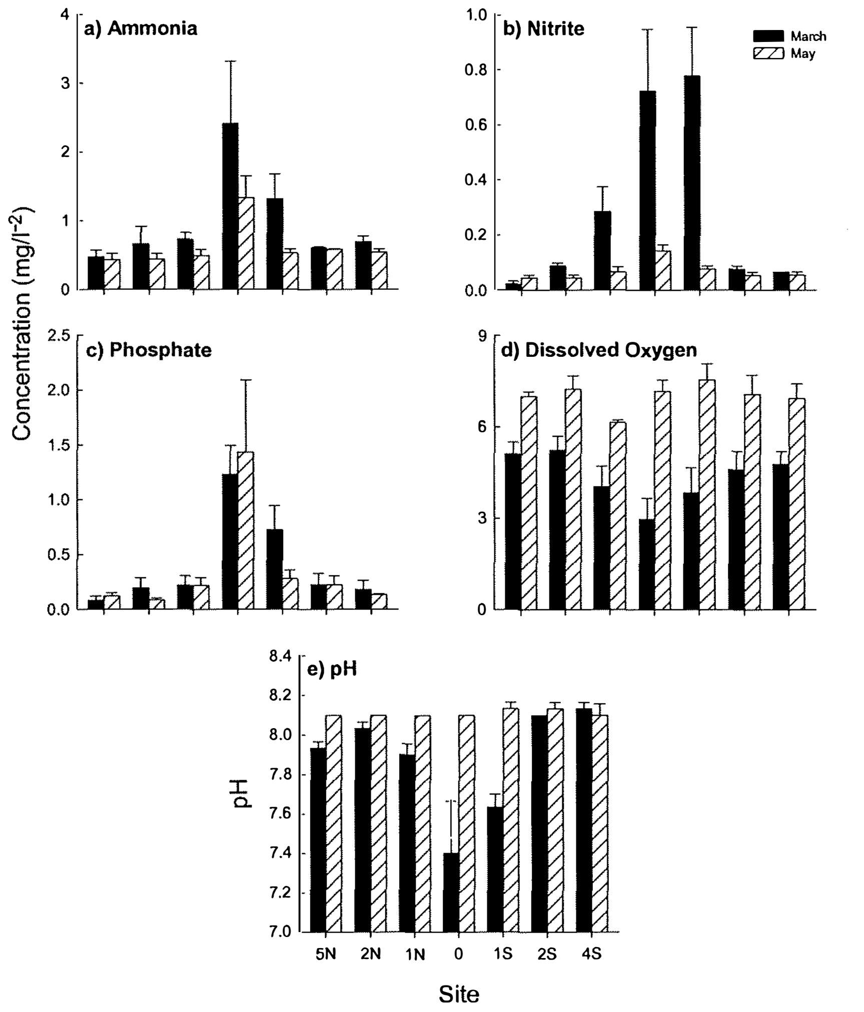

Figure 5.10. (a) Ammonia, (b) nitrite, (c) phosphate, and (d) dissolved oxygen concentration, and (e) pH at various distances from the Bolivar Outfall during March and May.

Relationship between Macrofaunal Abundances and Water Quality

Despite a highly significant difference in the macrofaunal assemblage and water quality between sites with distance from the outfall, the results from a canonical correlation analysis indicated that water quality explained just under 11.9% of the variation in macrofauna, with two significant canonical variates (Table 5.11a). When the same relationship was examined excluding those sites located 4 km south and 5 km north, water quality accounted for 18.5% of variation in the macrofaunal assemblage, with three canonical variates (Table 5.11b), indicating little biological significance. At these sites water quality explained just 17.0% and 27.8% of variation in macrofaunal assemblage in March and May, respectively, with two canonical variates (Table 5.11c, Table 5.11d). Graphical representation of the restricted data following a storm in March, fails to show any separation between sites (Fig. 5.11a), and the low percentage of variation in macrofaunal abundance explained by water quality parameters makes it difficult to pick up any relationship between those two data sets. In May, however, some separation, particularly of those sites adjacent to the outfall, is evident (Fig. 5.11b), and the biplots show that outfall sites contain high concentrations of ammonia, nitrite and phosphate, and high abundances of *Favongobius lateralis* and *Platycephalus bussesis* Cuvier.

Table 5.11. Results of four canaonical correlation analysis, testing the degree to which changes in water quality explain alterations in faunal assemblage.

	Source	Axis no.	Wilk's Λ	χ^2	df	P
a)	AS, March and May	1	0.016	124.35	80	0.001
		2	0.110	66.13	60	0.274
b)	RS, March and May	1	0.000	139.21	80	0.000
		2	0.010	82.08	60	0.031
		3	0.083	44.91	42	0.351
c)	RS, March	1	0.000	79.05	45	0.001
		2	0.002	41.25	32	0.127
d)	RS, May	1	0.001	56.96	35	0.011
		2	0.03	26.30	24	0.338

P value is the probability that at least one of the remaining axis is significant. AS = all sites included in analysis (4S, 2S, 1S, 0, 1N, 2N, 4N), RS = restricted data set, excluding peripheral sites(4S and 5N).

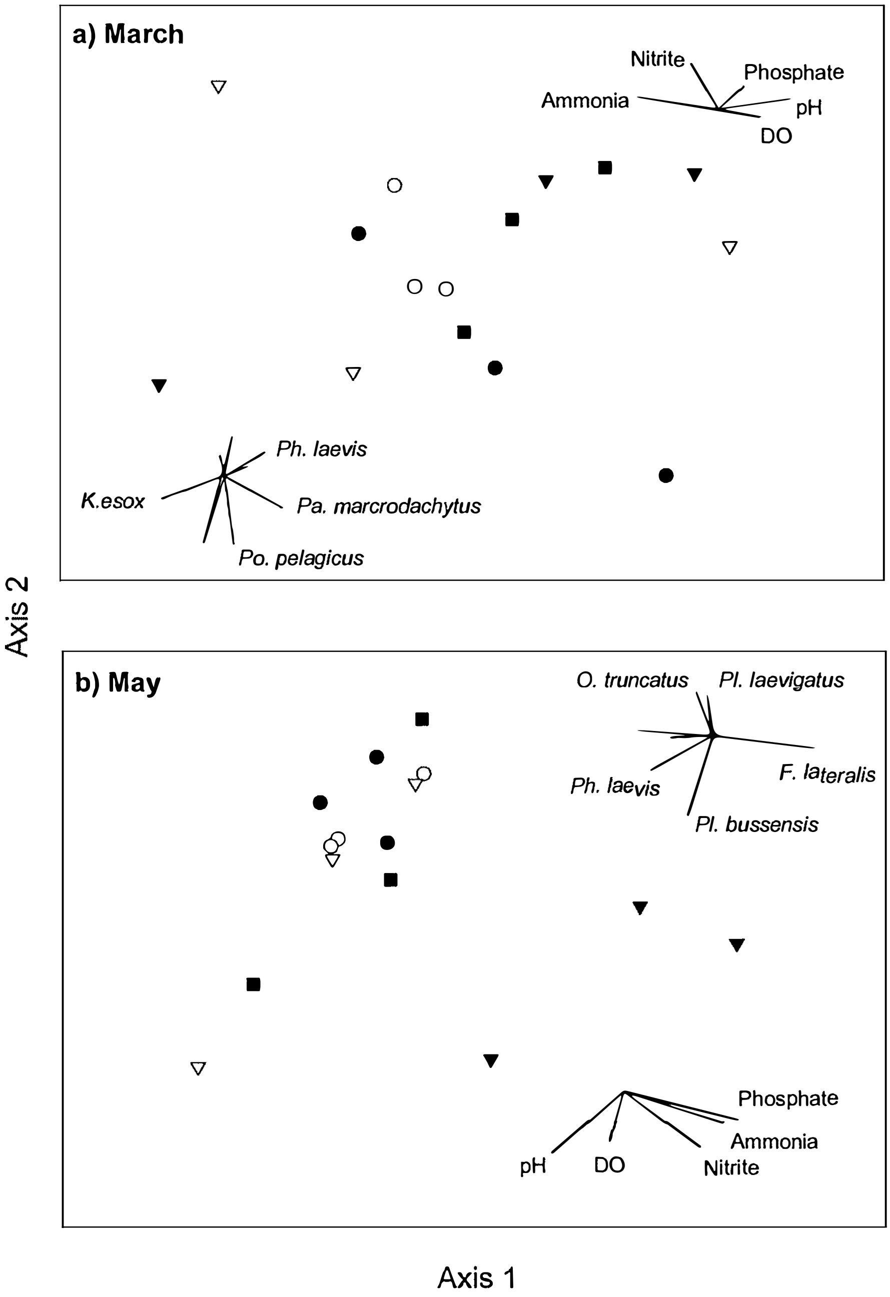

Figure 5.11. Canonical correlation analysis graphs of observations of the relationship between water quality and species abundances, with biplots of both water quality parameters and environmental variables. DO = dissolved oxygen, ▼ = 0, ▽ = 1S, ● = 2N, ○ = 1N, ■ = 2S.

Effect of nutrient enrichment on Melicertus latisulcatus *growth*

The addition of ammonia and phosphate in low and high concentrations did not affect the growth (change in weight and carapace length) of juvenile *M. latisulcatus*, over a period of approximately one month (Table 5.11). In both cases, however, there was a significant tank effect, which may have obscured differences between treatments. Growth was also a function of initial weight but not carapace length.

Table 5.11. Results of ANCOVA testing the effect of ammonia and phosphate on juvenile *Melicertus latisulcatus* growth in (a) weight and (b) carapace length, with initial prawn size (weight of carapace length) as a covariate.

a)

Source	df	Type III SS	*F*	*P*
Initial weight	1	0.104	10.746	0.001
Ammonia	2	0.031	0.654	0.532
Phosphate	2	0.054	1.156	0.337
Ammonia x Phosphate	4	0.038	0.404	0.803
Tank (Ammonia x phosphate)	18	0.422	2.430	0.002

b)

Source	df	Type III SS	*F*	*P*
Initial carapace length	1	0.014	0.384	0.536
Ammonia	2	0.063	0.205	0.816
Phosphate	2	0.302	0.977	0.396
Ammonia x Phosphate	4	0.219	0.355	0.837
Tank (Ammonia x phosphate)	18	2.788	4.390	<0.001

Discussion

The results of this study support the consensus that faunal communities undergo substantial changes in response to organic enrichment (Littler and Murray 1975; Pearson and Rosenberg 1978; Vanes *et al.* 1980; Dorsey 1982; Rygg 1985; Desrosiers *et al*. 1990; Anderlini and Wear 1992; Smith and Simpson 1992; Stark 1998; Inglis and Kross 2000). This response was not always obvious, however, indicating the importance of investigating the effects of pollution at several spatial and temporal scales. Not only was the response of the macrofaunal assemblage directly affected by pollution, but changes in habitat type, which are probably associated with the disposal of effluent (Shepherd *et al*. 1989), are also likely to have influenced community composition. Local environmental conditions were also important in determining the structure of the assemblage, emphasising the need to investigate pollution effects over time.

Spatial variation in fauna around Bolivar

Within 2 km of the Bolivar Outfall, spatial variation in abundance and distribution of marine macrofauna was evident, as has been reported generally for marine outfalls (Pearson and Rosenberg 1978). Abundances of many species including *F. lateralis, K. esox* and *O. truncatus* varied significantly between sites, but with no apparent trend with distance from the input of sewage. Other species, however, such as *M. latisulcatus* and *P. pelagicus* increased in abundance with distance from the outfall. This finding is in accordance with numerous other studies which found a similar trend in species abundance with distance from the point of effluent disposal (Belanger 1991; Tablado *et al.* 1994; Lui and Morton 1998; Smith and Suthers 1999). It must be noted, however, that the sampling method adopted in this study was designed specifically to collect juvenile *M. latisulcatus*, which bury themselves to avoid predation (Tanner and Deakin 2001). Consequently, species that are found submerged beneath the sand, including *P. pelagicus*, will also be effectively sampled by the water-jet net. The abundance of other species not targeted by the sampling method, however, are unlikely to be reliable, as a result no firm conclusions regarding their response to effluent discharge can be made.

Despite the fact that lower abundances of *M. latisulcatus* and *P. pelagicus* were observed adjacent to the disposal of sewage, their presence at the outfall suggests that the effect of pollution was marginal. Previous studies have found that while most species do not respond to the input of sewage, other species are particularly sensitive to its effects, and can be used as indicators for the detection of environmental disturbances (Pearson and Rosenberg 1978). Inglis and Kross (2000) recently determined that otherwise abundant species of filter-feeding bivalves and other molluscs were absent from polluted areas. Similarly, Rygg (1985) found that almost half of the species identified (approximately 45/100) along a putative pollution gradient were absent from disturbed sites. In conclusion, Rygg (1985) stated that the presence of one or more of these species will indicate that the pollution effect is low or moderate. Among the 45 species that were absent from polluted sites were a variety of crustacean species, adding support to the conclusion that effluent discharged at the Bolivar Outfall is having a marginal effect on those species investigated.

Traditionally, in investigations of organic enrichment effects, researchers have compared environmental variables adjacent to a discharge area to those of ‘cleaner’ sites located many kilometres away. Although researchers who have utilised experimental designs of this nature commonly detect changes between sites, differences due to the effect of effluent may be confounded by spatial variation (Hewitt *et al*. 2001). The importance of natural variation, which may occur through changes in sediment type, temperature, water quality, water circulation etc., is evident by the failure of some studies to detect pollution effects. In one such study, environmental variation in macrofaunal assemblages was found to be a more dominating factor influencing community structure than the effects of effluent (Smith 1994). Other studies have supported this finding, illustrating that while pollution significantly affects faunal assemblages, other environmental variables can be more influential (Growns *et al.* 1998; Ferraro *et al*. 1991; Lardicci *et al*. 1999). Ignorance of the importance and subsequent lack of investigation, of natural variation, may lead to misinterpretation of the effects of pollution. Given that there is a consistent pattern of faunal change with distance from the outfall in both directions, it is highly likely that the input of effluent is the primary factor influencing community structure within 2 km of the Bolivar Outfall.

Despite a similar trend in the abundance of *M. latisulcatus* and *P. pelagicus*, in both directions, counts of both species are consistently lower in the north compared to corresponding sites in the south. This pattern suggests that the effect of sewage disposal is more pronounced north of the point of discharge. A likely explanation for such a directional outcome in pollution effects is the northerly direction of wave induced littoral currents in the shallow waters of eastern Gulf St Vincent (Edyvane 1996). Such wave-induced currents are likely to cause a shift in the movement of effluent in a northerly direction, providing evidence to support the suggestion that lower abundances of *M. latisulcatus* and *P. pelagicus* in the north are a result of effluent discharge.

Although the response of macrofaunal communities to effluent pollution is relatively incontrovertible within 2 km of the Bolivar Outfall, sites located 4 km south and 5 km north do not conform with expected trends. While an increase in species diversity at these sites is apparent, and is commonly indicative of unpolluted areas (Pearson and Rosenberg 1978), a dramatic reduction in the abundance of *M. latisulcatus* was detected. The lack of seagrass at sites located within 2 km of the outfall, and increased percentage of seagrass at the outermost sites, is likely to explain the changes in macrofaunal community structure. Differences in faunal assemblages between seagrass meadows and sand-flats have been well established. In comparison to sand-flats, seagrasses support a higher diversity of species and number of individuals (Heck and Thoman 1984; Lewis 1984; Orth *et al*. 1984; Orth and van Monfrans 1987; Bell and Pollard 1989; Orth and van Monfrans 1990; Ferrell and Bell 1991; Edgar *et al*. 1994; Connolly 1997; Jenkins *et al*. 1997; Jenkins and Wheatley 1998) due to the protection from predators, food availability, and habitat structure provided by seagrass communities (Heck and Orth 1980; Ryer *et al*. 1990; Irlandi and Peterson 1991; Rooker *et al*. 1998; Tanner and Deakin – Chapter 6). Unlike most species, including the majority of crustaceans, however, *M. latisulcatus* actively select sand habitats to avoid predation (Tanner and Deakin, Chapter 6). Consequently, it is expected that higher abundances of juvenile *M. latisulcatus* occur at those sites which primarily consist of sand. Knowledge of changes in community composition between habitats and preference of *M. latisulcatus* for bare sand, combined with the increased percentage of seagrass at peripheral sites, helps to explain the increased species diversity, and decreased abundance of *M. latisulcatus* at those sites located further away from the disposal of sewage. Differences in water quality between sites is unlikely to explain the changes in community composition as water quality between those sites located 2 km north and south of the outfall and peripheral sites was rarely different.

The importance of habitat alteration, compared to pollution effects, is emphasised by Growns *et al*. (1998). Fish assemblages in the Hawkesbury-Nepean River, New South Wales, were affected by both nutrient enrichment and loss of riparian vegetation. Differences in the abundance of two prolific fish species suggested that although eutrophication had a major effect on fish assemblages, even greater effects may have resulted from the clearing of riparian vegetation. Sites with low nutrient enrichment or adjacent to vegetated banks contained a higher species diversity and total abundance of fish. The profound effects of habitat alteration in this study show that alteration in habitat type can exceed the impact of effluent and reiterates the importance of monitoring habitat changes between sites. It is possible that changes in habitat type in the current study caused the changes in macrofanua, this would be an indirect effect of pollution.

In any comparison of fauna from different habitats, demonstrated differences between habitat types are potentially attributable to differences in the effectiveness of the method of capture. In this study, for example, the water-jet net which was specifically designed to sample juvenile *M. latisulcatus* on bare substrate (Kangas and Jackson 1998; Kangas 1999) and works by disturbing and lifting organisms buried in the sand, may have been limited in its efficiency in vegetated habitats. Furthermore, the increased species diversity in seagrass habitats could be explained by the ability of some species to more easily avoid capture in unvegetated areas. However, documentation of increased species diversity but decreased *M. latisulcatus* abundances in seagrass, compared to sand habitats, as found in the present study, provides some evidence that differences in faunal communities described here are not due to a sampling artefact.

Temporal variation in fauna around Bolivar

Significant temporal variation in the response of the macrofaunal assemblage to effluent disposal was found. Investigations of temporal variation in intertidal communities have suggested several reasons for such variability including the recruitment of juvenile organisms at different times of the year, seasonal movement of individuals offshore, presence/absence of migrating communities and changes in patterns of predation and competition (Livingston 1987; Fitz and Wiegert 1992; Gibson *et al*. 1996; Pfister 1997; Vance *et al*. 1998). Daily, seasonal, and/or yearly differences in the quantity of sewage being discharged may also explain temporal variation in pollution effects. In the present study variability between all sampling periods was evident, particularly in those samples taken in March, compared to other times, and is likely to be attributed to differences in local environmental conditions prior to sampling. A reasonably severe storm preceded sampling in March, whereas sampling in February, May and August followed calm weather conditions.

The occurrence of storms has been found to cause unpredictable changes in community structure over both the short and long terms (Peckol and Searles 1984; Ebeling *et al*. 1985; Brey 1991; Ferraro *et al.* 1991; Anderlini and Wear 1992; Posey *et al*. 1996; Barnes 1998; Underwood 1999). Storms significantly influence the flow of water and sediment transport (Bock and Miller 1995), and consequently produce an unpredictable source of mortality (Sherman and Coull 1980; Ebeling *et al*. 1985; Dayton *et al*. 1989; Seymour *et al*. 1989) in addition to significant changes in community composition (Peckol and Searles 1984; Anderlini and Wear 1992; Posey *et al.* 1996). The influence of storms on faunal assemblages was particularly obvious in a study performed by Posey *et al.* (1996), where approximately one third of the common fauna exhibited a significant decline in abundance following a severe storm. As found by Posey *et al*. (1996), the effect of such natural disturbances varies among different species. In comparison to deep-burrowing organisms, the effect of storm disturbance on surface-dwelling taxa is pronounced (Tamaki 1987; Posey *et al*. 1996), presumably due to their increased susceptibility to movement of surface sediments. This response of organisms to disturbance by storms is outlined by Tamaki (1987), who demonstrated that the influence of storms on fauna is correlated with the vertical distributions of individuals within the sediment. Those species that remained unaffected by large waves had the ability to inhabit or reach greater depths compared to species that are restricted to within 1 cm of the sediment-surface water interface. The response of different species to the disturbance of storms emphasises the importance of local environmental conditions in community composition, and provides support for the conclusion that unpredictable temporal variations in faunal assemblages around the Bolivar Outfall are predominantly due to changes in local weather conditions.

Water quality

While the effects of pollution on faunal communities have been investigated by numerous authors (Littler and Murray 1975; Pearson and Rosenberg 1978; Vanes *et al.* 1980; Rygg 1985; Desrosiers *et al*. 1990; Stark 1998; Inglis and Kross 2000), a failure to quantify some variables including local conditions, habitat type and water quality can potentially lead to misinterpretation of pollution effects. In the present study significant differences in water quality were found between sites, with poorer water quality at the outfall site compared to those sites located further away. Ammonia, nitrite and phosphate concentrations at the outfall were considerably higher than values at other sites, while dissolved oxygen concentration and pH were lower. The increased ammonia, nitrite and phosphate concentrations observed at the outfall are a direct result of the input of sewage, while decreases in oxygen concentration are likely to be related to increased decomposition and microbiological activity as a result of organic enrichment (Vanes *et al*. 1980; Lapointe and Matzie 1996). A similar trend in water quality with distance from the input of sewage has been found in other studies. For example, Ruiz-Beviá *et al*. (1986) discovered elevated concentrations of phosphate and ammonia adjacent to a sewage outfall, which progressively decreased with distance from a sewage outfall. Lara *et al*. (1985) found a similar trend, and established that levels rapidly declined within 900 m of the outfall, reaching normal values at approximately 1700 m. In the present study it appears that various water quality parameters decline rapidly within 1 km of the outfall and stabilise at approximately 2 km.

While trends in water quality during March and May were similar, significant temporal variation was evident. In March, water quality showed more pronounced trends with higher concentrations of phosphate, ammonia and nitrite and lower dissolved oxygen concentration and pH at the majority of sites. Such temporal differences could have been influenced by a number of factors, including changes in water circulation and/or changes in the quantity of effluent disposed of. Such considerable changes, however, are likely to be a result of variation in the time of day sampling took place. Samples were collected during the daylight at high tide, consequently during March samples were taken between 0630 and 0800 (central standard time), whereas in May the collection of samples took place between 1630 and 1800. Considering that the secondary treated effluent is disposed into Gulf St Vincent during the night, it is expected that higher concentrations of pollutants are more common closer to this time and dissipate throughout the day. Highly significant temporal variation in water quality over a matter of hours is unlikely to cause dramatic changes in the macrofaunal assemblage, rather, long term variation (whether it be monthly, seasonal or yearly) in quantity of sewage discharge is likely to influence organism abundance and distribution.

Relationship between macrofaunal abundance and water quality

Although water quality and macrofaunal assemblages were found to vary significantly with distance from the point of effluent disposal, canonical correlation analysis suggested that there was little relationship between water quality and faunal composition. As previously outlined, various temporal and spatial effects have influenced the response of the macrofaunal assemblage to distance from the outfall, namely habitat alterations and the influence of local environmental conditions, such as storms. Such forms of variation which significantly altered the faunal assemblage are also likely to have influenced the result of this analysis. Similarly, the highly variable nature of water quality within a matter of hours, is likely to have similar implications. More importantly, canonical correlation analysis assumes a linear relationship between the two variable sets, an assumption that is unlikely to have been met. Thus it is still likely that the spatial variation in macrofaunal composition and abundance is related to changes in water quality, despite the failure of statistics to show this.

Effect of nutrient enrichment on Melicertus latisulcatus *growth*

The assessment of physiological responses by individual organisms to pollution is fundamental to determining its direct effects. Ecological monitoring of populations and communities is extremely beneficial when an appropriate experimental design is adopted, however, natural temporal and spatial variation can confound results. Direct measurements of physiological responses by individual species to pollution, however, provide information on the organisms' condition, its performance and the efficiency with which it functions under conditions of environmental stress (Widdows 1985). Oxygen to nitrogen ratios, mortality, accumulation of toxicants, and reproductive and behavioural responses, among other variables, are useful in assessing the effects of environmental stress (Robbins 1985; Belanger 1991; Qixing and Limei 1995; Vijayram and Geraldine 1996; Lye *et al.* 1997; Pablo *et al*. 1997; Escher *et al*. 1999; Smith and Suthers 1999; Hindell and Quinn 2000). Growth rates and size distributions of some species may also provide important information of the effect on stress (i.e. pollution), as such measurements provide an immediate assessment of the energy status of the animals.

Previous investigations into the size distributions of species at polluted sites, compared to control sites have revealed a variety of responses, and have often indicated that the input of sewage severely affects growth. For example, Hindell and Quinn (2000) discovered that mussels (*Brachidontes rostratus*) influenced by to the disposal of sewage exhibited slower growth than those located at control sites. Conversely, Tablado *et al*. (1994), found that a limpet species (*Siphonaria lessoni*) increased its growth rate in the vicinity of an outfall, as did limpets in a study performed by Lui and Morton (1998). In these studies, however, the response of growth to pollution was found to be highly influenced by the abundance of the species, with those species exhibiting a greater growth rate at polluted sites also having lower densities compared to control locations. While size distributions of *M. latisulcatus* and *P. pelagicus* varied between sites, there were no consistent trends with distance from the outfall. This suggests that the disposal of sewage does not affect the growth of juvenile *M. latisulcatus* and *P. pelagicus* which inhabit the area surrounding the Bolivar Outfall, or that there is substantial movement over the scale of several kilometres, so animals are only in the polluted area for a relatively short time. A relatively small and highly variable sample size, combined with the recruitment of prawns at different times of the year may also have confounded results. Monitoring the growth of juvenile *M. latisulcatus* exposed to various nutrient enriched treatments in the laboratory, however, also failed to show that growth rates of juvenile *M. latisulcatus* were directly influenced by varying concentrations of nutrients. Instead, there is an unexplained tank effect, whereby the growth of the prawns varied according to the tank they were housed in.

Conclusion

The comparison of faunal communities with distance from effluent outfalls, particularly in intertidal regions, is a necessary step in establishing how far from the point of sewage discharge community composition is altered. In summary, the results of this study demonstrate that while the input of nutrients from the Bolivar Outfall is an important factor controlling the response of macrofaunal assemblages with distance from the outfall, other unquantified factors, particularly changes in habitat type are just as influential. Changes in macrofaunal assemblages directly associated with nutrient enrichment are relatively localised, having a pronounced effect only within approximately 2 km of the outfall. Despite this pattern of faunal change with increasing distance form the point of nutrient input, significant temporal variation resulting in unpredictable alterations of the community composition is evident. Such temporal variation is explained by natural variability in local environmental conditions especially storms, and reiterates the importance of investigating pollution effects over time, to provide a more accurate assessment of pollution-induced disturbances. Overall the influences of the input of sewage from the Bolivar Outfall, into Gulf St Vincent on marine macrofauna appear to be minimal in contrast with other sites, indicated by the presence of negative indicators of pollution adjacent to the outfall, and the lack of the pollution effect on both *M. latisulcatus* and *P. pelagicus*.

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Chapter 6: Active habitat selection for sand by juvenile western king prawns, *Melicertus latisulcatus* (Kishinouye).

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Abstract:

This paper presents the results of a series of habitat selection experiments aimed at determining if juvenile *Melicertus latisulcatus* generally occur on intertidal sand- and mud-flats as a result of active selection of unvegetated areas, or due to extrinsic factors (e.g. differential predation). In the laboratory, juvenile *M. latisulcatus* showed a clear preference for habitats containing sand irrespective of the presence or absence of predators. If sand was not available, artificial seagrass was chosen as a secondary preference but was avoided when sand alone was also present. Importantly, the combinations of habitats chosen for testing allowed us to determine that artificial seagrass provided a good surrogate for real seagrass, and that the presence of potential food (epiphytes) did not appear to influence habitat selection. There was also no difference in the habitat selected between day or night, and only minor differences with prawn size. Thus juvenile *M. latisulcatus* appear to have a hierarchy of mechanisms for avoiding predators, with burying in sand being the preferred option. If burying is not possible, then seagrass is used for shelter. Active habitat selection to avoid predation appears likely to play a substantial role in determining the distribution of these animals on unvegetated sand- and mud-flats.

Introduction:

Seagrasses, mangroves and saltmarshes provide habitat for many species (e.g. Coen et al. 1981, Stoner 1983, Bell & Westoby 1986, Robertson & Duke 1987, Halpin 2000), some of which appear to use vegetation to reduce the risk of predation (Stoner 1982, Minello & Zimmerman 1983, 1985, Sogard & Olla 1993, Perkins-Visser et al. 1996). For other species, aquatic vegetation also provides food (Bologna & Heck 1999a). Many types of organisms prefer vegetated habitat in the presence of predators, but unvegetated areas when predators are absent (Holbrook & Schmitt 1988, Sogard & Olla 1993, Jordan et al. 1996, Bostrom & Mattila 1999), suggesting that there are costs associated with inhabiting vegetated areas for some species. A tradeoff has therefore been proposed between these costs and the benefits of avoiding predators (Gotceitas 1990, Bologna & Heck 1999b); costs associated with being in vegetation may mean that an individual would be less likely to seek shelter when predators are present.

Penaeid prawns (shrimp) frequently use seagrass habitats as nursery areas (Minello & Zimmerman 1985, Loneragan et al. 1994, 1998, Haywood et al. 1995). Prawns play an important role in many shallow water ecosystems, and also provide the basis for many important fisheries (Dall et al.1990). Habitat selection has been intensively studied in the juveniles of several species of penaeid prawns, although this work has concentrated on species which predominantly occur in seagrasses or other vegetation (Minello & Zimmerman 1985, Hill & Wassenberg 1993, Kenyon et al. 1997, Liu & Loneragan 1997). Other species, however, seem to avoid vegetated areas, and prefer to live on unvegetated intertidal sand- and mud-flats. *Metapenaeus affinis* in Kuwait follows tidal fronts, spending most of its time in intertidal areas. This behaviour may occur because these areas have few predators (Bishop & Khan 1999). In Australia, juvenile *M. latisulcatus* (Kishinouye) (formerly *Penaeus latisulcatus*, Perez Farfante & Kensley 1997) occur predominantly on intertidal sand- and mud-flats, generally located between shallow subtidal/intertidal seagrass beds and mangroves higher on the shoreline (Penn et al. 1989, Potter et al. 1991, Kangas & Jackson 1998). In East Africa, however, the same species often occurs amongst seagrasses (Subramaniam 1990). The larger densities reported on intertidal sand- and mud-flats in Australia may occur because of active selection of habitat, decreased survival in seagrass (possibly through increased predation), or may be a reflection of inadequate sampling of seagrass.

Coastal habitats in many areas of the world are becoming increasingly degraded. A major aspect of this degradation is the loss of extensive areas of seagrass, with potentially important consequences for species living in or near these seagrasses. To understand how these species will be affected, it is important to determine what microhabitats they use, and why they use them. Because *M. latisulcatus* is generally found over unvegetated substrates, we hypothesised that they actively selected this habitat. In addition, if this choice was driven by the need to avoid predators, selection should be intensified in the presence of predators. Alternatively, there may be no selection, but prawns in vegetated areas are exposed to higher rates of predation, reducing their abundance relative to unvegetated areas. Prawn size might also play an important role in the choice of habitat (e.g. Kenyon 1995, Loneragan et al. 1998) if small individuals are incapable of discriminating between habitats, or predation pressure changes in intensity and nature with ontogeny.

The aim of this study is thus to examine experimentally selection of habitat by juvenile *M. latisulcatus*. In particular, we want to determine if selection changes with size or the presence of predators. To do this, we offered animals a choice between two habitats in the laboratory. The habitats offered allow us to determine if *M. latisulcatus* displays a preference for artificial seagrass or sand and if these two structural elements interact, if food presence (in the form of a well developed epiphytic assemblage) modifies the choice of habitat, and if artificial seagrass provides a good surrogate for natural seagrass.

Methods:

To examine selection of habitat by juvenile *Melicertus latisulcatus* a series of 33 tanks were set up in controlled environment rooms. Each round tank was 58 cm in diameter, 43 cm deep, and filled to a depth of 35 cm (total volume ~87 litres). Fresh seawater was continuously supplied to each tank. Two different habitats were established in each tank, with combinations randomly re-assigned to tanks after each trial. Room temperature was maintained at 20ºC, but water temperature varied naturally from 19ºC in April, to 13ºC in June when the experiment finished. Juvenile prawns were collected at night using a beam trawl in the northern portions of Gulf St Vincent and Spencer Gulf, and held in 500 litre outdoor holding tanks with flow through seawater until needed. Three size classes of prawn were used to determine if the preferred habitat changed with size. A random sample of 50 prawns from each size class were measured for carapace length, with small prawns having a mean length of 4.6 mm (range 3.1-5.9), medium 7.6 mm (6.2-9) and large 12.8 mm (10.4-17.2). The influence of predators on selection of habitat by medium-sized prawns was tested by placing a single mullet (*Aldrichetta forsteri* (Valenciennes) – length approximately 200 mm) or blue crab (*Portunus pelagicus* (Linnaeus) – carapace width approximately 80-90 mm) into the appropriate tanks. Both species have previously been identified as predators of penaeid prawns (King 1977). All predators were starved for 24 hours prior to use to encourage active foraging during the experiment. To determine if the habitat selected varied with time of day, both day and night trials were run. We carried out five replicate trials for each combination of factors tested.

Six different habitat types were used, although only eight combinations of these were tested. To determine if prawns preferred some form of habitat structure to no structure, half the tank was left bare, and the other half either covered in coarse white silica sand to a depth of approximately 2 cm or filled with artificial seagrass. Two centimetres of sand was sufficient for all prawns to completely bury themselves, and nearly all buried prawns were found in the top 1 cm. The artificial seagrass was made from black polythene builders plastic, with 4 sheets welded together at the base and then cut into strips 5-6 mm wide. Leaves were 20 cm long, with 4 leaves per shoot, and about 18-20 shoots on each 10 cm long segment. This artificial seagrass was intended to mimic the locally abundant *Zostera muelleri* (Irmisch ex Aschers.). Fifteen segments were placed into half of the tank. To determine the preferred type of structure, sand was compared to artificial seagrass, and to determine if there was any interaction between these, artificial seagrass and sand combined was compared to each habitat alone. Six months prior to the commencement of the experiment, a series of artificial seagrass segments were placed into natural seagrass to accumulate a load of epiphytes, and these were used to determine if the extra structure or food source provided by epiphytes influenced habitat selection by comparing epiphytised artificial seagrass to clean artificial seagrass (both with sand). Finally, to check that prawns responded to artificial seagrass in the same manner as to real seagrass, selection between *Z. muelleri* (at a density of 300 shoots per 1/2 tank) and either epiphytised or non-epiphytised artificial seagrass was tested (again both with sand).

Day trials commenced at 18:00, with 5 prawns being placed in the centre of each tank. Lights were turned off at 19:00, and back on at 06:00, mimicking the natural light regime in April/May when the experiment was conducted. Predators were added to the appropriate trials at 08:00, and the trial terminated at 18:00 (after 12 hours of light) by placing a divider between habitats in each tank, removing any predators, and then thoroughly searching for and counting the number of prawns in each half of the tank. Night trials followed a similar procedure, except they commenced at 08:00, lights went off at 21:00, predators were added at 22:00, and the trial terminated at 08:00 the following morning (after 11 hours of darkness) before the lights were turned back on. Prawns were held in spare tanks in the experimental rooms for at least 24 hours prior to a trial, so they could adapt to minor changes from the natural light regime.

To determine if the proportion of prawns selecting a given habitat varied with any of the factors investigated, log-linear analyses were used. Each combination of habitats was analysed separately. Initially a single analysis was done incorporating both the three different size classes and two predator types, with the individual factor habitat, and all interactions between habitat and/or time (day/night) and size/predator (small, medium and large with no predators, medium + mullet, medium + crab). Time and size/predator and their interaction have zero deviance by definition as all animals had to select one of the two habitats. Significance was determined using an analysis of deviance testing against the χ^2 distribution (akin to ANOVA with continuous data, Chambers & Hastie 1993). If size/predator interacted with habitat (indicating that it had an influence on what habitat was selected), then separate analyses were conducted for the three size classes without predators, and for medium prawns under different predation regimes, to determine which factor was important (note that medium prawns without predators appeared in both of these later analyses).

Results:

Overall, juvenile prawns showed a distinct preference for habitats with sand irrespective of the presence of other structure. There were no significant differences between day and night for any habitat combination. Prawn size and the presence of predators only had an influence when one of the available habitats had no structure.

There was a significant preference for sand over a bare tank, which was influenced by size/predator (Table 6.1). The analysis comparing only the different size classes indicated that size influenced the choice of habitat (deviance=8.48, df=2, P=0.014), with medium prawns showing little preference, while small and large prawns showed a distinct preference for sand (Fig 6.1.a). The presence of predators also influenced the selection of habitat (deviance=10.78, df=2, P=0.005). Sand was preferentially selected in predation trials with fish, but was only slightly preferred in trials with crabs or without predators (Fig 6.1a).

Table 6.1: Habitat selectivity of juvenile *Melicertus latisulcatus* in different habitat combinations, as influenced by time of day, predator presence, and prawn size. (Results of analysis of deviance tests). S = sand, ASG = artificial seagrass, EA = epiphytised artificial seagrass, SG = live seagrass.

Source	df	Deviance	P	Deviance	P
		S vs Bare tank		ASG vs Bare tank	
Habitat	1	39.41	<<0.001	23.73	<<0.001
Habitat × Time	1	0.11	0.745	0.067	0.795
Habitat × Pred/Size	4	10.53	0.032	13.99	0.007
Habitat × Time × Pred/Size	4	3.54	0.471	1.00	0.909
		ASG vs S		ASG + S vs S	
Habitat	1	34.53	<<0.001	4.44	0.035
Habitat × Time	1	1.68	0.195	0.18	0.667
Habitat × Pred/Size	4	3.57	0.467	3.53	0.474
Habitat × Time × Pred/Size	4	3.34	0.503	1.87	0.760
		ASG + S vs ASG		ASG + S vs EA + S	
Habitat	1	39.39	<<0.001	0.25	0.617
Habitat × Time	1	0.11	0.744	0.09	0.764
Habitat × Pred/Size	4	7.61	0.107	1.12	0.891
Habitat × Time × Pred/Size	4	3.16	0.532	1.70	0.790
		ASG + S vs SG + S		EA + S vs SG + S	
Habitat	1	2.64	0.104	0.38	0.535
Habitat × Time	1	0.18	0.670	0.02	0.888
Habitat × Pred/Size	4	2.79	0.594	1.97	0.742
Habitat × Time × Pred/Size	4	2.20	0.698	2.19	0.702

Artificial seagrass was also significantly preferred to a bare tank, with this preference again being influenced by size and/or the presence of predators (Table 6.1). Partitioning the data indicated that size had an effect (deviance=10.76, df=2, P=0.046), with small prawns showing no preference, medium prawns a slight preference for artificial seagrass, and large a distinct preference for artificial seagrass (Fig 6.1b). The presence of a predator did not influence habitat selection (deviance=3.27, df=2, P=0.195), with artificial seagrass being preferred in all cases (Fig 6.1b).

Prawns showed a significant preference for one habitat in three comparisons for which the choice of habitat was not influenced by prawn size or the presence of a predator ($P > 0.1$ for the Habitat × Size/Predator term for all comparisons). Sand was preferred over artificial seagrass alone (Table 6.1, Fig 6.1c) and artificial seagrass with sand (Table 6.1, Fig 6.1d), while artificial seagrass and sand was preferred to artificial seagrass alone (Table 6.1, Fig 6.1e). There was no preference shown for either habitat, and no influence of prawn size or predator presence on the selected habitat, in the final three comparisons. These were artificial seagrass and sand vs epiphytised artificial seagrass and sand (Table 6.1, Fig 6.1f), artificial seagrass and sand versus live seagrass and sand (Table 6.1, Fig 6.1g), and epiphytised artificial seagrass and sand versus real seagrass and sand (Table 6.1, Fig 6.1h).

Discussion:

The results reported here support the contention that juvenile *Melicertus latisulcatus* actively select areas of sand, although predation rates were too low to analyse so we do not know if differential predation also has a role to play in determining relative abundance between habitat types. Provided sand was present, other structures (artificial or real seagrass) had little influence on which habitat was selected. These results suggest that seagrass may be avoided to a certain extent, although not completely. Thus there should be fewer prawns in seagrass than over bare substrate, although they should still be present in the former areas. If sand is available within seagrass beds, however, there appears to be no reason for prawns to avoid them. This preference for habitats containing sand appears to be related to the burying behaviour exhibited when inactive. Although it could not be accurately quantified, the majority of inactive prawns were buried in sand, especially when predators were present. An important point to note, is that in the laboratory trials the artificial seagrass had no sub-sediment structure, and the real seagrass only had minimal rhizome and root biomass. This structure might provide a barrier to prawns burying into the substrate, possibly further explaining the lower densities of *M. latisulcatus* in seagrass beds.

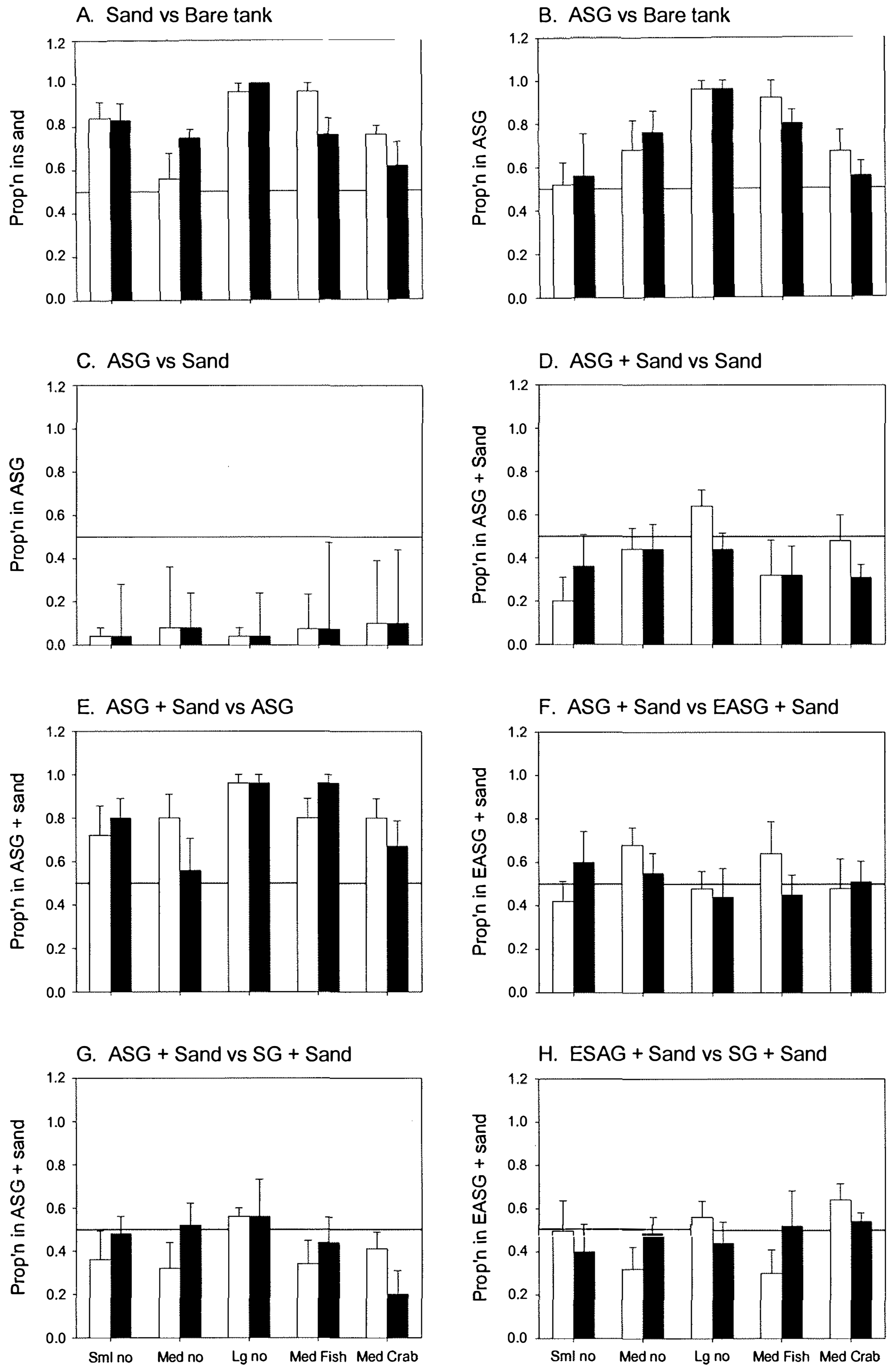

Figure 6.1. Habitat selection by juvenile *Melicertus latisulcatus*. Mean of 5 trials for each prawn size and predator combination (+ SE). ASG = artificial seagrass, EASG = epiphytised artificial seagrass. The x-axis indicates groupings according to prawn size and type of predator (no = no predator present). White bars indicate day-time selection, and black bars night-time. The line at 0.5 on the x-axes indicates the expected value if no selection between habitats occurs. Individual figure titles indicate the combination of habitats being tested.

When there was a large difference in the amount of structure in each habitat (i.e. one half of the tank was bare), the presence of predators enhanced selection for the preferred habitat. This suggests that the preference for structure is predominantly to avoid predation. There was no influence of predators on habitat selection when both habitats contained structure. Even though burying appears to be the main predator avoidance mechanism for juveniles of this species, prawns are still able to move into areas with complex structure in an attempt to avoid predation. This suggests that there might be a hierarchy of mechanisms for avoiding predators.

We also tested several other factors that are thought to influence the use of habitat by penaeids. The choice of habitat did not change between day and night, despite the fact that during the day most prawns were buried (or at least quiescent), while at night they tended to be active in the water column. Most previous studies that have examined the influence of time of day on habitat use by penaeids have found considerable differences between day and night. These studies have, however, concentrated on species that select vegetative structure as a resting spot during the day, but may move to unvegetated areas at night (Minello & Zimmerman 1985, Liu & Loneragan 1997, Sánchez 1997).

The chosen habitat also did not change greatly with the size of the prawns tested, although there were some small but significant differences – notably the lack of choice between artificial seagrass and bare tank by small prawns. This result is possibly due to the size range of prawns used. Studies on several species in northern Australia have shown that small post-larval prawns (< 2 mm carapace length) are not as selective as larger prawns (Liu & Loneragan 1997, Loneragan et al. 1998). The smallest animals in this study were 3.1 mm carapace length. *Penaeus esculentus* displays ontogenetic behavioural changes, with small animals (2.5 – 3.5 mm carapace length) burying less frequently than larger animals (11 – 13 mm carapace length) (Kenyon et al. 1995). Whether this change in behaviour was associated with a change in preferred habitat was not tested. At larger sizes, the preferred habitat must also change, as once animals reach about 20 mm carapace length they move offshore (Kangas 1999).

Finally, *M. latisulcatus* did not distinguish between seagrass, artificial seagrass or epiphytised artificial seagrass, although they did avoid artificial seagrass and sand when sand alone was present, suggesting that artificial seagrass may have hindered burying. Epiphytised and clean artificial seagrass elicited identical responses, indicating that the extra structure and potential food source offered by epiphytes had no effect on the habitat chosen. While epiphyte composition was not quantified, it consisted of turfing algae, crustose coralline algae, *Ulva*, and sessile and mobile invertebrates including bryozoans, sponges, ascidians, polychaetes and amphipods, as well as some sediment and detritus. Thus epiphytised artificial seagrass would have provided both greater habitat complexity and at least a minor source of food. Bologna & Heck (1999a) found that the presence of epiphytes on artificial seagrass increased the abundance of mobile epifauna, as they provided a source of food. As the epiphytised artificial seagrass had been in the ocean for six months prior to use, the lack of selection between it and new, clean artificial seagrass suggests that lack of preference for the latter in sand versus artificial seagrass trials was not due to avoidance of chemicals leaching from the plastic. This conclusion is further supported by the lack of selection between artificial seagrass and live *Zostera*, which validated our decision to use the former for most trials. Each trial with real seagrass required about as much time to set up and then search at completion as did all 6 trials employing combinations of other habitats, and thus use of artificial seagrass resulted in considerable savings in time.

The successful use of unvegetated habitat is mediated by behaviour. *M. latisulcatus* seem to have developed burying as their primary response to the presence of predators, and thus select habitats where they can bury if needed. When burying is not an option, as a secondary preference they move to habitats which are structurally complex. Whether *M. latisulcatus* have behavioural mechanisms that allow them to escape predation once in these habitats, or they simply rely on reduced foraging ability of the predator, is unknown. In many cases, simply moving into vegetation does not provide increased protection (Main 1987). Juvenile *P. esculentus* change their behaviour depending on the morphology of the seagrass in which they are sheltering (Kenyon et al. 1995). Predators may also switch tactics once they enter vegetated areas, and thus maintain predation rates (e.g. seahorses change from active searching in simple habitats to ambush predation in complex habitats, James & Heck 1994). The intertidal area frequently used by *M. latisulcatus* may also be a favourable habitat if the abundance of predators is less than in subtidal areas. Potential fish predators were found to be rare in the preferred unvegetated intertidal habitat of *Metapenaeus affinis* in Kuwait (Bishop & Khan 1999).

Given that juvenile *M. latisulcatus* rely on burying as a primary mechanism to avoid predators, characteristics of the substrate may play an extremely important role in habitat selection. Substrates that hinder burying will likely be avoided in preference for those that are easy to bury in. Thus areas with very coarse or very fine sediment, or with mats of decaying vegetation overlying the sediment, will probably have lower densities of prawns. As mentioned above, this may also explain low densities in seagrass areas if the rhizome and root mass of seagrasses prevents burying. However, while juvenile *P. esculentus* also bury as a predator avoidance mechanism, they do not seem to show any sediment type preferences (Loneragan et al. 1994, Kenyon et al. 1997), although they do prefer vegetated to unvegetated areas.

Our research suggests that *M. latisulcatus* may not be as affected by seagrass loss due to coastal development as it would if it depended on seagrass for habitat, although there are still several important life history aspects that need to be addressed before we can firmly conclude this. While seagrasses may not provide habitat, they may still be a primary source of food if prawns rely on exports from seagrass areas to their habitat. Many juvenile penaeids feed primarily on benthic diatoms etc. (Dall et al. 1990), which can be highly productive on intertidal soft sediments. To fully understand the consequences of seagrass loss, we need to determine to what extent *M. latisulcatus* relies on *in situ* production versus production exported from nearby seagrass beds. While detritus is not a major food source for penaeids (Dall et al. 1990), it may still be the basis for the food chain involving juveniles. Seagrasses might also modify the intertidal environment by trapping sediment and reducing water motion and turbidity, with possible consequences for organisms living inshore of them.

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Chapter 7: The influence of introduced European green crabs (*Carcinus maenas*) on habitat selection by juvenile blue crabs (*Portunus pelagicus*).

Jason E. Tanner

Abstract:

The European green crab (*Carcinus maenas*), is a highly successful marine invader, having established populations in a number of areas outside its natural range in the last 100 years. In South Australia, *C. maenas* is abundant on intertidal mud flats, which are used by juveniles of the native blue swimmer crab (*Portunus pelagicus*), and has the potential to cause substantial negative effects on this species. I tested the influence of adult blue and green crabs on habitat selection by juvenile blue crabs, to determine if they responded to both predators in a similar fashion. While the presence of predators did influence the habitat juvenile blue crabs were found in in laboratory experiments, there were no consistent preference shown, and no differences in their response to the two species. Juvenile behaviour in the selected habitat did differ between the two adult species, however. Many more crabs buried themselves beneath the substrate when adult conspecifics were present than when adult green crabs were present. Presumably, this makes them more vulnerable to predation by green crabs than by adults of their own species, indicating that if green crabs were to spread outside of their present localised distribution in South Australia they could have substantial negative impacts on blue crab populations.

Introduction:

The European green (or shore) crab, *Carcinus maenas*, has proven to be a highly successful invader around the world. Reproducing populations have become established in Australia, South Africa, and on both coasts of North America over the last century, and have spread rapidly over large areas (Fulton and Grant 1902; Zeidler 1978; LeRoux et al. 1990; Griffiths et al. 1992; Cohen et al. 1995; Grozholz and Ruiz 1995). Given that these crabs are highly effective predators of benthic invertebrates, have very cosmopolitan feeding habits, and can occur in high numbers, their presence has substantial implications for the native biota of invaded areas (Rangley and Thomas 1987; LeRoux et al. 1990; Griffiths et al. 1992; Cohen et al. 1995; Grozholz and Ruiz 1995). For instance, in California they have decreased the abundance of clams and native crabs by an order of magnitude in some instances, with concomitant increases in some polychaetes and amphipods (Grozholz et al. 2000). These effects were not obvious higher in the food chain, however, with the numbers of shorebirds remaining constant from 4 years prior to the invasion until 2 years after crab abundance had stabilised.

Green crabs have the potential to negatively effect other crab species through competition as well as predation. McDonald et al. (2000), found that juvenile *C. maenas* displaced juvenile Dungeness crab (*Cancer magister*) from both shelter and food, with adults also predating on the juvenile Dungeness crab. These interactions may be of limited importance, however, as most green crabs were found high in the intertidal, whereas juvenile Dungeness crabs were found in lower intertidal and subtidal areas. Similarly, in South Africa, the green crab shows little dietary or habitat overlap with native crab species, so is not expected to have a major effect on them (Griffiths et al. 1992). Subtidal populations of *C. maenas* do occur in other locations where they have been introduced (e.g. San Francisco Bay, Cohen et al. 1995), as well as in their native range (Crothers 1968; Hunter and Naylor 1993; Abelló et al. 1997), indicating that there is considerable potential for interactions with subtidal species in some areas.

In South Australia, the distribution of green crabs overlaps with the native blue swimmer crab (*Portunus pelagicus*), and they are particularly abundant in intertidal soft sediment areas which are heavily utilised as nursery areas by the native species. This distribution leads to a high potential for interactions between the two species, with possible negative implications for the native *P. pelagicus*. Juvenile *P. pelagicus* typically inhabit these shallower waters, whereas larger individuals tend to move offshore (Edgar 1990; Sumpton et al. 1994). Qualitative observations in Barker Inlet suggest that the 2 species use the same intertidal and shallow subtidal areas, and adult green crabs that have been kept in the same tanks as juvenile blue crabs have proven to be effective predators of the later (pers. obs.). *P. pelagicus* is highly abundant in South Australia's two large gulfs (Gulf St Vincent and Spencer Gulf), as well as along much of the rest of the Australian coastline. As the most abundant large predatory crab in the gulfs, it probably has an important ecological role, and forms the basis of an economically important fishery. Adult *P. pelagicus* are also active cannibals on the juveniles (de Lestang et al. 2000), although they predominantly prey on infauna and slow moving crustacea such as hermit crabs (Williams 1982; Edgar 1990). In this paper, I test the hypothesis that juvenile *P. pelagicus* shift their habitat use in response to the presence of adult green crabs in the same way that they do in the presence of conspecific adults. For many species (especially crustaceans and fish) the presence of a potential predator induces a change in the pattern of habitat use, with animals generally moving into habitats of higher structural complexity where predation rates are lower (e.g. Holbrook and Schmitt 1988; Sogard and Olla 1993; Jordan et al. 1997; Boström and Mattila 1999; Tanner and Deakin 2001). If juveniles respond in the same manner to adults of both species, then the introduced green crab will have less of an effect than if it is not perceived as a threat. In the same experiment, I also examine how juvenile behaviour changes within a habitat (by looking at the frequency of burrowing into the substrate, which is presumably a mechanism for avoiding predators), and whether the density of juveniles has any influence on either of these predator avoidance mechanisms.

Methods:

The influence of introduced green crabs on the selection of habitat by juvenile *P. pelagicus* was examined in a series of 33 tanks set up in two controlled environment rooms. Each tank was 58 cm in diameter, and filled to a depth of approximately 35 cm (total volume ~ 87 l), with a constant supply of fresh seawater. To determine the preferred habitat, crabs were allowed a choice between two out of three habitats in each trial, these being bare sand, artificial seagrass and sand, and live seagrass (*Zostera muelleri*) planted in sand. For each pair of habitats the influence of crab density on habitat selection was examined by running trials with either 1, 3 or 5 juvenile crabs per tank, and the influence of confamilial adults by placing either a single adult *P. pelagicus* or *C. maenas* into selected tanks (with a control treatment which lacked predators). The experimental design was thus a 2-way factorial ANOVA design for each habitat combination, with 5 replicates of each density/predator combination. As well as measuring habitat selection, the proportion of crabs that buried themselves in each habitat was also determined. So that this behaviour could be compared to behaviour when only one habitat was available, an equal number of trials were run with each tank containing only a single habitat. Trials commenced on the 28th January 2001, and continued until the 30th May 2001, as crabs became available. All trials were randomly allocated over this time to ensure that there was no confounding with any potential seasonal differences. Room temperature was maintained at 23°C throughout the experiment, but water temperature decreased from 22 °C to 18 °C through time. All juvenile crabs used were between 32 and 51 mm carapace width. Trials commenced at 08:00, predators were added to the appropriate trials at 12:00, and they were terminated at 16:00 by recording the location of all juvenile crabs, and whether they were buried or not.

The habitats chosen for this experiment allowed me to determine if crabs prefer habitat containing structure (seagrass or artificial seagrass) over habitat lacking structure (sand), as well as if artificial seagrass provides a good surrogate for live seagrass. All three habitats contained a base of ~ 3 cm of clean, coarse silica sand over the bottom of the tank, which provided sufficient depth for all crabs to bury themselves. As buried crabs invariably leave their eyes projecting above the sand no matter what the sand depth, it is unlikely that 3 cm was shallow enough to cause problems with crabs encountering the bottom of the tank, and thus not behaving naturally. Live *Zostera muelleri* was planted in the appropriate tanks at a density of 300 shoots per 1/2 tank (or 2270 shoots m^{-2}). Artificial seagrass was intended to mimic *Z. muelleri*, and was constructed from black polythene builders plastic. Four sheets of plastic were welded together at the base, and cut into strips approximately 5-6 mm wide and 20 cm long. Each segment of artificial seagrass was 10 cm long, and contained 18-20 shoots (with 4 leaves per shoot). Ten of these artificial seagrass segments were then placed into 1/2 a tank where required.

To determine if either crab density or predator presence affected habitat selection in juvenile crabs, log-linear analyses were used. For each of the three habitat combinations, a single model incorporating habitat, predator type and density, with all possible interactions, was examined. The proportion of crabs in the specified habitat was the dependent variable. Density and predator type (and their interaction) have zero deviance in these analyses by definition, as all animals had to select one of the two habitats on offer. The significance of each non-zero term in the model was assessed via an analysis of deviance, testing against the χ^2 distribution (Chambers and Hastie 1993. This is directly comparable to ANOVA with continuous data). The proportion of crabs in each habitat that had buried themselves under the sand was analysed in the same fashion for the trials containing two habitats, although both density and predation regime could have non-zero deviance in this case. For those trials containing only a single habitat, a similar procedure was used to examine the incidence of burying, but with only the terms density and predator type (and their interaction) included in the model.

To determine if the results of the above laboratory experiments are applicable to habitat selection in the field, a subset of trials were run in Barker Inlet, South Australia (where all crabs were collected). Crabs for this experiment were tethered to wire pegs with a 50 cm length of nylon monofilament fishing line, which was tied around the carapace of the crab. Qualitative behavioural observations suggested that tethering did not interfere with crab movement, or their ability to bury themselves. Tying also resulted in lower rates of tether shedding than did supergluing the fishing line to the crab's carapace. To examine habitat choice, individual animals were placed into the field along the boundary between a seagrass (*Zostera muelleri*) patch and a sand patch. Additional animals were also tethered entirely in seagrass, or entirely in sand, to examine their behaviour in these habitats. All trials lasted for 2 hours, and were carried out over low tide in a water depth of approximately 0.5 - 1 m. The influence of predator presence was examined by tethering either an adult *C. maenas* or adult *P. pelagicus* to the same stake as the juvenile in a subset of trials. Again, five replicate trials were run for all combinations of habitat (sand, seagrass, edge) and predation regime (no predator, *C. maenas*, *P. pelagicus*). As this was a field experiment, crabs in the no predator treatment would still have been exposed to naturally occurring predators, but the predation threat would presumably have been lower than in those trials with a predator added. At the end of each trial, the location of the juvenile, and whether it was buried or not, were recorded. Most of these trials were run between the 23rd & 25th of May 2001, with some being delayed until the 15th & 18th of June due to bad weather.

Results:

Both predators and crab density influenced the preferred habitat of juvenile *P. pelagicus* in two of the three habitat combinations in the laboratory (Table 7.1). The proportion of crabs selecting the seagrass habitat, as opposed to sand, increased with density, but was not influenced by the predation regime (Fig. 7.1). Averaging over predation regimes, 1/3 of juvenile crabs selected seagrass when only 1 animal was present, and 2/3 selected it when 3 or 5 were present. In contrast, artificial seagrass was preferred to real seagrass when predators were absent, but there was no preference shown for either habitat when predators were present. There was no effect of density in this habitat combination. Similarly, artificial seagrass was preferred to sand in the absence of predators, but when predators were present predation and density interact in determining the preferred habitat (Fig. 7.1), with single juveniles selecting sand in the presence of *C. maenas*, and artificial seagrass in the presence of adult *P. pelagicus*. At higher juvenile densities, there was no preference in the presence of either predator.

Table 7. 1: Influence of density and predator regime on the preferred habitat of juvenile *P. pelagicus* (results of analysis of deviance tests). Factors showing a significant interaction with habitat influence habitat selection.

Source	df	Deviance	P
Seagrass vs Sand			
Habitat	1	0.80	0.37
Habitat×Density	2	8.40	0.015
Habitat×Predation	2	4.58	0.10
Habitat×Density×Predation	4	1.45	0.84
Residual	72	55.67	
Seagrass vs Artificial Seagrass			
Habitat	1	1.47	0.23
Habitat×Density	2	0.24	0.89
Habitat×Predation	2	12.67	0.0018
Habitat×Density×Predation	4	3.47	0.48
Residual	72	54.64	
Artificial Seagrass vs Sand			
Habitat	1	10.47	0.0012
Habitat×Density	2	1.21	0.55
Habitat×Predation	2	12.09	0.0024
Habitat×Density×Predation	4	15.78	0.0033
Residual	72	33.44	

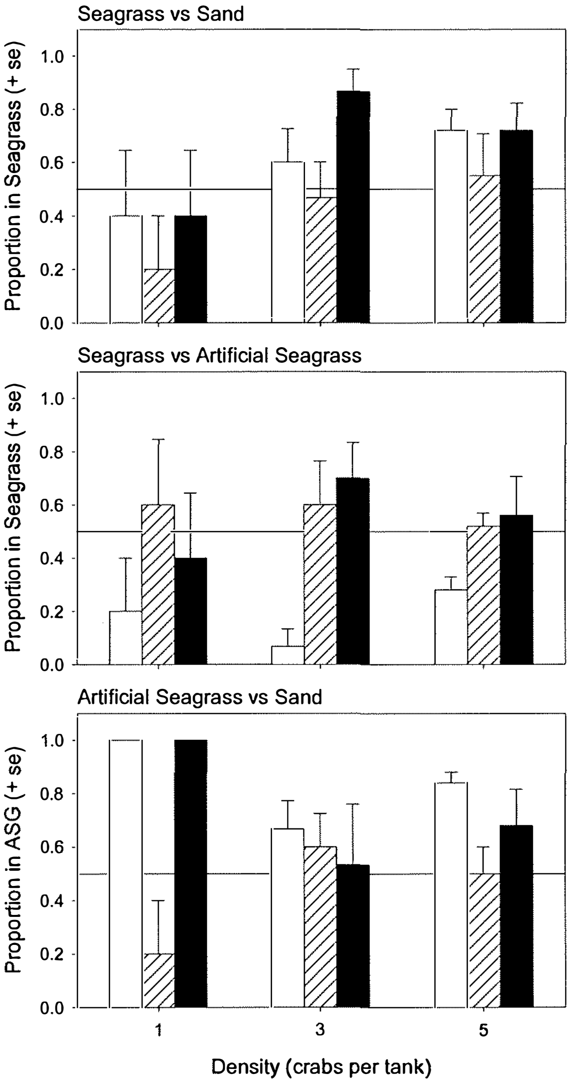

Figure 7.1: Effect of density and predator regime on habitat selection in juvenile blue crabs. Empty bars - no predators, Hatched bars - Adult *C. maenas*. Solid bars - Adult *P. pelagicus*. The horizontal line indicates the expected value if no habitat selection is occurring.

Burying behaviour was influenced by predators in the single habitat trials with seagrass and artificial seagrass, with an obvious response to the presence of adult conspecifics, although there was no effect in sand only trials (Table 7.2, Fig 7.2). In no case did density, or the interaction between predation and density, have an effect. In seagrass, 28% of crabs buried when no predator was present, 19% when *C. maenas* was present, but 66% with adult conspecifics. The corresponding figures in artificial seagrass are 28%, 28% and 77%. In sand, however, 81% of crabs buried, irrespective of density and predators. Similar patterns in burying behaviour occurred in the habitat choice experiment (Table 7.3, Fig 7.3). In all three habitat combinations, the proportion of crabs in either habitat that were buried increased when predators were present, and rates of burying were higher in bare sand as compared to either live or artificial seagrass. In the seagrass versus sand combination, both predators caused juvenile blue crabs to bury more frequently, although the effect was stronger in the presence of conspecifics. In the other two habitat combinations, only adult conspecifics induced higher rates of burying, with rates being the same in the absence of predators and the presence of *C. maenas*. The apparently high rate of burying in the seagrass versus artificial seagrass combination when no predators were present and there were three crabs per tank is because only one animal selected artificial seagrass, and this animal buried.

Table 7.2: Influence of predator treatment and density on the burying behaviour of juvenile *P. pelagicus* in single habitat trials (results of analysis of deviance tests).

Source	df	Deviance	P
Seagrass			
Predation	2	7.60	0.022
Density	2	0.73	0.69
Predation×Density	4	0.46	0.98
Residual	36	31.23	
Artificial Seagrass			
Predation	2	10.19	0.0061
Density	2	0.23	0.89
Predation×Density	4	0.97	0.91
Residual	36	28.16	
Sand			
Predation	2	1.86	0.40
Density	2	1.83	0.40
Predation×Density	4	2.00	0.74
Residual	36	29.52	

In the field trials, crabs invariably selected seagrass over sand (in 15 trials only 1 crab was found on sand). 76% of animals had buried themselves by the end of the 2 hour trial, and this did not vary with either habitat or predation regime (Table 7.4).

Discussion:

While there is some evidence of a similar change in habitat use by juvenile *P. pelagicus* in the presence of adult conspecifics and adult *C. maenas*, there are clear differences in burying behaviour in response to adults of the two species. Although the presence of adult conspecifics induced juveniles to bury themselves beneath the substrate, adult *C. maenas* elicited no such response, suggesting that they were not perceived to be as great a threat. While adult *P. pelagicus* are known to be important predators of conspecific juveniles, predation rates in this experiment were too low to meaningfully analyse (2 juveniles were eaten by *P. pelagicus*, 3 by *C. maenas*). The pattern of predation observed, however, does suggest that *C. maenas* may be as important a predator as adult *P. pelagicus*. Preliminary trials run over 24 hrs (cf 8 hrs used here), resulted in higher predation rates, but adult crabs also dug up and redistributed much of the seagrass, making comparisons between habitats ineffective. Thus the consequences of these behavioural differences could not be investigated in the laboratory. To my knowledge, no studies on the diet of *C. maenas* have been conducted in Australia. The diet of *P. pelagicus* has been studied, with de Lestang et al. (2000) finding that the remains of large decapods (primarily *P. pelagicus* and *Ovalipes australiensis*) made up ~ 10% of the dietary volume, suggesting that cannibalism can be important.

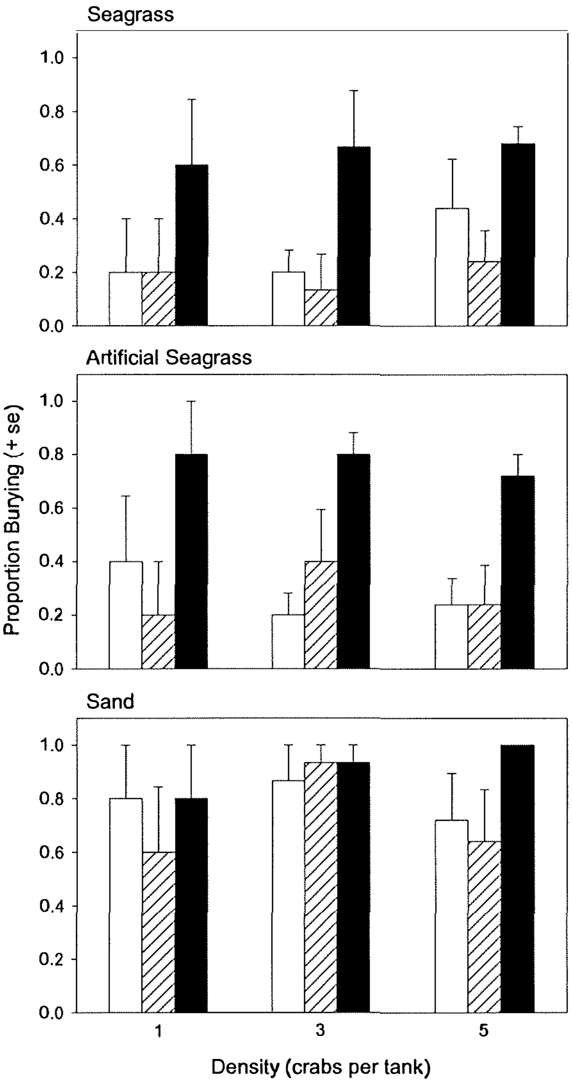

Figure 7.2: Effect of density and predator regime on burying behaviour in juvenile blue crabs. Empty bars - no predators, Hatched bars - Adult *C. maenas*. Solid bars - Adult *P. pelagicus.*

If adult green crabs are effective predators of juvenile blue crabs, then the relative lack of response of the later to the former is likely to make them much more vulnerable. While the adults of both species are similar in being large-bodied predacious portunid crabs, there are obviously enough differences between the two for the introduced species to present a novel stimulus, which the native species does not appear to perceive as a substantial threat. The only response to green crabs was for juveniles to lose their preference for artificial seagrass habitat over live seagrass, and to treat the two habitats equally. Given that juvenile *P. pelagicus* show a strong preference for artificial seagrass in the absence of predators, it is obvious that it is not acting as a good mimic of live seagrass (unlike for penaeid prawns – Chapter 6), although its shelter value in the presence of predators appears to be viewed as being the same. Alternatively, burying may not be an effective avoidance response to *C. maenas*, which is able to detect prey buried several centimetres under the substrate (Cohen et al. 1995). *P. pelagicus* shows very similar feeding behaviour to *C. maenas*, with a high proportion of infauna in its diet (Williams 1982; Edgar 1990; de Lestang et al. 2000) and thus is also likely to be able to effectively detect buried prey. Grapsid crabs also seem to not recognise *C. maenas* as a predator, and their numbers are substantially depressed in areas where it has invaded (Thresher 1997).

Table 7.3: Influence of predation, density and habitat on burying behaviour of juvenile *P. pelagicus* in different habitat combinations (results of analysis of deviance tests).

Source	df	Deviance	P
Seagrass vs Sand			
Habitat	1	3.88	0.049
Density	2	0.56	0.75
Predation	2	6.22	0.045
Habitat×Density	2	0.45	0.80
Habitat×Predation	2	6.81	0.033
Density×Predation	4	2.36	0.67
Habitat×Density×Predation	4	3.84	0.43
Residual	49	46.34	
Seagrass vs Artificial Seagrass			
Habitat	1	0.70	0.40
Density	2	2.54	0.28
Predation	2	7.26	0.027
Habitat×Density	2	0.32	0.85
Habitat×Predation	2	0.18	0.91
Density×Predation	4	2.05	0.73
Habitat×Density×Predation	4	5.92	0.21
Residual	49	43.96	
Artificial Seagrass versus Sand			
Habitat	1	13.83	0.0002
Density	2	2.15	0.34
Predation	2	17.93	0.0001
Habitat×Density	2	2.58	0.28
Habitat×Predation	2	2.47	0.29
Density×Predation	4	2.23	0.69
Habitat×Density×Predation	4	0	1
Residual	49	38.03	

Interestingly, despite clear changes in behaviour in the presence of adult conspecifics, juvenile blue crabs did not show any strong selection between available habitat types in the laboratory experiment (although they did lose their preference for artificial seagrass over live seagrass). Many other species are known to actively select (generally complex) habitats in the presence of predators, presumably as a means of decreasing predation risk (e.g. Main 1987; Holbrook and Schmitt 1988; Fernandez et al. 1993; Dittel et al. 1995; Jordan et al. 1997), although sometimes behavioural adaptations lead to selection of less complex habitats (e.g. Tanner and Deakin 2001, Chapter 6), or other factors such as food availability may outweigh predator avoidance (e.g. Boström and Mattila 1999). In contrast, the field experiment indicated strong selection for seagrass irrespective of the predation regime, suggesting that the lack of selection seen in the laboratory trials might be related to constant disturbance by the confined predator. The field results could also be affected by tethering artefacts (see page 158). At low densities (1 crab/tank), however, active habitat selection did frequently occur despite any unnaturally high levels of predator disturbance, so results at high densities may also be confounded by small juveniles selecting sub-optimal habitat to avoid larger, potentially cannibalistic, juveniles. Unfortunately, the difference between live and artificial seagrass meant that follow-up trials could not be conducted in larger tanks under more natural conditions because of the

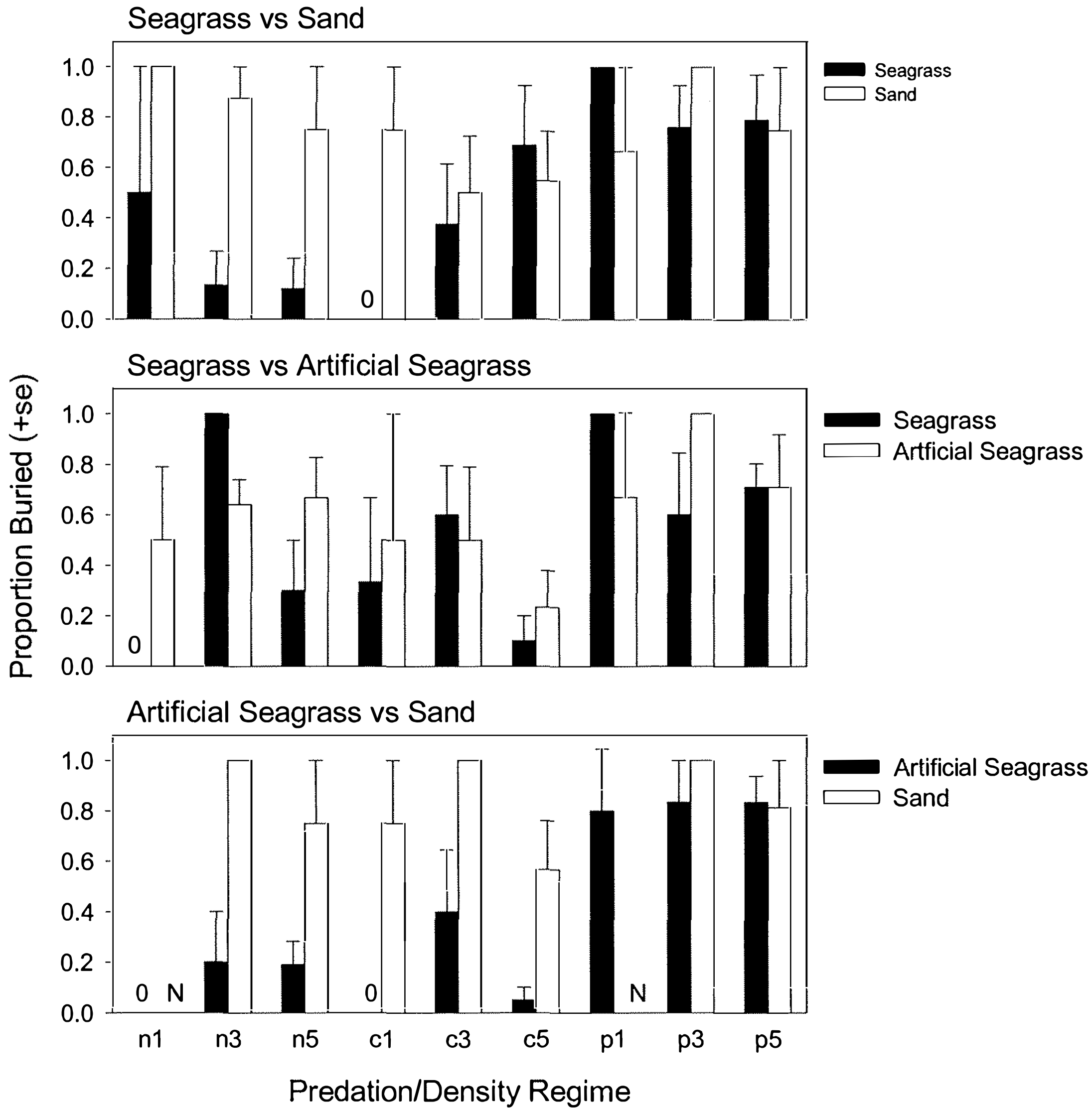

Figure 7.3: Effect of predator regime and crab density on burying behaviour of juvenile blue crabs in habitat selection trials. 0 indicates that crabs occupied the habitat but none were buried, N indicates that no crabs occupied the habitat. n - no predator, p - adult *P. pelagicus*, c - adult *C. maenas*.

Table 7.4: Influence of habitat (edge, seagrass or sand) and predation on burying behaviour of juvenile *P. pelagicus* in the field (results of analysis of deviance tests).

Source	df	Deviance	P
Habitat	2	5.08	0.079
Predation	2	1.82	0.40
Habitat×Predation	4	5.27	0.26
Residual	37	38.44	

excessive time required to plant them with seagrass. The habitat a crab was in did have an effect on its behaviour, however, with a greater proportion of crabs burying in bare sand than did in real or artificial seagrass. This suggests that the crabs perceived a greater predation risk in the less complex sand habitat.

In determining the potential implications of introduced species for the native biota, it is important to take into account the effects of other native species. If, for example, green crabs are major predators of juvenile blue crabs, but only to a similar extent as adult blue crabs, then if the former are simply displacing the later, the implications for juvenile blue crabs may be minor (see also Lafferty and Kuris 1996). If, on the other hand, green crabs are placing a significant additional predation pressure on the juvenile blue crabs, the consequences could be a substantial decrease in the population size of blue crabs. Other studies of the interactions between introduced green crabs and large native crabs have shown that while there is considerable potential for severe negative effects on the native species, this potential is rarely realised because of differences in habitat use (e.g. Griffiths et al. 1992; Cohen et al. 1995), possibly related to predation pressure on *C. maenas* by large native crabs restricting it to intertidal areas (McDonald et al. 1998). Other smaller crabs which show a high degree of habitat overlap with *C. maenas* have suffered from severe predation, however, with one species showing a 10 fold decline in abundance in Bodega Bay (California) within 3 years of invasion by green crabs (Grozholz et al. 2000). It remains to be seen if actual predation rates of juvenile blue crabs by green crabs in the field are sufficiently high to have substantial negative consequences, especially if green crabs were to spread from their currently relatively restricted distribution along the Adelaide metropolitan coastline.

It is unlikely that predation pressure by *C. maenas* on juvenile *P. pelagicus* is substantially decreased by a limited overlap of habitats in South Australia, as occurs for native crabs interacting with *C. maenas* in some other areas (e.g. Griffiths et al. 1992; McDonald et al. 2000). Juvenile *P. pelagicus* predominantly utilize intertidal and shallow subtidal areas in protected embayments (Edgar 1990; Sumpton et al. 1994; pers. obs.), which is also the preffered habitat of *C. maenas* (e.g. Griffiths et al. 1992; Hunter and Naylor 1993; Cohen et al. 1995; Abelló et al. 1997; Grozholz et al. 2000). In Barker Inlet, seine netting for juvenile blue crabs frequently also resulted in the capture of both juvenile and adult green crabs, and in a series of drop net samples in shallow subtidal areas, Hooper (2001) obtained roughly equal numbers of both species.

In conclusion, juvenile blue crabs fail to show the same predator avoidance responses in the presence of the introduced portunid crab *C. maenas* as they do to adult conspecifics. This is despite adults of the two species having similar foraging modes and diets, and an apparent similarity between the two species in their ability to prey upon juvenile blue crabs. The high degree of habitat overlap between the two species thus means that green crabs have the potential to have a substantial negative impact on the blue crab population. To determine if this is in fact the case, the diet of *C. maenas* in South Australia needs to be studied in detail, as well as its patterns of microhabitat use in relation to *P. pelagicus*.

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Chapter 8: The role of habitat edges in determining predation rates in seagrass beds

Mandee J. Smith.

Abstract

Seagrass meadows are becoming increasingly fragmented due to human disturbance, which increases the amount of habitat edge. In this study, predation rates on three decapod crustaceans, *Portunus pelagicus* (Linnaeus) (blue swimmer crab), *Penaeus latisulcatus* Kishinouye (western king prawn), and *Macrobrachium intermedium* (Stimpson) (shrimp), were shown to decrease 2 m from the patch edge in seagrass, but increase 2 m into sand. It is likely that changes in habitat complexity accounted for changes in predation rates. In particular, predation rates were dramatically enhanced along the edge in seagrass. However, predation rates did not vary when the boundary between sand and seagrass (hard or soft edge) was manipulated in aquaria. Over a larger spatial scale (4 m) predation rates indicated that the edge effect did not penetrate further than 2 m into seagrass. Predation rates on *P. pelagicus* and *M. intermedium* changed dramatically at the seagrass/sand edge, whereas predation rates on *M. latisulcatus* were very similar. Despite changes in predation rates between sand and seagrass and at the patch edge, a visual survey failed to detect any predators in these habitats. The results of this study suggest that edge effects on predation rates are an important consequence of increasing levels of fragmentation in seagrass beds.

Introduction

Landscape ecology, predominantly a terrestrial discipline, includes the study of the effects of spatial patterning of habitats on biotic and abiotic processes. (Forman and Godron 1981; Turner 1989; Miller *et al*. 1997; Silver *et al*. 2000). Recently, ecologists have emphasized the effect of spatial patterns on ecological processes such as competition, predation and nutrient flow (e.g. Forman and Godron 1981; Franklin and Forman 1987: Danielson 1991; Silver *et al.* 2000). This research is largely a response to increased levels of fragmentation and habitat loss due to human activities (Thayer *et al*. 1975; Edyvane 1999; Sih *et al*. 2000). The effect of spatial patterns is also important when studying natural systems, as natural processes have been shown to fragment habitats (e.g. Duarte and Sand-Jensen 1990; Andrén 1997; Aguiar and Sala 1999; Halg *et al*. 2000). Habitat fragmentation creates a greater number of habitat patches that are usually smaller in size than the original continuous tract(s) of habitat (Bender *et al.* 1998; Bowers and Dooley 1999; Delin and Andrén 1999). As habitat is lost and patch size decreases, species diversity declines. Species diversity is widely believed to increase with increasing habitat size, but it does so at a decreasing rate (Arrhenius 1921; Gleason 1922; Preston 1962; Mc Guiness 1984). Thus, larger areas hold proportionally fewer species than smaller areas (species area relationship). Consequently, the influence of habitat fragmentation on biological systems has become a critical factor in ecology (Forman *et al*. 1976; Ambuel and Temple 1983; Andrén 1997; Bender *et al.* 1998; Bowers and Dooley 1999; Delin and Andrén 1999; Villard *et al*. 1999).

The influence of habitat fragmentation on faunal abundance, species diversity and biological interactions has mainly been examined in terrestrial landscapes (e.g. Ambuel and Temple 1983; Andrén 1992; Bowers and Dooley 1992; Suarez *et al*. 1997; Delin and Andrén 1999). Even though the principles and concepts of landscape ecology are based in terrestrial systems, the techniques are directly applicable to the marine environment. The consequences of habitat fragmentation, however, have not been widely studied in marine systems (but see Bell and Hicks 1991; Irlandi 1994; Robbins and Bell; 1994; Irlandi *et al*.1995). One habitat that frequently occurs in a fragmented nature and dominates many coastal marine areas is seagrass meadows. Due to the sheltered, shallow nature of their coastal location, seagrass beds are vulnerable to the effects of human activities in many locations, which frequently leads to habitat loss and increased levels of fragmentation (Edyvane 1999; Laurance 2000). Seagrass meadows are highly productive, supporting a high density and diversity of fishes and invertebrates (Heck and Thoman 1981; Orth *et al*. 1984; Ferrell and Bell 1991; Connolly 1994). In estuarine systems, seagrasses support a large number of juveniles (e.g. Rooker *et al* 1998; Petrik *et al*. 1999) of many animal species and provide one of the predominant nursery habitats for numerous ecologically and commercially important species (Heck and Thoman 1981; Orth *et al*. 1984; Connolly 1994).

An important consequence of habitat fragmentation that has recently been recognised is the dramatic increase in the amount of habitat edge (Donovan *et al*. 1997; Bowers and Dooley 1999; Laurance *et al.* 1998; 2000). Early research mainly emphasized the positive effects of edges, such as high biodiversity (e.g. Gates and Gysel 1978) due to movement of animals between two different habitats and increased abundance of some game species (e.g. Reimoser and Gossow 1996). There is increasing evidence, however, that edges created by fragmentation negatively affect many species and ecological processes (Andrén and Angelstam 1988; Paton 1994; Murcia 1995), and may allow invasion of exotic species (Suarez *et al.* 1998; Cadensso and Pickett 2001). For example, fragmentation and habitat loss may influence rates of predation on patch inhabitants (Brittingam and Temple 1983; Small and Hunter 1988; Andrén 1992; Aguiar and Sala 1999; Bowers and Dooley 1999; Bologna and Heske *et al.* 1999). The proportion of edge habitat associated with small patches and fragmented habitats is greater in comparison to large patches (ie. they have greater edge to interior habitat) (Paton 1994; Baldi and Batary 2000). An increase in the amount of edge habitat increases the accessibility of prey sheltering in patches to predators foraging from patch to patch (Andrén and Angelstam 1988). A similar process has also been suggested for seagrass beds. For example, bivalve predation rates are higher in small seagrass patches than in large patches (Irlandi 1994; 1997; Irlandi *et al*. 1995; 1999).

There are several ways in which species abundance can change in response to an edge. An edge effect can be characterised by emergent properties occurring at the edge, where the organism’s response is not explained by its behaviour in the two habitat types. Furthermore, the organism’s response to the emergent properties is impossible to predict by observing the organism in a single habitat (Lidicker 1999). In this case, predation may increase or decrease abundance in either habitat at the edge or asymmetrically affect abundance at the edge. This category of edge influence has been termed an ‘ecotonal effect’. Alternatively, when the response of organisms at the edge can be explained by the organism’s response pattern to the adjacent habitat-types, the type of edge effect is termed a ‘matrix effect’ (Lidicker 1999). The organism may respond abruptly or gradually at the edge, depending on how the two habitats are divided. If the organism does not respond to the edge, as a function of distance from the patch edge, then no edge effect is present (Summerson and Peterson 1984).

Predation rates are often highest at patch edges (Andrén and Angelstam 1988; Paton 1994; Brand and George 2000) and lowest in patch interiors and with increasing distance from the patch edge. For example, nest predation and parasitism of forest dwelling birds by other species of bird common to agricultural land and grasslands is less in large patches than small, and with increasing distance from the forest edge (Brittingam and Temple 1983; Small and Hunter 1988; Andrén 1992; Heske *et al.* 1999; Flaspohler *et al*. 2001). To my knowledge, however, no studies have looked at the response of predation to proximity from the patch edge in seagrass beds. Earlier research on predation in seagrasses has mainly compared predation rates at patch edges to that in patch interiors. For example scallop predation rates at patch edges are significantly higher than in the interior of seagrass beds or over open sediment (e.g Bologna and Heck 1999). Also, seagrass patch edges tend to have greater abundances of fish compared to interior vegetated sites (e.g. Holt *et al.* 1983).

A few studies have examined faunal change as a function of distance from the sand/seagrass edge. For example, Ferrell and Bell (1991) examined the response of fish assemblages and found that fish abundance over seagrass was similar to that over sand close (10 m) to seagrass, but was higher than over sand distant (100 m) from seagrass. Summerson and Peterson (1984), however, failed to detect a response of infauna to distance from the sand/seagrass edge on a scale of 1-15 m, rather assemblages differed between the two habitats. Predation rates can also differ between sand and seagrass habitats, with sand having higher predation potential than seagrass (Heck and Thoman 1981; Holt *et al*. 1983; Orth *et al.* 1984; Summerson and Peterson 1984; Irlandi and Peterson 1991).

Rates of predation on patch inhabitants, however, may depend on the nature of the boundary dividing the two habitats (e.g. Paton 1994; Suarez *et al*. 1997). Natural edges are usually a gradual blending of two habitats. Vegetation increases in height and density, allowing predators to easily penetrate the patch. Alternatively, an abrupt transition between habitats creates a dense edge that is difficult for predators to penetrate, which is typical of human created edges (but natural abrupt edges also occur). For example, nest predation rates were found to be lower along abrupt or “hard” edges and higher in gradual or “soft” edges (Ratti and Reese 1988). Thus, abrupt edges are expected to have greater species abundance compared to soft edges, but lower abundance of species that can penetrate the edge. This response of species to edge type is an example of a matrix effect. To my knowledge, however, the concept of edge type has not been studied in seagrass beds. Research has primarily examined the influence of density and below ground material on abundance and predation of animals in seagrass (Heck and Thoman 1981; Crowder and Cooper 1982; Worthington *et al*. 1991; Worthington *et al*. 1992; Irlandi 1997; Horinouchi and Sano 1999).

The above examples indicate that ecological processes may differ between edge and interior habitats. In particular, species that only inhabit patch interiors respond negatively to edges, and are greatly endangered by increased levels of habitat fragmentation (Bender *et al*. 1998). Thus, from a conservation perspective, fragmentation of natural habitats is a major threat to biodiversity. The aim of this study is to examine the response of predation to seagrass edges in an area where seagrass habitat is lost due to fragmentation. Of predominant interest is how predation rates change in response to distance from the patch edge and edge tyM. To determine the effect of habitat edges on predation rates, a variety of decapod crustaceans were used as prey items in field and laboratory experiments. Even though predation rates are often influenced by edge habitat, prey survival rates can ultimately be governed by the behaviour and distribution of predators throughout the landscape, which may differ between locations (Andrén 1994; Donavon *et al*. 1997; Villard *et al*. 1999). Hence, I aim to determine how predators respond to fragmented seagrass beds by surveying predator assemblages and behaviour in sand and seagrass habitat, and at the boundary between the two.

Materials and Methods

Habitat Edge Type

To examine the influence of habitat edge type on predation rates of juvenile *Portunus pelagicus* (Linnaeus) predation experiments were run in a series of outdoor tanks. Each square tank was 95 cm x 95 cm x 50 cm deep and filled with a layer of clean beach sand (2 cm deep). Seawater pumped from Gulf St.Vincent flowed through each tank continuously to maintain a water depth of 30-35 cm (total volume ~270 L). Habitats (sand, seagrass, hard edge and soft edge) were established in each tank randomly and were randomly re-assigned to tanks after each trial. Water temperature varied naturally from 19ºC in April to 13ºC in July 2001 when the experiment finished. Green shade cloth over each tank provided shade from direct sunlight.

Collection of animals

Adult *Portunus pelagicu*s (blue swimmer crab), a known predator of juvenile *P. pelagicus* (Hines *et al.*1990; Wilson *et al.* 1990; Smith and Hines 1991; Moksnes *et al.* 1997), and adult *Carcinus maenas* (Linnaeus) (European green shore crab), an active introduced predator (Edgar 1997), were collected by hand or seine net in sand and vegetated habitats in Barker Inlet, Port Adelaide. Juvenile blue crabs were collected at night using a 1.5 m beam trawl off Outer Harbour, Port Adelaide. All animals were held in 500-l outdoor tanks with flow through seawater until needed.

Tethering procedure

To estimate relative predation intensity between different habitat edge types, predation rates were measured using tethered animals. The tether served to restrain motile prey that would otherwise crawl or swim away from the treatment (Zimmer-Faust *et al*. 1994). Tethering, however, may have potential artefacts associated with it such as interference with escape behaviour. The between-habitat difference in predation, as estimated from mortality of prey on tethers, could be inaccurate if the increase in predation induced by tethering is not constant across habitats (Barbeau and Scheibling 1994; Peterson and Black 1994; Aronson and Heck 1995; Kneib and Scheele 2000). This experiment included a comparison of predation on tethered verses unteathered juvenile crabs in each habitat, to determine if tethering had a differential effect across habitats.

Juvenile *P. pelagicus* were attached to individual tethers using a similar procedure to Heck and Thoman (1981), shortly before an experiment began. A small amount of “Quick Tite Super Glue” was placed on the animal’s carapace and the end of a 20 cm length (after tying) of monofilament fishing line was firmly held against it until attached. Animals were then securely tied to individual sinkers (50 g) ready for use in the experiments. The effective tether length of 20 cm was determined from preliminary experiments (observations only) with varying tether lengths (5, 10, 15, 20, 35, and 55 cm). Tether lengths of 5-15 cm resulted in juvenile *P. pelagicus* being prone to predation, as the tether hindered their escape response. When tethered with 35 and 55cm long tethers, juveniles became excessively tangled in the seagrass. Hence artefacts due to the tether were least when it was 20 cm long. Due to an increasing number of prey becoming untethered later in the experiment, the tethering method was revised. The new method of tethering was similar to the procedure used by Zimmer-Faust *et al*. (1994), where the fishing line was attached by looping the line around the posterior margin of the carapace, just above the last abdominal segment and tightened. The effective tether length remained the same and the technique did not physically affect juvenile escape behaviour in comparison with the original method.

Experimental Procedure

The influence of habitat edge type on predation on juvenile *P. pelagicus* was tested by placing a single adult blue crab (*P. pelagicus* - carapace width approximately 85-90 mm) or adult European green shore crab (*C. maenas* - carapace width 60-65 mm) into each treatment tank. A variety of other predators were also trialed, but their predation rates were too low to produce useful results. All predators were starved for 24 hrs prior to use to encourage active foraging during the experiment. In each tank, five tethered juvenile blue crabs (*P. pelagicus* – mean carapace width 45 mm ± 0.06 SE) were placed as prey items along the habitat edge, but were randomly placed in tanks containing sand and seagrass habitat. Juvenile blue crabs were randomly selected for each treatment and were only used once as prey items in experiments. Due to the lack of adult crabs (only seven *P. pelagicus* and ten *C. maenas* were collected), adults were randomly selected for each treatment. Predator and prey were placed in experimental tanks at 10:00 am and removed 24hrs later and evidence of predation recorded. Five replicate trials were carried out for each combination of habitat (sand, seagrass, hard edge and soft edge) and predator. To determine if tethering affected predation rates, survival of untethered juvenile *P. pelagicus* was compared to survival of tethered animals in the above four treatments.

Construction of seagrass habitats

Artificial seagrass was used to create edge and seagrass habitats similar to the dominant seagrass in shallow waters of Barker Inlet (*Zostera muelleri*). The artificial seagrass was made from black polyethylene builders plastic: four sheets were welded together at the base and then cut into strips 6-7 mm wide. Seagrass blades were 22 cm long, with four blades per shoot, and about 12-14 shoots in each 10 cm. Each 880 mm long segment of seagrass was tied to an aluminium frame (880 x 880 mm) with monofilament fishing line to fit into the experimental tanks. Experimental treatments were sand, seagrass (5530 shoots per 0.88 m^2), hard edge and soft edge. A hard edge was created by filling half the frame with artificial seagrass (3017 shoots per 0.44 m^2), leaving the other half of the tank as bare sand (Fig 8.1). To create a soft edge, 1/3 of the frame contained full seagrass (2011 shoots per 0.3 m^2), and 1/3 of the frame had blades gradually decreasing in size (22, 20, 15, 10, 5 cm), leaving only 1/3 of the frame to expose sand (Fig 8.1).

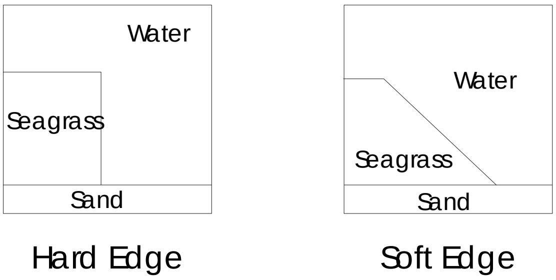

Figure 8.1: Habitat edge types used in laboratory experiments (profile view of tanks)

Analysis

To determine if the proportion of juvenile *P. pelagicus* that survived in a trial varied between any of the habitats investigated, generalised linear models (GLM) were used, assuming a binomial distribution. GLM's provide a summary of the relationship between a response variable (survival) and predictor variables (predator, habitat and tethering) (Yee and Mitchell 1991; Swartzman *et al*.1992; Reckhow and Quin 1994), resulting in an analysis analogous to ANOVA. Significance values for the relationship between the response and the predictor variables were determined by using analysis of deviance (Hastie and Tibshirani 1990). The factor (predator, habitat and tethering) explaining the greatest amount of variation in the data was fitted to the model first, with the remaining factors added in order of importance. At each step, the new model was compared to the previous model to determine the significance of the added term.

Proximity to edge habitat

To determine if predation rates varied with distance from seagrass habitat edge, a field experiment was carried out with juvenile *Portunus pelagicus* (blue swimmer crab), *Penaeus latisulcatus* (Kishinouye) (western king prawns) and *Macrobrachium intermedium* (Stimpson) (Shrimp). Prey were tethered at different distances (0.2 m, 0.5 m and 2 m) from the patch edge in a series of 4 m long transects extending from a sand patch into a seagrass patch.

Study site

Field predation experiments were carried out between May and July 2001 in *Zostera marina* seagrass patches in Barker Inlet (34°46'S, 138º31'E), a sheltered, marine dominated estuary with extensive intertidal areas, near Port Adelaide. The estuary is strongly tidal, typically with two tides per day, with maximum tidal amplitude of about 2.5 m.

Collection of animals

Juvenile *P. pelagicus* and *M. latisulcatus* were collected from Outer Harbour, Port Adelaide, at night using a 1.5 m beam trawl*. Macrobrachium intermedium* were collected form Barker Inlet using a seine net. The animals were held in 500-l outdoor tanks with flow through seawater until needed.

Experimental procedure

To determine if predation rates varied with distance from habitat edge, predation experiments were run in areas of patchy *Z. marina* and sand. A series of transects were laid out in seagrass and sand patches. Each transect was 4 m long, and extended from a sand patch into a seagrass patch perpendicular to the boundary between the habitats. Patches at least 4-5 m wide were chosen to ensure the furthest point of the transect was >2 m from the opposite patch edge. Seagrass patches with a clear transition (edge) between seagrass and sand were also chosen. Prey were tethered at fixed distances (0.2 m, 0.5 m and 2 m) from the edge, in either sand or seagrass. The tethering procedure for crabs, prawns and shrimp was similar to that of Zimmer-Faust *et al*. (1994). A 20 cm long tether (after tying) of monofilament fishing line was attached by looping the line around the carapace, and then tightened. The free end of the tether was attached to a wire stake which was pushed into the substrate at the selected locations. Tethering was conducted in the laboratory approximately 2 hrs before experimentation using animals of a uniform size (blue crabs – carapace width 45-55 mm, shrimp – total length 35-45 mm, and prawns – total length 40-50 mm).

Three replicate transects were placed approximately 1m apart in each patch, with patches 5-10 m apart. For each prey species, four replicate patches were used, with the experiment being repeated after three weeks for *P. pelagicus.* The replicate patches resulted in 24 replicate transects for *P. pelagicus* and 12 each for *M. intermedium* and *M. latisulcatus*. To identify each transect, stakes were flagged with coloured tape and placed on the patch edge. To ensure that *P. pelagicus* abundance was not excessively elevated above natural levels, animals were placed at only three of the experimental locations (randomly chosen) in a patch on any one day, with the experiment extending over six days. *Macrobrachium intermedium* and *M. latisulcatus* were placed at all experimental locations in a patch edge in one day as they were naturally more abundant than *P. pelagicus*. Once tethered at a desired distance from the edge, the stakes were not flagged to ensure that the animals visibility to predators was not enhanced. To relocate stakes 24 hrs later, a 4 m long rope was placed along each transect with knots corresponding to the fixed distances (0.2, 0.5, 2 m). The stakes were removed and the survival of the attached animals assessed.

Larger spatial scale

To determine if relative predation rates changed over a larger spatial scale, the above experiment was repeated for *M. intermedium* using 8 m long transects. Twelve transects were laid out in patches as indicated above, but the distances of tethered animals from the patch edge into seagrass and sand were 0.2, 2 and 4 m. Shrimps were relocated 24 hrs later and evidence of predation was recorded.

Analysis

To determine if relative predation rates varied with distance from the patch edge, Generalised Additive Models (GAM) (analogous to ANOVA), were used, assuming a binomial distribution. GAM is a non-parametric extension of GLM where instead of assuming a linear response the data determines the shape of the response curves (Hastie and Tibshirani 1990). This regression technique fits a non-linear smooth curve to the data, rather than being limited by the shapes available in a parametric class. For each prey species, models were fit separately with Splus (Math-Soft Inc., Seattle) and transect was included as a nested factor in the analysis to account for any small-scale variation between transects. Significance values for survival in response to distance and transect (and time for crabs) were determined using an analysis of deviance where distance from patch edge was included as a continuous variable and transect as a random factor. Time was also included as a random factor in the blue crab analysis to account for any temporal variation between the two experimental periods. If the non-linear component for distance was not significant, it was replaced by a linear term, resulting in a Generalised Linear Model (GLM – Dobson 1990; Yee and Mitchell 1991; Swartzman *et al*.1992; Reckhow and Quin 1994).

To determine if the response of predation to distance from the patch edge changed at the patch edge, a discontinuous piece-wise linear fit was included in the analysis. The analysis incorporates regression splines by representing the fit as a piece-wise polynomial. A knot or breakpoint in the fitted function (distance) separates the regions that define the pieces (sand and seagrass habitat). The piece-wise polynomials are then joined smoothly at the break. As a result, the sand and seagrass habitat were separated with a break at the patch edge (0 m). Significance was determined by testing between the results of analysis of deviance for the GAM and the piece-wise model.

Habitat use by predators

To examine predator use of different habitats in situ, a video camera was used to record predator presence in different habitats. The habitats surveyed were sand, seagrass and the edge between the two, with the camera being left to record for 30mins in each habitat. Due to seagrass obstructing the camera view, a large crate was used to position the camera above the height of the seagrass. The first 10 mins recorded were disregarded due to the area becoming disturbed by my presence, leaving the remaining 20 mins to be analysed. For predator identity and abundance, five replicate surveys of each habitat type were conducted in at least 1m of water in Barker Inlet.

Results

Habitat edge type

Even though figure 8.2 suggests that *C. maenas* predation rates increased in soft habitat edge compared to hard habitat edge, habitat had no significant effect on juvenile *P. pelagicus* survival (Table 8.1). Thus, the type of habitat edge did not significantly alter predation rates on *P. pelagicus.* Adult *P. pelagicus* seemed to forage inefficiently in vegetated habitats, where all prey survived (Fig. 8.2). Conversely, *C. maenas* foraged actively in all habitats (Fig. 8.2). Predation rates on *P. pelagicus* by both predators, however, were not significantly different (Table 8.1). Figure 8.2 suggests that the presence of vegetation enhanced the survival of tethered prey, compared to sand habitat, although this isn't statistically significant. Habitat and tethering also did not significantly interact with both predators. Untethered prey survived equally well in all habitats.

Table 8.1: GLM results for the effect of habitat type, predator and tethering on juvenile

Source	df	Deviance	P
Predator	1	14.3	0.12
Habitat	3	12.1	0.53
Tethering	1	11.4	0.40
Predator x Habitat	3	9.9	0.70
Predator x Tethering	1	9.8	0.74
Habitat x Tethering	3	9.4	0.94
Predator x Habitat x Tethering	3	9.4	1
Residual	64	9.4	

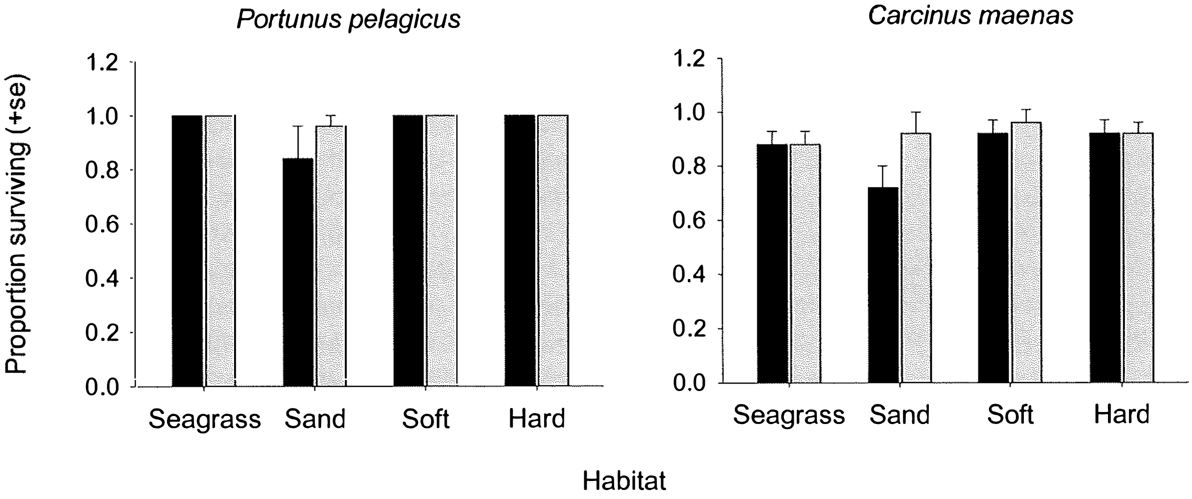

Figure 8.2: Habitat effect on survival of juvenile *P. pelagicus*. Mean of five trials for each habitat type, including predator and tethering (+SE). Black bars indicate tethered crabs, and grey bars untethered.

Proximity to patch edge

Overall, survival of juvenile *P. pelagicus*, juvenile *M. latisulcatus* and *M. intermedium* differed in response to distance from the habitat edge. At the furthest distance (2 m) from the patch edge into seagrass, survival was greatest, but generally declined rapidly towards the boundary between the habitats and into sand where survival was greatly reduced. An overall response of survival to distance indicates that edge effects are occurring in seagrass beds.

Survival of juvenile *P. pelagicus* responded to distance from the patch edge nonlinearly, with survival abruptly increasing from the edge into seagrass, and decreasing smoothly into sand (Table 8.2, Fig. 8.3a, 8.4a). Distance from the patch edge, however, only had a marginally significant effect on survival (*P* = 0.07, Table 8.2). There was a significant interaction, however, between distance and time. Thus, the response of predators to distance from the patch edge differed over time (Table 8.2). Even though survival during time 1 and time 2 changed with distance from the patch edge, the trends were not statistically significant. Both days, however, show obvious edge effects, where survival decreased near the patch edge (Fig. 8.3b, 8.3c). During time 1, survival was highest at 2 m in seagrass (100%), and lowest at 0.2 m in seagrass and 0.5 m in sand (20%) (Fig. 8.3b). Conversely, survival during time 2 was highest at 2 m in sand (100%) and lowest at 0.2 m in sand (65%) (Fig. 8.3c). Survival between 0.5 m and 2 m in sand, however, did not change, indicating the edge effect may have extended further than 2 m in sand (Fig. 8.4c).

Survival of juvenile *M. latisulcatus* responded to distance from the patch edge linearly, rather than abruptly increasing or decreasing away from the edge (Table 8.2, Fig. 38.d). At 0.2 m in seagrass, 50% of *M. latisulcatus* survived, whereas 85% survived at the furthest distance from the patch edge in seagrass (2 m) (Fig. 8.4d). Survival in sand was highest (60%) at 0.2 m in sand and lowest at 2 m in sand (25%). *Macrobrachium intermedium* survival also responded significantly to distance from the patch edge, with survival responding to distance from the patch edge non-linearly (Table 8.2, Fig. 8.3e). Survival in seagrass decreased from 65% at 2 m to 20% at 0.5 m (Fig. 8.4e). At 0.2 m in seagrass, only 2% of *M. intermedium* survived. Survival then increased again in sand, from 20% at 0.2 m, to 35% at 2 m. At a larger spatial scale, *M. intermedium* survival showed a linear response to distance (Fig. 8.3f). Distance and transect, however, significantly interacted (Table 8.2). Thus, the effect of distance differed between transects, indicating small-scale variation in survival. However, Figure 8.4 (f) shows a general trend in survival with distance from the patch edge.

Table 8.2: GAM results for prey survival as a function of distance from seagrass patch edge

Source	**df**	**dev**	**P**[a]	**P(nl)**[b]
P. pelagicus				
Distance	4	8.7	0.07	0.043
Time	1	3.0	0.08	
Distance x Time	1	6.0	0.02	
Transect/Distance x Time	6	10.8	0.10	
Residual	131	107.7		
M. latisulcatus				
Transect	3	2.3	0.52	
Distance	1	10.5	0.001	0.823
Distance x Transect	3	0.9	0.82	
Residual	64	84.0		
M. intermedium				
Transect	3	0.7	0.86	
Distance	4	15.7	0.003	0.025
Distance x Transect	3	5.8	0.12	
M. intermedium *(larger spatial scale)*				
Transect	3	4.4	0.23	
Distance	1	10.3	0.001	0.33
Distance x Transect	3	10.2	0.02	
Residual	64	74.1		

a. Probability that the term is significant with the given df (df=1specifies linear fit, df = 4 a non-linear fit). b. Probability that the term is non-linear.

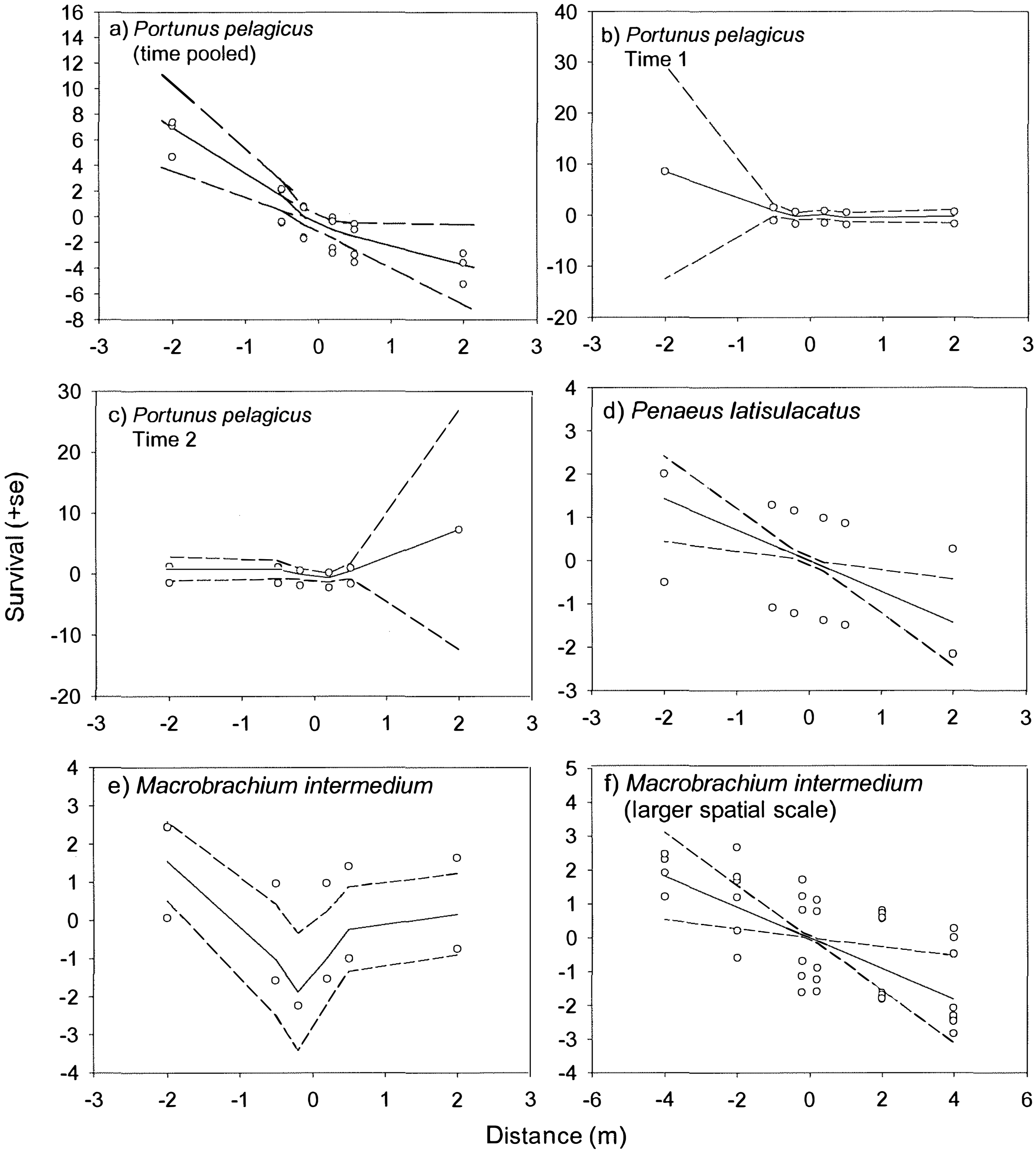

Figure 8.3: GAM fit for survival as a function of the distance from the patch edge. –ve distances indicate seagrass, +ve distances indicate sand. Points connected by solid line indicate observed survival. Dashed lines indicate ± 2 x se.

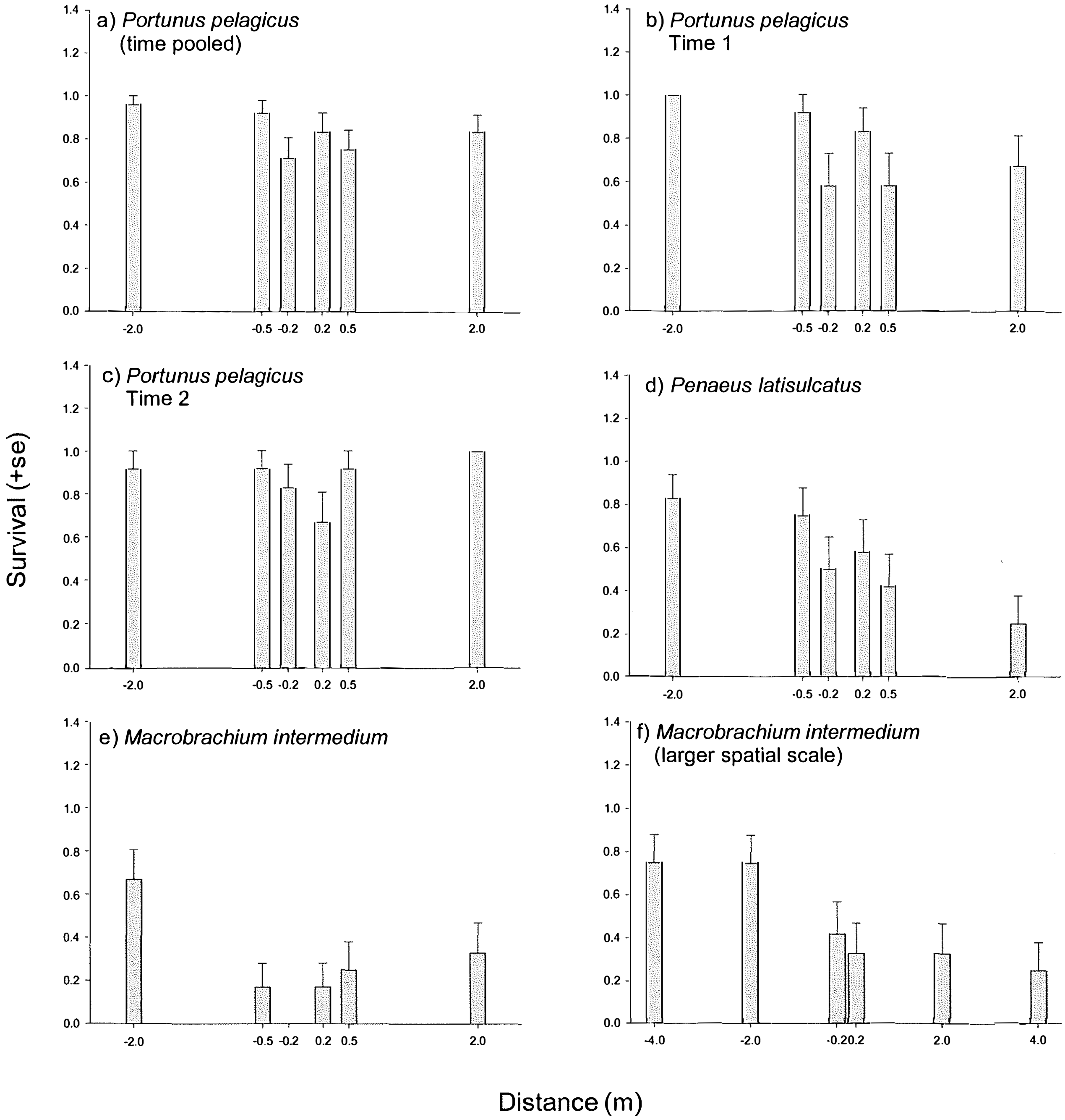

Figure 8.4: Survival of *P. pelagicus, M. latisulcatus, M. intermedium* and *M. intermedium* (over a larger spatial) as a function of distance from patch edge.

Changes in predation rates at the patch edge

A discontinuous piece-wise linear fit showed that the response of predation rates on *P. pelagicus* to the distance from the patch edge, dramatically changed at the patch edge (Table 8.3, Fig. 8.5a). Predation on *P. pelagicus* during time 1 was higher in the sand interior, which was similar to the seagrass edge, compared to the seagrass interior (Fig. 8.5b). During time 2, predation rates were dramatically higher in the seagrass interior and at the sand edge compared to the sand interior (Fig. 8.5c). When the discontinuous piece-wise model for time 1 and time 2 were compared to the GLM's for time, however, the changes in predation at the edge were not statistically significant for time 1 or time 2. Conversely, predation rates on *M. latisulcatus* did not change at the patch edge (Table 8.3). Instead *M. latisulcatus* predation rates declined consistently from the interior of the seagrass patch to the interior of the sand patch (Fig. 8.5d). Predation on *M. intermedium* at 2 m in sand was slightly higher than at 2 m in seagrass. At the patch edge predation rates were dramatically higher at 0.2 m in seagrass than 0.2 m in sand (Fig. 8.5e). The analysis of deviance between the *M. intermedium* model in Table 8.2 and the discontinuous piece-wise linear model, however, was statistically insignificant (Table 8.3).

Table 8.3: GAM tests to determine if response of predation rates to distance changed at the habitat boundary.

Source	**df**	**dev**	***P***
P.pelagicus	1	4.14	0.04
M. latisulcatus	2	0.01	0.99
M. intermedium	1	0.37	0.50
M. intermedium (larger spatial scale)	8	17.8	0.02

Results of analysis of deviance tests between model in Table 2 and model allowing a break in the fitted function at 0 m.

Over a larger spatial scale (4 m) a discontinuous piece-wise linear fit also detected a change in *M. intermedium* predation rates at the edge (Table 8.3, Fig 8.5f). The effect of distance in each habitat, however, can not be interpreted as small-scale variation in predation rates was detected in the GLM.

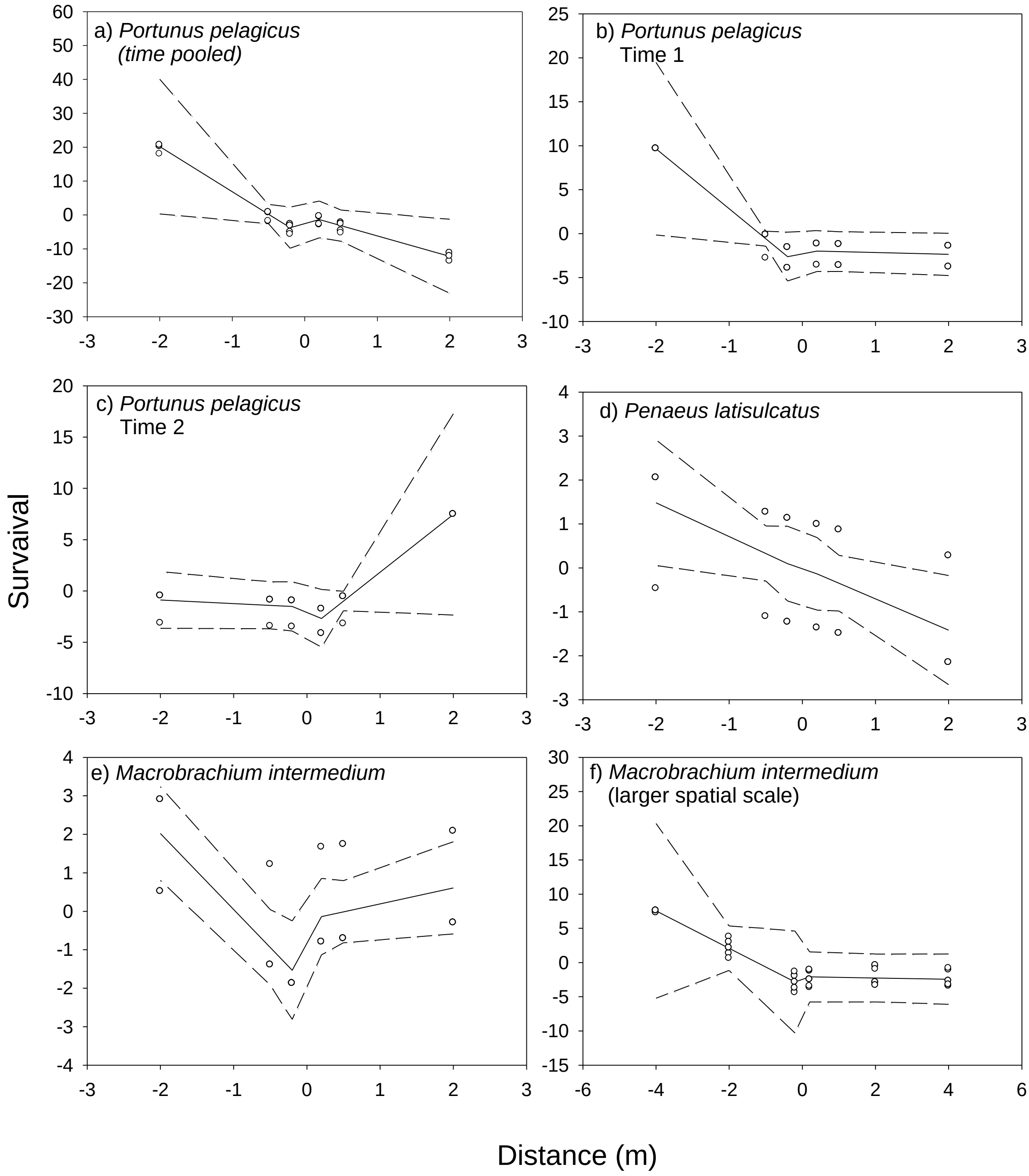

Figure 8.5: Discontinuous piece-wise linear fits for *P. pelagicus*, *M. latisulcatus, M. intermedium* and *M. intermedium* over a larger spatial scale (4 m) as a function of distance from the patch edge. Points connected by solid lines indicate observed survival. Dashed lines indicate ± 2 x se.

Habitat use by predators

In all three habitats surveyed, there was no sign of any predatory species, giving no indication of predator foraging behaviour in the area.

Discussion

At the spatial scale examined in the field the prediction that predation rates change in response to distance from the seagrass patch edge was supported. Predation rates were also distinctly different between sand and seagrass. Predation rates in seagrass were highest at the patch edge and lowest at the furthest distance (2 m or 4 m) from the patch edge. It is possible that this trend in predation was correlated with changes in seagrass complexity as a function of distance from the edge. Predation rates in sand were generally higher than in seagrass and with increasing distance from the patch edge. Between 0.5 m and 2 m in seagrass, however, prey survival did not appear to level off. Consequently, edge effects on decapod crustaceans could potentially extend further than 2 m into seagrass.

Effects of habitat and distance on predation

Predation on *P. pelagicus*, *M. latisulcatus* and *M. intermedium* was greatly enhanced close to the patch edge (0.2 m) in seagrass. In particular, *M. intermedium* experienced greater predation rates along the habitat boundary than in either habitat. Earlier research considered an increase in predation at the patch edge to be unusual, given that seagrasses have been demonstrated to be a predator deterrent (Heck and Orth 1980; Heck and Thoman 1981; Crowder and Cooper 1982; Orth *et al*. 1984). Edge effects, however, have recently been documented for sand/seagrass edges, with an increase in scallop predation rates along the habitat boundary compared to either habitat (Bologna and Heck 1999). A similar process has been well documented in terrestrial landscapes, where nest predation is often found to be higher along forest edges than in the interior (e.g. Andrén and Angelstam 1988; Paton 1994; Donovan *et al*. 1997; Brand and George 2000). This pattern in predation is largely due to predators altering their foraging behaviour (Brittingam and Temple 1983; Small and Hunter 1988; Andrén 1992; Andrén 1994). Highly mobile mammals use forest edges as “travel lanes” and may move parallel to the edge for some distance, resulting in increased predation potential for bird eggs in forest fragments (Small and Hunter 1988). Consequently, large mobile predators are expected to alter their foraging behaviour in response to the spatial patterning of seagrass habitats. The unvegetated sediments associated with seagrass patches may facilitate the movement of predators into and among the seagrass patch. As a result, seagrass patch edges are expected to increase the accessibility of prey sheltering in patches to predators foraging from patch to patch (Andrén and Angelstam 1988), which is consistent with the edge effect found in this study.

Predators might increase the predation rate at the patch edge for several different reasons. Angelstam (1986) suggested that the intensity of the edge related predation rate could be explained by the productivity difference between the habitat patch and the surrounding habitat. Consequently, a more productive habitat (e.g. seagrass) is expected to support more predators than a less productive one (e.g. sand). The high densities of predators in the productive habitat are expected to increase the predation rate on prey close to the edge. Predators may be spending more time in the habitat edge than in other parts of the habitat patch because prey are either more abundant there, or are more easily detected. In terrestrial systems, predators view habitat edges as good foraging grounds as they have high densities of prey (Gates and Gysel 1978). Faunal abundance in seagrasses, however, increases with increasing distance from the edge. Thus, predators foraging along an edge are probably not responding to increased food availability, but are confronted by a trade off between increased detection and capture of prey, and increased predation from their own predators. For example, the bay scallop (*Argopecten irradians*) has been shown to select habitat edges in response to increased flow rate and food availability, but at a cost of higher mortality than in interior habitat (Bologna and Heck 1999).

The distance to which an edge effect can penetrate a patch depends on a range of biotic and abiotic factors (Laurance *et al.* 1997). The distance a predator will penetrate is likely to depend on which of these factors are most relevant to the organism. For example, microclimate changes across a forest edge and significantly impacts on species composition, structure and ecological processes (Baldi 1999; Davies-Colley *et al*. 2000). As a result, nest predation has been shown to decrease with increasing distance from a forest edge (Gates and Gysel 1978; Brittingham and Temple 1983; Andrén 1992; Brand and George 2000). In seagrass beds, hydrodynamics change as a function of distance from the patch edge, which is likely to influence seagrass complexity and faunal abundance (Fonseca *et al*. 1982). Flow rate is greatly reduced towards the patch interior, where the habitat is physically more complex than at the patch edge (Fonseca and Fisher 1986; Gambi *et al*. 1990). The net benefit of foraging in seagrass closer to the patch edge is therefore likely to be greater than at the furthest distance from the edge. While seagrass biomass was not quantified in the present study, increased habitat complexity has been shown to reduce predator capture success by interfering with mobility and visual detection of prey (e.g. Heck and Thoman 1981; Coen *et al*. 1991), while below-ground roots and rhizomes act as a barrier to digging predators (e.g. Peterson 1982). Thus, changes in seagrass complexity could possibly account for the observed decrease in predation rates on *P. pelagicus, M. latisulcatus* and *M. intermedium* with increasing distance from the edge.

A variety of studies have examined the effect of habitat complexity on prey vulnerability (e.g Nelson 1979; Heck and Orth 1980; Heck and Thoman 1981; Crowder and Cooper 1982; Nelson and Bonsdorff 1990), with the overwhelming conclusion being that predation rates decrease as seagrass complexity increases. As a result, many individuals respond to reduced predation pressure in denser or more complex seagrass beds by choosing to shelter in these habitats (Heck and Thoman 1981; Orth *et al*. 1984; Bell and Westoby 1986; Connolly 1994). According to Heck and Orth (1981), predators are attracted to invertebrates inhabiting vegetated areas as long as the density of vegetation is insufficient to reduce foraging efficiency to less than it would be in other habitats. The low predation rates found in the seagrass interior in this study suggest that the seagrass density was sufficient to reduce foraging efficiency. Heck and Thoman (1981) suggested that reduced foraging success could be related to a threshold density of seagrass. Thus, the threshold density of seagrass in this study was reached between 2 and 4 m, where predation was lowest. To my knowledge, however, only one study has aimed to determine if a correlation exists between habitat complexity and faunal abundance as a function of distance from the seagrass patch edge. Seagrass biomass and the associated epifaunal assemblage were shown to change significantly as a function of the distance from the patch edge (Chapter 9). There were few responses, however, by infauna, but rather a large amount of unexplained small-scale variation in abundance and composition. Consequently, further research of this type is required to help explain why predators choose to forage over habitat edges. Research by Bell and Westoby (1986) has suggested that predation is the agent driving prey to select complex habitat, but not the direct cause of low prey abundance among poor seagrass cover. Thus, active predator avoidance is at least partially responsible for the observed patterns of differential habitat selection within mosaics of sand and seagrass habitats (Heck and Orth 1980; Stoner 1982; Holbrook and Schmitt 1988; Jordan *et al*. 1996).

The marginal effect of distance on *P. pelagicus* predation is likely to represent natural variability. Time significantly explained much of the variation in predation rates, with predation rates being slightly higher during time 1 compared to time 2. The relatively high survival rates in seagrass compared to sand are likely explained by habitat complexity. Seagrass may have reduced predator foraging activity, while enhancing *P. pelagicus* protection. Despite the fact that low habitat complexity enhances foraging activity, survival rates in sand habitat were still high. This lack of predation in sand suggests that the size range of juvenile *P.pelagicus* used in the experiment may not experience high rates of predation. Potential predators (e.g. adult blue crabs, green crabs, fiddler rays) may have difficulty in capturing and feeding on animals of this size range, as it has been previously established that predators select prey depending on their size (Vince *et al*. 1976). In addition, predation rates were higher close to the patch edge in sand than in sand distant from the patch edge. Predators of *P. pelagicus* are therefore making active decisions about habitat use, which incorporate relative risk of predation. Clearly more research is needed to evaluate the general importance of behaviorally mediated habitat selection by predators.

Predation rates on M. *intermedium* (over a small and large scale) and *P. pelagicus* changed at the patch edge. *Macrobrachium intermedium* (small scale study) survival in sand was lower than seagrass and with increasing distance from the patch interior. This pattern of survival suggests that predators are leaving the protection of seagrass to forage in sand, but not at great distance from the seagrass edge. Predators that forage in sand close to seagrass not only benefit from enhanced detection of prey, but also can seek cover when encountered by their own predator. Fish are potential predators of small crustaceans, and are found in large numbers in sand near seagrass patches (e.g. Sogard 1989; Ferrell and Bell 1991). A similar pattern of predation has been suggested to influence infaunal abundance near rocky habitats (Posey and Ambrose 1994). Infaunal abundance increased in sand with increasing distance from the reef. Thus, predators foraging in sand may be balancing predation risk with food availability in order to maximize net energy gain.

Over a larger spatial scale, however, survival rates of *M. intermedium* in the sand decreased with increasing distance from the patch edge. This trend may suggest that over a larger spatial scale predators were not moving between seagrass and sand habitat. Instead, predators that predominantly inhabit sand (e.g. crabs) were foraging more actively at the sand interior than in sand close to seagrass. Juvenile *P. pelagicus* (time 1), which are predominantly preyed on by adult blue crabs, also experienced higher predation rates in sand distant from seagrass. In addition, the observed differences in predation rates on *M. intermedium* and *P. pelagicus* between sand and seagrass are consistent with previous studies documenting that sand habitats have higher predation potential than seagrass habitats (e.g. Heck and Thoman 1981; Holt *et al*. 1983; Orth *et al*. 1984; Summerson and Peterson1984; Irlandi and Peterson 1991).

The response of predation rates on *M. latisulcatus* to distance from the patch edge did not dramatically change at the patch edge. Despite predation rates being lower in seagrass than in sand, seagrass was expected to inflate predation rates, given that *M. latisulcatus* predominantly inhabit sand (Chapter 6). Burying in sand is the preferred option for avoiding predators for *M. latisulcatus* (Chapter 6), however, they have also been shown to use seagrass as shelter when burying in sand is not possible (Chapter 6). Furthermore, a distinct linear relationship exists between predation and distance from the patch edge. This linear trend suggests that predators of *M. latisulcatus* are moving between seagrass and sand habitats over a small scale (2 m). Summerson and Peterson (1984), however, found that infauna moving over a scale of 1 m from the seagrass/sand edge was insufficient to mask differences in predation rates. At a larger spatial scale, the later study also failed to detect an edge effect at distances up to 15 m from the sand/seagrass boundary. Instead, they found infaunal assemblages to differ between sand and seagrass. On the other hand, highly mobile animals, such as fish, respond to edge effects over 100’s of m (Ferrell and Bell 1991), while terrestrial animals respond over 10’s of km (Laurance 2000). Thus, the relative mobility of different species may be important in causing edge effects to occur over different scales.

The larger spatial scale (4 m) examined in this study established that edge effects on predation of decapod crustaceans do not extend further than 2 m from the sand/seagrass boundary in both directions. Although predation rates in seagrass were generally consistent with those found over a smaller spatial scale (2 m), predation did not change between 4 and 2 m before gradually decreasing into the sand interior. Consequently, a seagrass patch 2 m in diameter is not expected to contain interior habitat as the edge effect would extend to the opposite edge of the patch. The proportion of edge habitat associated with small patches is greater compared with large patches. Larger seagrass patches are therefore expected to reduce predation rates on species requiring seagrass interior. For example, bivalve predation rates are greater in small patches than large patches (Irlandi 1994; 97: Irlandi *et al*. 1995; 1999). Furthermore, Wilcove (1985) established that a long narrow fragment, with a high proportion of edge habitat, has greater predation potential than a similar sized, but circular fragment. Further research is required to determine if seagrass patch size and shape influence predation rates as a function of distance from an edge.

While there were distinct changes in predation rates between seagrass and sand and at the boundary between the two, the survey technique failed to detect any predator activity in these habitats. While the activity of predators was not quantified during the night, the results from 3 hour predation trials indicated a lack of predator activity during the day. The lack of predator activity during the day may suggest that predators are more active during the night, which is consistent with the edge effect found over a 24 hr period in this study. Predators' choice of habitat may therefore have been influenced by natural variation, including tidal fluctuations, light intensity (time of day) and season. Connolly (1994) showed that fish in Barker Inlet move in over tidal flats and choose a new habitat (eelgrass or unvegetated habitat) on each tide. Consequently, a revaluation of the survey technique is required before longer and more intense surveys are conducted to examine variations in predator abundance and behaviour over sand and seagrass and the boundary between the two. Other studies, however, have established that fish abundance is greater over sand/seagrass patch edges than sand and seagrass interior (Holt *et al*. 1983; Ferrell and Bell 1991). These suggestions concerning predator activity along the sand/seagrass edge, could explain the increased level of predation at edges found in this study.

Habitat edge type

Several terrestrial studies have established that predation rates in patches depend on the nature of the boundary dividing the two habitats (Ratti and Reese 1988; Paton 1994; Suarez *et al*. 1997; Heske *et al*. 1999). Laboratory results did not support my predictions about the influence of habitat edge type on predation rates, however. Predation rates were predicted to be higher in gradual or 'soft' habitat edges and lower in abrupt or 'hard' habitat edges, as reported by Ratti and Reese (1988), but no effect was detected. The majority of terrestrial studies, however, have found that predation rates are highest along abrupt habitat edges (e.g. Paton 1994) and lowest along gradual habitat edges (Suarez *et al*. 1997). Differences in vegetation associated with habitat edges in terrestrial and marine landscapes vary in structure, composition and scale. Consequently, I predicted the opposite effect of edge type on predation rates in seagrass beds. For example, a gradual seagrass edge, which has reduced blade complexity and height, was expected to enhance visual detection and capture of prey by predators, whereas gradual forest edges often contain dense regenerating shrub layers that may provide numerous places where birds can hide their nests, and may obstruct predator vision when searching for nests from the edge. Conversely, a mammalian or avian predator moving along an abrupt edge may have an unobstructed view of the adjacent vegetation, whereas a hard seagrass edge contains dense vegetation, which is expected to deter predators (Bider 1968). Some other studies, however, have also failed to find an effect of edge type (Yahner *et al*. 1989, Heske *et al*. 1999).

Abrupt edges have also been found to act as ecological traps because they attract large populations that fail to produce enough young to compensate for adult mortality (possible population sinks) (Pulliam 1988). Gates and Gysel

(1978) suggested that birds perceive these edges as adequate nesting sites due to food availability, cover and structure, whereas they are unable to assess the increased risk of predation. Consequently, less than ideal habitats are more attractive than ideal habitats, and are inversely related to nest success (Misenhelter and Rotenberry 2000). Ecological traps can occur in natural systems, but are mostly common in anthropogenically altered landscapes (Gates and Gysel 1978). For example, birds may be attracted to vegetation that develops along the boundary between field and forest habitat, but may suffer substantial nest losses due to predators or brood parasites, whose activities may be concentrated along these edges. Misenhelter and Rotenberry (2000) suggested that it is not an animal’s innate preference that changes, but rather the correlation of cues with expected outcomes; instead of being linked with positive outcomes, those cues are now linked with negative ones. Consequently, ecological traps have the potential to enhance adverse effects of edges in fragmented forest landscapes (Temple and Cary 1988).

Predators also perceive abrupt edges as barriers, because movement across the edge is difficult (Stamps *et al*. 1987). As a consequence, predators can become habitat specialists, as they are restricted to only one habitat tyM. An edge related increase in predation rate is therefore expected to be confined to only a narrow band. On the other hand, soft edges can allow the movement of predators between two different habitats (Stamps *et al.* 1987). Thus, the edge related increase in predation rate is expected to occur on both sides of the edge.

A number of variables can explain the general lack of difference in predation rates between habitat edge types. For example, similar sized prey could not always be used, however, the size range was not great and those eaten (or lack thereof) showed no size-dependent pattern. Due to the lack of predation, however, I suggest that the prey used were too large for the predators to pursue and consume. Previous research has established that prey size selected will increase as the size of the predator increases (Vince *et al.* 1976), suggesting that the predators selected for this experiment were too small to prey on *P. pelagicus*. Physical conditions (e.g. temperature) have also been shown to influence predation rates in aquaria (Elliott and Leggett 1996). In this case, there seems to be a seasonal influence (ie. temperature) on *P. pelagicus* and *C. maenas* activity. During predation trials in autumn, both species were active predators, however, predatory activity declined towards the winter months. Predation rates have been shown to change on a seasonal basis. For example, Heck and Thoman (1981) showed that predation rates on crabs were higher in spring than in summer and varied considerably among prey taxa. Thus, this experiment needs to be repeated to determine whether temporal patterns in predation are consistent with seasons. Furthermore, to eliminate a biased outcome due to controlled variables, the experiments on the influence of habitat edge type on predation rates should be repeated in the field. Seagrass biomass across an abrupt and hard edge should also be sampled as complexity is expected to influence predation rates as a function of distance from the patch edge.

Tethering artifacts

The use of tethering for restraining prey in predation experiments has been examined in a large number of studies, with the general conclusion being that tethering may bias comparisons of relative predation intensity among different habitats (Peterson and Black 1994; Scheibling and Barbeau 1994; Zimmer-Faust *et al*. 1994; Kneib and Scheele 2000). Tethers have been shown to constrain movement of live prey or to interfere with the predators ability to carry away prey for consumption. Previous predation experiments have investigated habitat and tethering interactions in the laboratory (Scheibling and Barbeau 1994; Zimmer-Faust *et al*. 1994; Kneib and Scheele 2000). A limitation of laboratory trials using tethering to restrain prey is that aquaria themselves constrain movements and limit escape responses of untethered prey. Unless the size of aquaria reflect the natural range of movement of prey (e.g. Smith 1995), laboratory trials are likely to introduce an additional, uncontrolled bias in relative comparisons of predation intensity between different habitat types (Kneib and Scheele 2000). If tethering artefacts exist and are habitat specific, then individuals tethered in habitats where entanglement may decrease tether length should show a disproportional increase in relative mortality compared to those tethered in less complex habitats (see Heck and Wilson 1987; Aronson and Heck 1995). In the field, prey tethered at the furthest distance from the patch edge (2 m), where seagrass shoot densities are higher than edge densities, did not experience inflated predation potential relative to the edge. At the furthest distance from the patch edge prey survival was higher in seagrass than in sand. Predation rates also changed with distance from the edge in both habitats, suggesting that tethering artifacts were constant within each habitat. In aquaria, prey tethered in the seagrass habitat did not experience inflated mortality in comparison to the sand habitat. As a result, I believe that tethering artefacts have little effect on the interpretation of my lab and field results.

Conclusion

In summary, the results confirm that predation rates vary as a function of distance from the seagrass/sand edge. In particular, predation rates were distinctly different between sand and seagrass, suggesting that predators were not moving across the seagrass/sand edge. When there was no distinct change in predation rates at the edge, predators were suggested to be moving across both seagrass and sand habitats. The difference complies with the notion that predation rates are directly related to habitat structure. Changes in seagrass complexity are predicted to be positively correlated with the observed trend in predation. Before further predictions can be made regarding predation rates, seagrass biomass needs to be quantified during predation trials in the field. The dramatic increase in predation rates at 0.2 m in seagrass, suggests that predators perceive seagrass edges as favourable habitat. Further surveys need to be conducted to determine if this observed increase in predation at the edge is a consequence of increased predator abundance or a change in predator behaviour. However, predation rates did not vary with edge tyM. Further field research is needed to determine if habitat edge type and the corresponding seagrass biomass influences predator foraging behaviour. I suggest that the main mechanism creating the above patterns of predation is a change in habitat utilisation and foraging behaviour of predators in response to the spatial patterning of seagrass meadows. Thus, seagrass habitat fragmentation is likely to effect habitat selection and community composition of prey species.

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Chapter 9: Edge effects in fragmented seagrass meadows.

Jason E. Tanner

Abstract:

Increasing levels of habitat fragmentation in many systems have lead to an emphasis of research on the response of organisms to this process. Most studies have been carried out in terrestrial systems, however, where fragmentation is both ubiquitous and obvious. The effects of the fragmentation of marine habitats are less well known. Seagrass beds are often naturally fragmented, but are also being increasingly exposed to anthropogenically induced dieback and fragmentation. In this paper I examine how the characteristics of the faunal assemblage associated with seagrasses in the genus *Zostera* change as a response to the distance from the sand/seagrass boundary in areas subject to extensive small-scale fragmentation. Seagrass biomass changed gradually as a function of the distance from the patch edge, with maximum biomass occurring within about 1m of the edge. Belowground components of seagrasses were often present in what were considered to be sand patches, indicating that patches may be relatively ephemeral in nature. While patch edges were defined visually based on the presence of seagrass foliage, the presence of rhizome/root material outside the "patch" may have obscured edge effects for infaunal species. Epifaunal assemblage composition tended to change significantly as a function of distance from the edge, with greater abundance and taxon richness in seagrass than in sand. There were few effects for infauna, however, with assemblages in seagrass being very similar to those in sand. When differences between habitats were found, there tended to be a direct change from one habitat to the other, without the formation of a unique edge assemblage. Thus the edge effects are purely matrix effects, and are not due to emergent processes operating at the patch edges.

Introduction:

The response of biological systems to habitat fragmentation has become a major concern in ecology (e.g. Quinn & Harrison 1987; Golden & Crist 1999; Bolger *et al.* 2000; Debinski & Holt 2000). This concern has been driven by the increasing levels of habitat loss and fragmentation caused by human activity (e.g. Edyvane 1999; Sih *et al.* 2000), although many habitats are also naturally fragmented (e.g. Duarte & Sand-Jensen 1990; Aguiar & Sala 1999). Much of this research effort has focussed on the consequences of fragmentation in terrestrial habitats, and relatively little attention has been paid to marine systems (but see Bologna & Steneck 1993; McNeill & Fairweather 1993; Frost *et al.* 1999; Bowden *et al.* 2001). Many marine species, especially those that live in inshore areas, are increasingly having to deal with fragmented habitats (Neverauskas 1987; Bowden *et al.* 2001). The consequences of habitat fragmentation may be inherently different in marine versus terrestrial systems, however, because of differences in some of the major ecological processes structuring them. For instance, while terrestrial animals tend to disperse as adults or subadults, marine animals often disperse in the plankton as eggs or juveniles (e.g. Scheltema 1986; Palmer *et al.* 1996), potentially resulting in greater connectivity between sub-populations. Conversely, because such dispersal is largely passive, sub-populations located in close proximity to each other may be poorly connected if local hydrodynamics are not favourable (e.g. Shepherd & Brown 1993). Thus we cannot extrapolate the existing body of knowledge on the consequences of habitat fragmentation in terrestrial systems to their marine counterparts.

One important aspect of fragmented habitats that has received considerable attention is the role of habitat edges in influencing both species abundance and ecological processes, especially predation (e.g. Murcia 1995; Laurance 2000; Heliölä *et al.* 2001). Although unfragmented habitats have edges, as the level of fragmentation increases, the proportion of the habitat that is edge also increases (Murcia 1995; Ranta *et al.* 1998). For many years it was considered that edges were areas of high biodiversity and productivity due to the mixing of biotas from two separate habitats (e.g. Fox *et al.* 1997; Davies-Colley *et al.* 2000), and they were thus considered favourably, especially from a game management perspective (e.g. Leopold 1933). More recently it has been realised that edges may also have negative influences on some species, being sites of increased predation risk (Paton 1994; Flaspohler *et al.* 2001) and for invasion of exotic species (Fox *et al.* 1997; Harrison 1999). The ecological processes associated with edges may thus differ from those in interior habitats (Fagan *et al.* 1999). Those species requiring interior habitat, in particular, respond negatively to edges, and can be greatly endangered by increased levels of habitat fragmentation (Wilcove 1985; Yahner 1988; Fox *et al.* 1997). Thus from a conservation perspective, habitat edges are generally regarded negatively.

Species abundances (or any other measure of interest) can change in response to an edge in several ways (see Lidicker 1999). Firstly, the edge may be unimportant, with no difference in abundance on either side. Secondly, there may be a direct change from the abundance in one habitat, to that in the other, which can occur either gradually or abruptly at the edge, depending on how sharply the two habitats are divided. This type of edge response has been termed a matrix response (Lidicker 1999), and is due to organisms responding purely to changes in the habitat. In some cases an abrupt change from one habitat to another, with no response in either habitat due to the proximity to the edge, has been defined as no edge effect (e.g. Summerson & Peterson 1984). Alternatively, there could be emergent processes occurring at the edge, which cannot be predicted from the organism's response to the habitats on either side. In this case abundance may change asymmetrically about the edge, or may be elevated above or depressed below that of either habitat at the edge. Such responses have been termed ecotonal effects (Lidicker 1999).

Matrix effects are likely to be predominantly mediated by responses to physical factors such as microclimate or habitat structure. It is well known that microclimate can vary greatly across a forest edge, and can play a large role in determining biotic responses to the edge (Laurance *et al.* 1998; Baldi 1999; Davies-Colley *et al.* 2000). Similarly, in seagrass meadows hydrodynamics change as a function of the distance from an edge (Fonseca *et al.* 1982), with likely consequences for both the seagrasses and their associated fauna. Ecotonal responses, on the other hand, are probably largely due to biotic interactions, such as enhanced predation or competition, which may occur along the edge (e.g. Heck & Orth 1980, Paton 1994).

One marine habitat that is often fragmented is seagrass meadows. While many areas of seagrass are naturally fragmented, their location in shallow coastal waters exposes them to a large degree of human disturbance, which frequently leads to habitat loss and increased levels of fragmentation (e.g. Neverauskas 1987; Walker & McComb 1992; Edyvane 1999; Frost *et al.* 1999). In this study, I examine the response of seagrass fauna to edges in locations subjected to small-scale habitat fragmentation which is thought to be predominantly natural. I concentrate here on the infauna (those organisms living in the sediment), and smaller epifauna (those that live amongst the seagrass leaves), rather than on larger species such as fish. I am predominantly interested in how the faunal assemblage changes as a response to distance from the edge of a seagrass patch in shallow intertidal areas that are a mosaic of seagrass and sand. It is well documented that there are substantial differences in most groups of fauna between seagrass and sand areas (e.g. Stoner 1980; Lewis 1984; Peterson & Black 1986; Edgar 1990), but there have been few studies which have looked at how the fauna change as a function of the distance from the edge of these two habitat types. One of these examined the response of fish assemblages (Ferrell & Bell 1991), and found that total abundance in seagrass was similar to that over sand close (10 m) to seagrass, but was substantially higher than over sand distant (100 m) from seagrass. The other looked at responses of infauna to distance from a sand/seagrass edge, and found that while the assemblage differed between the two habitats, there were no other effects of the edge on a scale of 1-15 m (Summerson & Peterson 1984). Conversely, Bowden *et al.* (2001) found distinct differences in the assemblage structure of infauna and small epifauna between the centre of patches and the edges.

Methods:

To examine the influence of distance from patch edge on both seagrass biomass and the composition of the associated faunal assemblage, a series of transects were laid out at three sites in Gulf St Vincent, South Australia. At all sites, areas of *Zostera muelleri* or *Z. macronuta* located slightly (~5-10 cm) below the level of the lowest predicted low tide were sampled along seven individual transects. Each transect was 4 m long, and extended from a sand patch into a seagrass patch perpendicular to the boundary between the habitats. Transects were limited to 4 m in length due to the small-scale patchiness of the habitat studied, and the requirement that the ends of the transect be > 2 m from the opposite edge. Sediment cores were taken at 9 locations along each transect; at the boundary between seagrass and sand, and at 0.25, 0.5, 1 and 2 m from the edge in each direction. Cores were taken with a length of PVC pipe (88 mm internal diameter) to a depth of 20 cm, and immediately sieved on a 1 mm mesh screen before being preserved in formalin. All motile fauna remaining were later removed from the sample and identified to family when possible. Seagrass was divided into above and below ground components and dried to constant weight to determine the biomass of each component. Barker Inlet was sampled on the 31st January and 1st February 2000, Price on the 28th & 29th February and Edithburgh on the 27th & 28th March. Although this sampling protocol confounds sites with time, it does not intend to make a strict comparison between sites but rather to examine the generality of any patterns. For ease of terminology comparisons between sites/times are referred to as site comparisons.

The variation in seagrass biomass (above-ground, below-ground and total) with distance from edge was examined using Generalised Additive Models (GAM - Hastie & Tibshirani 1990) assuming a normal distribution. GAM is a regression technique that fits a non-linear smooth curve to the data. The shape of this curve is defined by the data, rather than pre-defined by the analyst. Models were fit for each site separately with Splus (Math-Soft Inc., Seattle) using cubic splines with 4 df. Transect was included as a factor in these analyses to account for any small-scale variation between transects, resulting in an analysis analogous to a 1-way ANCOVA but with a non-linear fit for the covariate. If the non-linear component for seagrass biomass was not significant, it was replaced by a linear term, resulting in a generalised linear model (GLM - McCullagh & Nelder 1989).

To determine if the composition of the faunal assemblages differed with distance from the patch edge, a non-parametric MANOVA (NPMANOVA -

Anderson 2001a) was used. Because only 1 replicate core was taken at each distance on each transect, distances were initially grouped as sand (-0.5, -1 & -2 m), seagrass (0.5, 1 & 2 m) and edge (-0.25, 0 & 0.25 m) to determine if there was any interaction between distance and transect. Sites were analysed separately as there were substantial interactions between distance and transect, and distance and site, when all 3 sites were included in a single analysis. There were no interactions between distance and transect for individual sites, so analyses were subsequently conducted with the 9 individual distances as separate levels of the factor distance. The resultant analyses were 2-way NPMANOVAs, with transect being treated as random, and distance fixed. Bray-Curtis similarities were used to quantify the differences between samples as this measure does not give any weight to joint absences, and data were 4th root transformed to reduce the influence of abundant taxa. Significance probabilities for each factor were calculated using 4999 permutations of the residuals under a reduced model, as per Anderson (2001a, b). If the assemblages responded to distance, individual distances were compared using a-posteriori pairwise tests, again with 4999 random permutations of the data to calculate probability values for each pair (Anderson 2001a). As the faunal assemblage could be divided into several components that were expected to respond differently to the patch edge, analyses were conducted separately for Polychaetes (the dominant component of the infauna), Other Infauna, and Epifauna (which included some taxa with both infaunal and epifaunal representatives).

The assemblage level effects of proximity to an edge were further examined by determining how total faunal abundance and taxon richness for each of the above groups varied with distance. GAM was used with both distance from the edge and seagrass biomass as continuous variables, and transect as a factor (i.e. a 1-way ANCOVA design with two non-linear covariates). The model was fitted using a poisson distribution as all response variables were counts. To determine if above-ground, below-ground or total seagrass biomass provided a better fit to the data in each case, models were examined with each of these measures of biomass and the best selected for further analysis. As I was primarily interested in the response to distance from the patch edge, which is not independent of seagrass biomass, the importance of the later was determined only after distance had already been introduced into the model (i.e. the question being asked is does seagrass biomass have any influence on the assemblage independent of distance). If the non-linear component in any model was non-significant, it was replaced by a linear fit, with the resultant model then compared to a model without the term to determine its importance (using analysis of deviance, Hastie & Tibshirani 1990). Similar analyses were conducted for the most abundant taxa at each site (abundant being defined as those taxa that occurred in more than one third of the samples at the site), although for brevity only results for Edithburgh are presented.

Results:

Seagrass biomass tended to respond smoothly with distance from the patch edge, rather than abruptly increasing from zero to maximum density at the edge (Fig 9.1, Table 9.1). At all three sites, below-ground biomass was present for at least some distance into the sand patches, suggesting that patch locations may be transient (at least when patches are defined by the presence of seagrass leaves), and that for infauna patch edges were not as distinct as they appear to human observers. Above-ground components of the seagrass were, however absent (or almost so) at all distances in the sand patches. Most of the variation in total and below-ground seagrass biomass occurs within 1 m of the edge, with the response being almost linear in this region. Changes in above-ground biomass occur over a smaller spatial scale, from about 0.25 m into the sand patch to 0.5 - 1 m into the seagrass patch. Samples 1 & 2 m from the edge in each direction showed little difference from each other for any component.

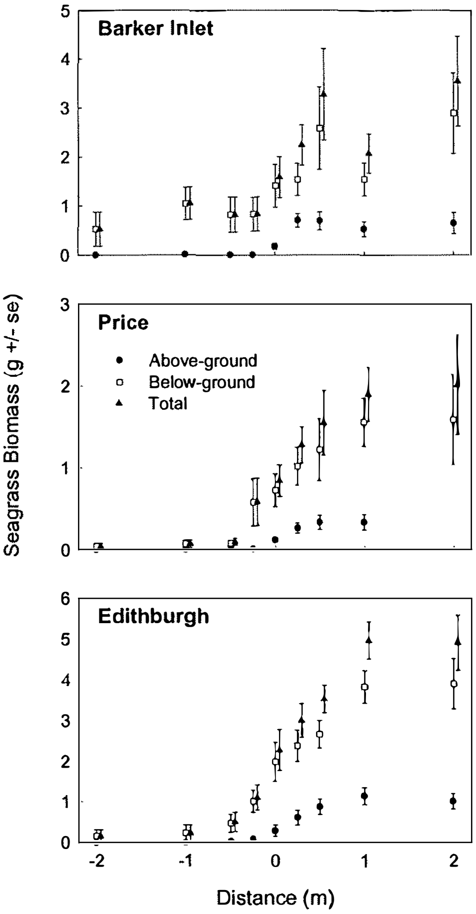

Figure 9.1: Seagrass biomass (dry weight) as a function of distance from the sand/seagrass boundary (negative distances are in sand, positive in seagrass)

Table 9.1: GAM results for variation in total seagrass biomass as a function of distance from patch edge.

	df	dev	F	P[a]	P (nl)[b]
Barker Inlet					
Transect	6	16.8	1.43	0.22	
Distance	1	45.1	23.07	<0.001	0.14
Residual	54	105.5			
Price					
Transect	6	10.8	4.65	<0.001	
Distance	4	36.4	16.9	<0.001	0.014
Residual	50	19.3			
Edithburgh					
Transect	6	22.1	4.90	<0.001	
Distance	4	204.1	48.27	<0.001	<0.001
Residual	52	39.2			

a. Probability that the term is significant with the given df (df = 1 specifies a linear fit, df = 4 a non-linear fit). b. Probability that the term is non-linear.

Table 9.2: NPMANOVA results for effects of seagrass edge on faunal composition.

	Barker Inlet			**Price**			**Edithburgh**		
	SS	F	P	SS	F	P	SS	F	P
Polychaetes									
Transect	2.54	7.38	0.0002	1.06	2.21	0.003	2.54	1.68	0.013
Distance	0.63	1.37	0.13	0.99	1.42	0.085	3.68	1.82	0.002
Residual	2.76			3.84			12.16		
Other Infauna									
Transect	0.76	8.43	0.0002	0.85	3.08	0.011	0.62	2.20	0.054
Distance	0.15	1.29	0.27	0.63	1.71	0.10	0.38	1.01	0.48
Residual	0.72			2.21			2.27		
Epifauna									
Transect	2.32	2.04	0.019	1.77	1.94	0.037	1.72	1.32	0.24
Distance	3.98	2.62	0.0006	1.82	1.50	0.099	2.81	1.62	0.049
Residual	9.11			7.27			10.40		

The response of the faunal assemblage to patch edges was more variable, depending on both the faunal group and site (Table 9.2). Polychaete assemblages only responded to the edge at Edithburgh, although there are indications of a possible response at Price (there was a significant difference between sand, seagrass and edge when distances were grouped ($P = 0.014$), with pair-wise tests indicating sand and seagrass were different ($P = 0.0006$)). Pair-wise comparisons for Edithburgh indicated that -2 m (sand) differed from all other distances, and that there were significant differences between just outside the seagrass (-0.25 m) and just inside (0.25 & 0.5 m). There was substantial variability at the transect level at all sites. There was no difference in the Polychaete assemblage between sand and seagrass habitats at Barker Inlet, which is the only site where seagrass root and rhizome material is present in abundance at all distances into the sand patches. The composition of Other Infauna did not show a response to patch edge at any of the sites, and behaved as though sand and seagrass were a single habitat, although again there was substantial variability at the transect level. Epifaunal composition, on the other hand, responded to the patch edge at both Barker Inlet and Edithburgh, with some slight indication of an edge effect at Price. Again the differences at Price were clearer when distances were grouped ($P = 0.006$), with sand being different from edge ($P = 0.003$) and seagrass ($P = 0.025$), but edge and seagrass being the same ($P = 0.47$). At Barker Inlet, all distances in sand (and the edge itself) were different from all distances in seagrass, but both of these groups were homogenous (pairwise comparisons, $\alpha = 0.05$), indicating an abrupt transition between assemblages. Differences were less clearly related to seagrass presence/absence at Edithburgh, where only the 1 m (seagrass) samples differed from all sand samples, as well as the edge and 0.5 m seagrass samples. Analysis with distances grouped, however, did indicate a difference in epifaunal composition between sand and seagrass ($P = 0.004$), but neither group differed from the edge ($P = 0.15$ & 0.13 respectively).

Total Polychaete abundance only varied slightly as a function of distance from the edge, although this was significant at all three sites (Table 9.3, Fig 9.2). The strongest response was obtained at Edithburgh, where abundance declined linearly from the sand patch into the seagrass patch. However, distance accounted for less than 10% of the variation in abundance for each site, and thus probably has little biological meaning. There was also a relationship between abundance and seagrass biomass at all three sites, with abundance decreasing as seagrass biomass increased at both Barker Inlet and Price, while it increased at Edithburgh. Again, however, seagrass biomass accounted for less than 10% of the variation in abundance at all sites. The number of families of polychaetes was not influenced by distance at any site, although it did increase slightly with total seagrass biomass at Edithburgh (Table 9.3, Fig 9.3). The only family present in at least 1/3 of samples at Edithburgh was the Capitellidae, which decreased linearly from sand to seagrass, but conversely increased with seagrass biomass (Table 9.4, Fig 9.4).

The abundance of Other Infauna was also weakly but significantly related to both distance and seagrass biomass (Table 9.3, Fig 9.2). At Edithburgh, there is some indication of an increase in abundance at the edge, with responses at the other two sites being variable. The clearest relationship with seagrass biomass was with below-ground biomass at Price, with abundance increasing as seagrass abundance increased. Taxon richness in this group only varied with distance at Price (Table 9.3, Fig 9.3), with richness increasing from sand to seagrass. Again only a single taxon, the bivalve family Solemyidae, was present in more than a third of samples at Edithburgh, with the only significant relationship being a variable response to seagrass biomass (Table 9.4, Fig 9.4).

Epifauna tended to show stronger responses to distance from the edge and seagrass biomass than the preceding two groups of fauna. Again total abundance varied with both distance and seagrass biomass at all sites (Table 9.3, Fig 9.2). A strong response in epifaunal abundance was detected at Edithburgh, with an increase between 1 m into the sand patch and 0.25 m into the seagrass patch. At Barker Inlet, abundance increased moving from sand towards the edge, then stayed relatively constant. Price showed a similar although weaker pattern. The response to seagrass biomass was variable at all three sites. Epifaunal taxon richness also showed strong responses to distance, although it was unrelated to seagrass biomass (Table 9.3, Fig 9.3). There was a linear increase in taxon richness moving from sand to seagrass at Price, while the increase at the other 2 sites occurred predominantly within 0.5 - 1 m of the edge. There is some indication that richness continues to decline in sand at Barker Inlet at the furthest distance from the edge sampled (2 m), and that there is also a decline at the furthest distance into seagrass sampled at Edithburgh. The only individual taxon abundant enough to analyse at Edithburgh was the Gammaridea, which showed a strong response to the edge, although they declined in abundance as seagrass biomass increased (Table 9.4, Fig 9.4).

Table 9.3: GAM results for influence of distance from patch edge and seagrass biomass on total abundance and taxon richness.

	Barker Inlet				**Price**					**Edithburgh**				
	df	Dev	P[a]	P(nl)[b]		df	Dev	P[a]	P(nl)[b]		df	Dev	P[a]	P(nl)[b]
Polychaete Abundance														
Transect	6	3765.5	<0.001		Transect	6	30.8	<0.001		Transect	6	45.1	<0.001	
Distance	4	399.9	<0.001	<0.001	Distance	4	21.6	0.0002	0.004	Distance	1	5.7	0.017	0.17
SG (A)	4	235.2	<0.001	<0.001	SG (T)	4	28.9	<0.001	0.036	SG (T)	1	15	0.0001	0.30
Residual	47	1254.5			Residual	47	146.4			Residual	54	93.1		
Polychaete Richness														
Transect	6	60.5	<0.001		Transect	6	20.3	0.0025		Transect	6	25.2	0.0003	
Distance	1	1.36	0.24	0.81	Distance	1	0.12	0.72	0.88	Distance	1	0.61	0.44	0.35
SG (T)	1	2.67	0.26	0.78	SG (T)	1	0.29	0.59	0.92	SG (T)	1	7.5	0.006	0.55
Residual	53	22.6			Residual	53	15.9			Residual	54	48		
Other Infauna Abundance														
Transect	6	2757	<0.001		Transect	6	94	<0.001		Transect	6	215.7	<0.001	
Distance	4	15.3	0.004	0.01	Distance	4	29.2	<0.001	0.004	Distance	4	106.7	<0.001	<0.001
SG (B)	4	157	<0.001	<0.001	SG (A)	4	26.2	0.0002	0.048	SG (T)	4	6.4	0.18	0.037
Residual	47	171.8			Residual	46	106.1			Residual	48	241.8		
Other Infauna Richness														
Transect	6	4.23	0.65		Transect	6	1.71	0.94		Transect	6	2.83	0.83	
Distance	1	0.95	0.33	0.93	Distance	1	5.34	0.02	0.69	Distance	1	0.44	0.51	0.87
SG (A)	1	0.79	0.67	0.85	SG (A)	1	0.13	0.72	0.67	SG (T)	1	0.05	0.82	0.88
Residual	53	7.07			Residual	53	14.88			Residual	54	14.56		
Epifauna Abundance														
Transect	6	1065	<0.001		Transect	6	82.8	<0.001		Transect	6	8.86	0.18	
Distance	4	283.5	<0.001	<0.001	Distance	4	82.9	<0.001	0.011	Distance	4	49.38	<0.001	<0.001
SG (T)	4	283	<0.01	<0.001	SG (A)	4	32.2	<0.001	<0.001	SG (T)	4	16.77	0.002	0.005
Residual	47	639.2			Residual	46	197.8			Residual	48	88.9		
Epifauna Richness														
Transect	6	22.8	0.0009		Transect	6	8.4	0.21		Transect	6	0.39	1	
Distance	4	54.5	<0.001	0.008	Distance	1	15	.0001	0.91	Distance	4	19.43	0.0007	0.0016
SG (T)	1	4.5	0.10	0.11	SG (T)	1	1.1	0.57	0.67	SG (T)	4	2.53	0.64	0.65
Residual	51	60.2			Residual	53	39.6			Residual	48	48		

a. Probability that the term is significant with the given df (df = 1 specifies a linear fit, df = 4 a non-linear fit). b. Probability that the term is non-linear. SG(A), SG(B) & SG(T) are above-ground, below-ground and total seagrass biomass respectively.

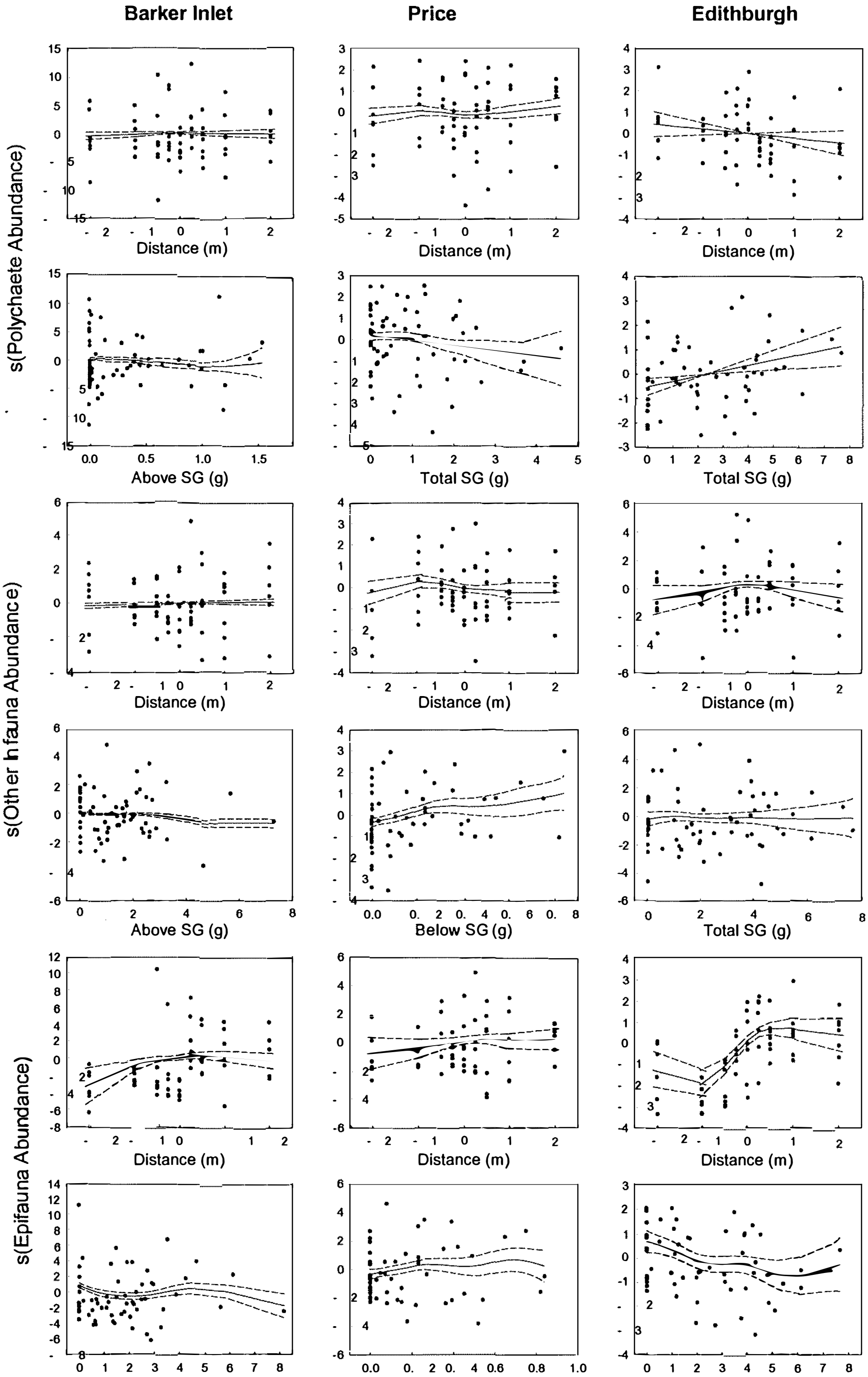

Figure 9.2: Response of faunal abundance to distance from the habitat edge, and seagrass biomass. The solid line indicates the GAM fit (statistics are presented in Table 9.3), and the dashed lines +/- 2 times the se. Plots are standardised, and centred to a mean of zero, with the y-axis representing standardised abundance for the taxon. Note that seagrass biomass can be either Total, Aboveground or Belowground depending on which explained the most variation in the dependent variable.

Table 9.4: GAM results for influence of distance from patch edge and seagrass biomass on abundance of individual taxa at Edithburgh (only those taxa for which at least one of these terms was significant are presented).

	df	Dev	P^a	$P(nl)^b$
Capitellidae				
Transect	6	17.79	0.0068	
Distance	1	6.04	0.014	0.086
SG (A)	1	5.28	0.022	0.77
Residual	54	92.85		
Solemyidae				
Transect	6	15.85	0.015	
Distance	1	0.01	0.93	0.48
SG (T)	4	12.66	0.013	0.002
Residual	47			
Gammaridae				
Transect	6	9.81	0.13	
Distance	4	19.18	0.0007	<0.001
SG (T)	1	7.8	0.005	0.065
Residual	51	80.5		

a. Probability that the term is significant with the given df (df = 1 specifies a linear fit, df = 4 a non-linear fit). b. Probability that the term is non-linear. SG(A), SG(B) & SG(T) are above-ground, below-ground and total seagrass biomass respectively.

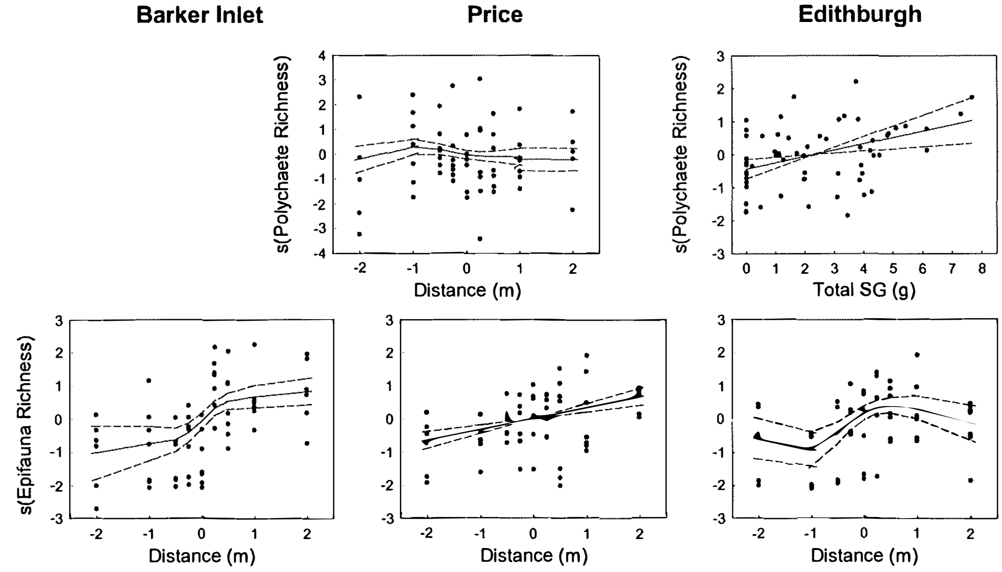

Figure 9.3: Response of faunal richness to distance from the habitat edge and seagrass biomass. Plots are only presented when the GAM (see Table 9.3), indicated that there was a significant association between the variables. See Fig. 9.2 for an explanation of the plots.

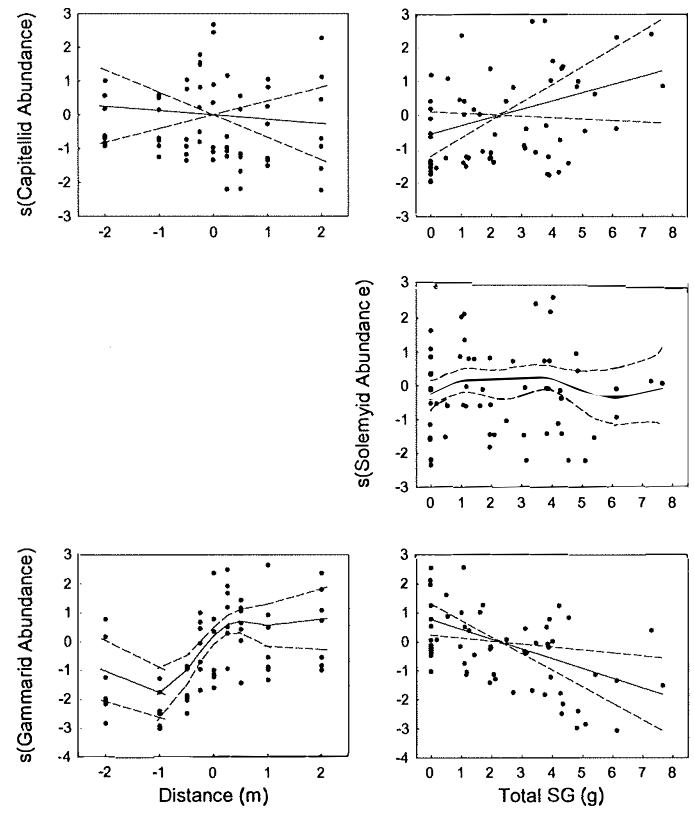

Figure 9.4: Responses of individual taxa to distance from the habitat edge and seagrass biomass at Edithburgh. Plots are only presented when the GAM (see Table 9.4) indicated that there was a significant association between the variables. See Fig. 9.2 for an explanation of the plots.

Discussion:

While there were distinct changes in seagrass biomass with distance from the patch edge, and concomitant changes in the epifaunal assemblage, there were surprisingly few changes in the infaunal assemblage. Although the sampling method was not optimal for epifauna, the distinct differences between sand and seagrass were easily detected. These differences are likely to be directly related to changes in habitat structure, which plays an important role in decreasing predation pressure on many epifaunal species living in seagrass (Heck & Orth 1980; Lewis 1984; Peterson 1986; Hindell *et al.* 2000). Many species also preferentially select complex habitats (e.g. Lewis 1984; Bell & Westoby 1986; Levin *et al.* 1997). Increased habitat complexity interferes with both the ability of a predator to detect its prey, and capture success once detected (Main 1987; Gotceitas 1990, but see James & Heck 1994). Some species also respond to increased food availability in seagrass, rather than to its shelter function (Bologna & Heck 1999). It is generally thought that similar processes operate for infauna as well, with the root and rhizome mass of seagrasses affording a refuge from predation (Stoner 1980; Peterson 1982; Summerson & Peterson 1984), although increased sediment stability can also be important (Orth 1977). When both epifauna and infauna have been examined together, however, the differences between habitats were generally less distinct for infauna (e.g. Summerson & Peterson 1984; Lee *et al.* 2001).

Differences in infaunal assemblages between seagrass and sand have been examined in a large number of studies, with the overwhelming conclusion being that seagrass assemblages are both richer in species, and have a higher total abundance (e.g. Peterson & Black 1986; Edgar 1990), although the opposite has sometimes been reported (e.g. Decho *et al.* 1985). Many of these studies, however, sample sand assemblages at some considerable distance from the nearest seagrass (10's - 100's of m if not more), and few have explicitly looked at assemblages close to seagrass. Several studies have also found that infaunal abundance is correlated to seagrass biomass (Stoner 1980; Webster *et al.* 1998), although this is not always the case (Lewis 1984). Interestingly, when the effects of above- and below-ground seagrass biomass were differentiated, infaunal abundance and diversity responded to the above-ground component, and was not influenced by below-ground biomass (Webster *et al.* 1998). Similar results were obtained here for Polychaetes at Barker Inlet and Other Infauna at Price. Other Infauna at Barker Inlet showed a stronger response to below-ground biomass, similar to infauna in Hong Kong (Lee *et al.* 2001). In general, however, the response of infauna to seagrass biomass was of a similar magnitude as the responce to distance (Table 9.3). Faunal abundance and assemblage composition can also be related to the amount of detrital material (an important food source for many infaunal species) present in the sediment (Fitzhardinge 1983, Edgar 1990; Lee *et al.* 2001). Due to the close proximity of the sand samples to seagrass in the present study, it is possible that there were still substantial amounts of detritus present, even at the greatest distance from seagrass sampled. If this is the case, and infauna are responding predominantly to food availability rather than predation pressure, then abundance would not be expected to vary as strongly with distance from the habitat edge.

Edge effects may occur over larger spatial scales, and at the small scale examined here (2 m) there may be sufficient movement between sand and seagrass habitats to mask differences in predation rates. Nevertheless, Summerson & Peterson (1984) found substantial differences between seagrass and sand 1 m from the habitat edge, suggesting that movement at this scale is unlikely to mask such patterns. The later study also failed to detect any edge effects (other than a difference between sand and seagrass) at distances up to 15 m from the sand/seagrass boundary. More mobile species, such as fish, exhibit edge effects on the scale of 100's of m (Ferrell & Bell 1991), while in terrestrial forests they can occur over 10's of km (Laurance 2000). Several other studies have documented edge effects in seagrass, predominantly related to either physical processes, or proximity to reefal areas. Water flow decreases from the edge of a seagrass patch towards the interior, due to the baffling effect of the seagrass (Fonseca *et al.* 1982). Changes in hydrodynamics may be important in causing the difference in faunal assemblages between vegetated and unvegetated areas (e.g. Tegner & Dayton 1981 for kelp). If so, then faunal composition should also change with distance from the patch edge. Seagrass beds in close proximity to reefal areas can be subject to strong gradients in grazing and predation pressure with distance from the reef. For example, urchins may leave the shelter of the reef at night to feed in nearby seagrass beds, causing distinctive urchin halos (e.g. Ogden *et al.* 1973), and grazing by herbivorous fishes may also decrease with distance from the reef (Thayer *et al*. 1984). Edge effects have also been documented for sand/seagrass edges, with predation on scallops being higher along the habitat boundary than in either habitat (Bologna & Heck 1999). A similar process operates in terrestrial forests, where nest predation is sometimes found to be higher along the forest edge than in the interior (e.g. Donovan *et al*. 1997; Flaspohler *et al.* 2001). In contrast, Summerson & Peterson (1984) found predator abundance along sand/seagrass edges to be intermediate between sand and seagrass, suggesting that edges do not always promote predation. Infaunal communities in sand habitats have also been shown to vary as a function of distance from rocky habitat, over a scale of 10's of m (Posey & Ambrose 1994). At the Barker Inlet site, we have experimentally determined that predation pressure on decapods increases linearly from seagrass to sand along 4 m transects as used here (Chapter 8), indicating that predation is likely to play an important role in determining these patterns.

The most likely explanation for the general lack of a difference in the infaunal assemblage between sand and seagrass can be found by examining the patterns of seagrass biomass, especially below-ground biomass, presented in Fig 9.1. At Barker Inlet, where there were no differences in infauna, there was still a substantial amount of below-ground seagrass biomass at 2 m into the patch. Thus while from the perspective of the human observer there are distinct differences between sand and seagrass, these are mostly due to the above-ground component of the seagrass, which is likely to have little relevance to the infauna (but see Webster *et al.* 1998). At Price, where there was some suggestion of a difference (in abundance, but not assemblage structure), there is little, if any, seagrass present in the sand samples, but seagrass density is considerably lower than at the other sites in the seagrass samples. Thus there may be insufficient predator protection in seagrass areas to have a substantial affect on the infaunal assemblage. The greatest differences in infauna between seagrass and sand occurred at Edithburgh, where the difference in below-ground seagrass biomass between these habitats was greatest. Studies that have examined differences in both infauna and epifauna between sand and seagrass have also tended to find lesser effects for infauna (Peterson & Black 1986; Howard *et al.* 1989), presumably due to the already complex nature of their habitat.

The high below-ground seagrass biomass in sand patches at Barker Inlet suggests that seagrass patches in this location are ephemeral, with changes occurring either on a seasonal or longer term basis. It is known that *Zostera* does have a tendency to die back at the height of summer (February, Seddon *et al.* 2001), and this may already have commenced when sampling occurred. There may thus be a constant change-over between sand and seagrass, with insufficient time for the infauna to respond to changes in habitat before they are reversed, especially if the seagrass persists below the sediment surface. Stoner (1980) has documented that temporal patterns of change in seagrass biomass are not reflected in patterns of change in the infauna, suggesting that there is a time lag between when the habitat changes and when the fauna changes. If this lag is sufficiently long there may be no change in the fauna before the seagrass has regrown (see also Connolly 1994).

Even when distance had a highly significant effect on infaunal abundance (either total or for an individual taxon), the proportion of variance explained was generally considerably (and often an order of magnitude) less than that explained by transect. Thus there is a large amount of small-scale variation in infaunal abundance and composition which swamps any variation due to distance from the seagrass/sand edge, making the later factor of little biological importance. Posey & Ambrose (1984) also found a great deal of small-scale spatial variation in infaunal abundance, although this was less than the variation attributable to distance from a rocky reef. Few other studies have examined the levels of spatial variability in infauna associated with different factors, although Boström & Bonsdorff (1997) found abundance and species richness to be more variable in seagrass than sand. In contrast, Rainer (1981) noted that the infauna associated with seagrass displayed greater temporal stability than that associated with sandflats.

Overall, in these seagrass meadows with a large amount of small-scale patchiness in seagrass presence and absence, there are few responses of the infauna to habitat edges. Instead, there is a large amount of unexplained small-scale variability in the abundance and composition of the infauna, which makes those edge effects that were detected relatively trivial. Whether similar patterns occur in response to larger-scale patterns of fragmentation, where there is less opportunity for continual switching over time between seagrass and sand habitats, remains to be seen (although Summerson & Peterson 1986 did not pick up such larger-scale patterns). The response of the epifauna contrasts strongly with the infauna, however, in that they tended to show relatively strong edge effects on a scale of about 1 m from the edge. However, there was no real indication that distinctive edge associated faunas occurred, instead there was a gradation from the sand fauna to the seagrass fauna, which occurred over a distance of 1-2 m centred on the actual edge. The seagrass also showed a gradation between full sand and full seagrass over a similar scale. Thus at the small spatial scale studied, habitat fragmentation seems to have little influence on the infauna, and results in a simple loss of habitat (i.e. a matrix effect) for the epifauna.

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Chapter 10: Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities

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Abstract:

While there have been theoretical arguments supporting the importance of the shape and orientation of habitat patches for determining species abundances, there have been few empirical demonstrations that these processes actually operate. Instead, most field studies have focussed on the importance of patch area, isolation and edge effects. I demonstrate that passively dispersed seagrass epifauna respond to the shape and orientation of artificial seagrass patches when currents, the dispersal mechanism, are strong, but not when they are weak. Orientation is important because animals dispersing via tidally induced water currents move predominantly in a single direction, and thus patches oriented across the current intercept more potential colonists than do those patches oriented perpendicular to the current. Taxa that actively disperse, or that are relatively sedentary, are less affected by currents. Fish species that tend to use intertidal areas at high tide, however, were more abundant in patches perpendicular to shore (and parallel to the current), presumably because these patches offer the greatest amount of edge to animals undergoing tidal migrations.

Introduction:

Habitat fragmentation is becoming increasingly ubiquitous in most areas of the world, as human disturbance results in the removal of natural habitat (Forman and Godron 1986). As a result, once continuous tracts of habitat are replaced by a network of smaller patches of varying size, shape and orientation. It is generally accepted that smaller patches contain smaller populations of most species, and fewer species, than larger patches (Keough 1984, Bell et al. 1995, Bolger et al. 2000, Bowden et al. 2001, Davidson and Knight 2001), and that they favour species adapted to living along habitat edges (Leopold 1933, Paton 1994, Harrison 1999). Transient species may also have higher densities in smaller patches (Debinski and Holt 2000), due to the increased probability of encounter per unit area (Eggleston et al. 1999). Species richness can decrease in smaller patches because they contain fewer microhabitats, fewer species encounter them, and/or some species go extinct as they are unable to maintain a viable population size (Kunin 1997, Bevers and Flather 1999).

The influence of patch shape and orientation, however, are not so well understood. Early hypotheses suggested that compact habitat patches (i.e. circular) were likely to support more species and greater population sizes than elongate patches, as the probability of animals emigrating and being lost from the system was reduced (Diamond and May 1976, Bevers and Flather 1999). Later, it was realised that the converse could also apply, with elongate patches receiving greater numbers of immigrants than compact patches, especially if they were oriented across the flow of dispersing individuals (Hamazaki 1996, Keyser et al. 1998). Thus the influence of patch shape is determined by the interplay of extinction and colonisation processes, which can vary for different species and under different conditions. For example, extinction processes may be more important in established habitat, whereas colonisation processes are more likely to be important in newly created habitat (Game 1980). While theoretically important, it has been difficult to show for any species that elongate patches differ from compact patches in their colonisation potential. This difficulty may be related to the confounding of patch shape with orientation - elongate patches may only have higher population densities if they are oriented across the direction of dispersal. If little is known about dispersal direction, it becomes difficult to determine if elongate patches are likely to receive increased numbers of immigrants or not. Species for which dispersal is not directed may also show little response to patch shape/orientation.

Here, I examine how both patch shape and orientation affect colonisation of artificial seagrass patches by adults of a range of taxa. Dispersal in many marine organisms is strongly influenced by currents (Scheltema 1986, Palmer et al. 1996), and at many locations it is relatively easy to determine the direction of the prevailing currents and thus orient patches with respect to dispersal pathways. Patch orientation is potentially important in seagrasses, as there have been a number of reports of seagrass patches having a consistent orientation, either parallel to the prevailing wave direction, parallel to channel banks or parallel to moving sand waves (Duarte and Sand-Jensen

1990, Marba and Duarte 1995, Turner et al. 1999). Several terrestrial habitats also consist of patches oriented in a consistent direction, such as arid zone vegetation (Aguiar and Sala 1999) and crop weeds (Dieleman and Mortensen 1999). Thus patch orientation may play an important role at the landscape level and not just at the level of the patch.

Methods:

The effects of patch shape and orientation on colonisation of seagrass patches by mobile epifauna were examined using artificial seagrass units (ASUs). Patches were all 1m^2 in area, and were either square, elongate and parallel to the current, or elongate and perpendicular to the current (n=5). Each patch consisted of four square 0.25 m^2 ASU's constructed of black polythene builders plastic, intended to mimic the locally abundant *Zostera muelleri*. Each steel-framed unit contained six strands of artificial seagrass that were constructed by welding four 50 cm long sheets of plastic together at the base and slicing it into strands 5-6 mm wide. Each strand thus contained approximately 90-100 shoots of four 20 cm long leaves connected at the base. Total shoot density was thus about 2400 m^{-2}, which is consistent with moderate shoot densities at the study location (JE Tanner unpublished data). Patches were placed close to (5-10 m) natural seagrass beds in Barker Inlet, South Australia, on July 3rd 2000 and sampled using a 1 mm mesh size net on the 28th July, 14th & 29th August and 12th September 2000 (spring tide series, tidal range on each day was 1.58, 2.14, 2.19, & 2.04 m respectively). A second set of patches were placed out on the 10th November 2000, and sampled on the 24th November, 8th & 22nd December 2000, and 5th January 2001 (neap tide series, tidal ranges 1.99, 1.35, 1.08 & 0.35 m respectively). Note there is some overlap in tidal range between the two series as there was originally no intention to sample on a set tidal phase. At each sampling time, a single randomly chosen unit was sampled from each patch, with each unit only being sampled once. To preserve patch shape over time, sampled units were returned to the patch within approximately 5 min of removal. The target unit was first surrounded by a drop net to ensure that no fauna escaped, and then a scoop net was gently slid underneath both the ASU and the drop net, picking up the entire unit and its associated fauna. The unit was then shaken vigorously for 30 sec in water and a further 30 sec out of water to dislodge all fauna. Visual observations during the sampling process indicated that fauna did not move out of the ASU when it was approached for sampling, but rather retreated further into it.

After sampling, the fauna from each unit were preserved and later identified and enumerated in the laboratory. Identification was carried out to the lowest taxonomic level possible, generally species for decapod crustacea, fish and molluscs, and family for polychaetes and amphipods. Species level identification of these later groups was not possible because of the poor degree of taxonomic knowledge of these groups in southern Australia. Each of these taxonomic groups were analysed separately, due to the likely differences in their response to patch shape and orientation mediated by their greatly different life histories, dispersal abilities and general ecology (although there is also a great deal of variation within each group). In addition, a single analysis incorporating all taxa, including some not in the above groups, was carried out.

While the sampling design used is strictly a repeated measures multivariate design, ecological data are generally unlikely to meet the assumptions of parametric MANOVA (e.g. Anderson 2001), and analysing repeated measures data using the available nonparametric techniques is problematic. The alternative is to treat time as an orthogonal factor and use a standard 2-way MANOVA, which requires the assumption that the assemblage present in a given patch at time t+1 does not depend on what was present at time t. This assumption can only be tested for the entire assemblage using a repeated measures MANOVA, but can be tested for each individual taxon by correlating abundance at time t+1 with that at time t. Thus, for each taxonomic group analysed, the abundance in the five samples taken on a given date from a given patch type was correlated with the abundance found for the same patch on the previous sampling date. Permutation procedures (Manly 1991) were used to calculate significance probabilities by comparing the observed correlation coefficient to all 120 possible correlations that could be obtained by rearranging the data. Only 5 of 30 correlations were significant (at $\alpha=0.05$, with only 2 being significant if a Bonferonni correction is made), suggesting that in general, abundance at one sampling date was not related to abundance at the previous sampling date, allowing replicate samples from a patch over time to be treated as independent. Separate patches could not be established for each sampling date due to the excessive labour required to manufacture the ASUs.

To examine the influence of patch shape/orientation and sampling date on total abundance and richness of all taxa identified, Poisson GLMs (McCullagh and Nelder 1989) were used. The results presented here pertain only to the higher level taxonomic groups identified above (amphipods, decapods, fish, molluscs, polychaetes), but reflect those obtained for individual species or families. Changes in assemblage structure for the above groups were examined using NP-MANOVA (Anderson 2001), followed by canonical discriminant analysis to present the differences between groups visually. The data were 4th root transformed prior to analysis to reduce the influence of abundant taxa. NP-MANOVA is a permutation based procedure that does not rely on the assumption of multivariate normality. Bray-Curtis dissimilarities were used in the analysis, and probability values were obtained using 4999 permutations of the residuals under a reduced model (Legendre and Anderson 1999, Anderson 2001). While an analysis was also done on all taxa combined, it was expected that these different groups would respond differently to shape because of their different life-history strategies and characteristics.

Results:

There was a clear difference in the response of different taxa to patch shape and orientation when sampling was conducted during spring tides, when current speeds are high, with some taxa being most abundant in patches oriented either parallel or perpendicular to the current. Relatively mobile taxa such as amphipods showed the greatest response to patch shape and orientation (Table 10.1, Fig. 10.1). Total amphipod abundance was clearly greatest in patches perpendicular to the current over all sampling dates (Fig. 10.1), and this was also true for each individual family in the order (JE Tanner unpublished data). Square patches had marginally greater abundances than patches parallel to the current, although this varied somewhat with family. In contrast, the only other taxon to respond to patch type, fish, showed decreased abundance in perpendicular patches compared to either square or parallel patches (Fig. 10.1). Given that patches perpendicular to the current were also perpendicular to the shore, this pattern may be related to small-scale tidal migrations, with fish using the seagrass patches as refugia during low tides. Fish, being more powerful swimmers than amphipods, are less likely to rely on currents for dispersal to new patches.

These patterns in abundance during spring tides are reflected in the assemblage composition for amphipods, but not for fish (Table 10.2, Fig. 10.2), indicating that different amphipod taxa responded differently to shape, whereas all fish species responded similarly. Parallel and perpendicular patches differed significantly in amphipod composition, with square patches being intermediate between the two and not differing from either, lending support to the idea that it is the length of border perpendicular to the current that is important in determining abundance, and not simply patch shaM. These differences between shapes (and dates) are shown for spring tides in Fig. 10.2, where the perpendicular patches (solid shapes) are clearly separated from the parallel (hollow) and square (dotted) patches. The biplot indicates that most families contribute to these differences, and also that most (apart from the Corophidae and Ischyroceridae) become more abundant as the soak time increases. Conducting separate analyses on each taxonomic group is justified by the significant effect of shape on the overall assemblage (Table 10.2).

In contrast, groups with more limited adult dispersal, or which rely less on currents for dispersal, showed no response to patch shape or orientation, either for total abundance (Table 10.1, Fig. 10.1) or for assemblage composition (Table 10.2, Fig. 10.2). These groups were polychaetes, decapod crustaceans and molluscs. As an example, canonical discriminant analysis for decapods (Fig. 10.2) shows that during both spring and neap tides there is a separation between sampling dates, but none between patch types. The biplots also show much greater differences in response between individual taxa within the decapods than within the amphipods. This diversity reflects the greater diversity in dispersal modes and abilities within the group. For none of the groups examined was taxon richness related to shape (GLM, $p>0.05$ for all taxa).

Sampling conducted during neap tides, when current speeds were relatively low, resulted in different patterns emerging. Total abundance of amphipods was no longer related to patch shape or orientation, although fish are still influenced (Table 10.1, Fig. 10.1). Unlike during spring tides, however, during neap tides fish are more abundant in perpendicular patches than parallel. Polychaetes and molluscs also showed a significant shape effect during neap tides (Table 10.1, Fig. 10.1). The polychaete response was caused by a substantial reduction in abundance in perpendicular patches compared to square and elongate on one day only (with this pattern being shown by 10 of 13 families present).

Table 10.1. Effect of patch shape/orientation and sampling date on total abundance within each taxonomic group (results of GLM analyses with Poisson distribution).

			Spring tide sampling			Neap tide sampling		
Taxon	Source	df	Deviance	F	P	Deviance	F	P
All Fauna	Date	3	12121	48.60	<0.001	8772	13.27	<0.001
	Shape	2	1453	8.74	<0.001	158	0.36	0.70
	Date×Shape	6	253	0.51	0.80	1579	1.19	0.33
	Residual	47	3700			10339		
Amphipods	Date	3	11475	76.29	<0.001	4193	6.56	<0.001
	Shape	2	1534	15.30	<0.001	177	0.42	0.66
	Date×Shape	6	71	0.24	0.96	1215	0.95	0.47
	Residual	47	2312			9697		
Decapods	Date	3	359	22.90	<0.001	433	14.35	<0.001
	Shape	2	27	2.63	0.083	30	1.50	0.23
	Date×Shape	6	23	0.73	0.63	85	1.41	0.23
	Residual	47	287			461		
Fish	Date	3	39	12.03	<0.001	28	7.22	<0.001
	Shape	2	8	3.57	0.036	8	3.21	0.049
	Date×Shape	6	7	1.06	0.40	10	1.35	0.25
	Residual	47	55			71		
Polychaetes	Date	3	983	13.15	<0.001	4721	35.80	<0.001
	Shape	2	68	1.36	0.27	432	4.91	0.012
	Date×Shape	6	107	0.72	0.64	565	2.14	0.066
	Residual	47	1127			2217		
Molluscs	Date	3	476	33.15	<0.001	212	11.20	<0.001
	Shape	2	28	2.89	0.065	58	4.60	0.015
	Date×Shape	6	34	1.17	0.34	11	0.29	0.94
	Residual	47	255			354		

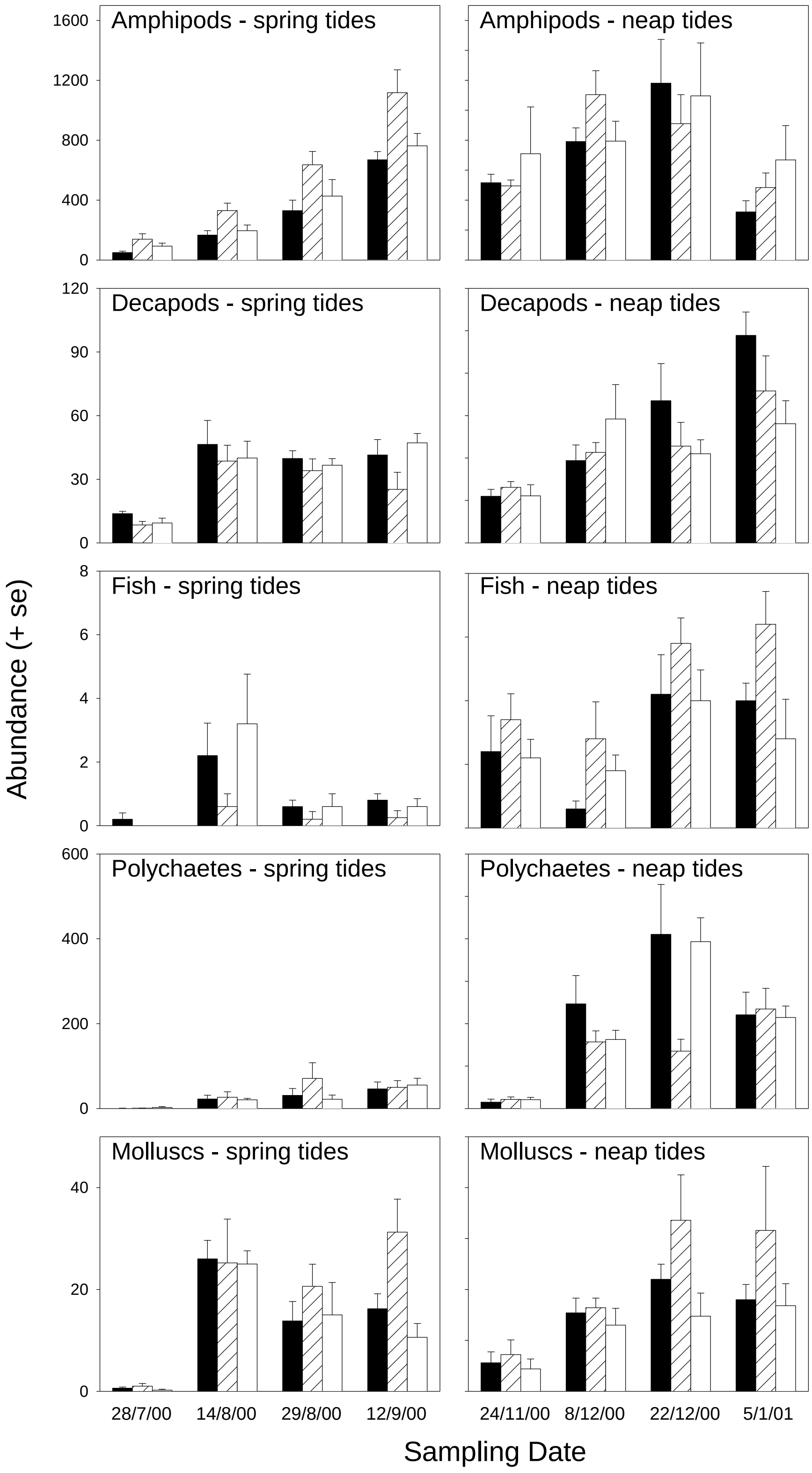

Figure 10.1. Patch shape influences on higher level taxonomic groups in artificial seagrass. Solid bars represent patches parallel to the prevailing currents, hatched bars perpendicular patches, and empty bars square patches. Amphipods and fish showed the strongest patch type effects (Table 10.1).

Mollusc abundance was consistently elevated in perpendicular patches, especially when tidal range was least, with this pattern due to the three most abundant species, all of which occurred as adults that would have colonised by benthic movement. Again, the other taxa showed no response to patch shape or orientation. These patterns in abundance were not always reflected in the composition of each group, however. Composition varied with patch type for both polychaetes and amphipods (Table 10.2), but there were no significant pairwise differences between patch types. There was still some separation present between patch types for amphipods (Fig. 10.2), especially during the first two sampling periods when the neap tidal range was greatest (1.99 & 1.35 m for census 1 & 2 respectively), but for the last two sampling periods patch types are intermingled (tidal range 1.08 & 0.35 m respectively). This adds further support to the hypothesis that the importance of patch shape and orientation are mediated by current speed. Again taxon richness was not affected for any group (GLM, p>0.05).

Table 10.2. Effect of patch shape/orientation and sampling date on assemblage composition within each taxonomic group (results of NP-MANOVA analyses).

			Spring tide sampling			Neap tide sampling		
Taxon	Source	df	SS	F	P	SS	F	P
All Fauna	Date	3	25810	14.71	0.0002	12307	14.53	0.0002
	Shape	2	1819	1.56	0.042	941	1.67	0.035
	Date×Shape	6	2676	0.76	0.89	1362	0.80	0.86
	Residual	48	28079			13551		
Amphipods	Date	3	11879	17.30	0.002	4462	11.14	0.0002
	Shape	2	1724	3.77	0.0026	607	2.27	0.03
	Date×Shape	6	311	0.23	0.997	498	0.62	0.90
	Residual	48	10987			6410		
Decapods	Date	3	29045	18.70	0.0002	6713	7.28	0.0002
	Shape	2	760	073	0.65	520	0.85	0.54
	Date×Shape	6	2666	0.86	0.64	1793	0.97	0.50
	Residual	48	24851			14763		
Fish	Date	3	38433	5.38	0.0002	17550	3.89	0.0012
	Shape	2	4575	0.96	0.41	7450	2.48	0.051
	Date×Shape	6	22094	1.55	0.10	12529	1.39	0.17
	Residual	48	114269			72112		
Polychaetes	Date	3	41860	7.36	0.0002	32018	14.79	0.0002
	Shape	2	5993	1.58	0.11	2848	1.97	0.021
	Date×Shape	6	14540	1.28	0.17	4655	1.07	0.36
	Residual	48	91017			34643		
Molluscs	Date	3	61665	14.24	0.0002	12072	2.77	0.012
	Shape	2	2430	0.84	0.52	2058	0.71	0.62
	Date×Shape	6	17230	1.99	0.017	5370	0.62	0.87
	Residual	48	69289			69640		

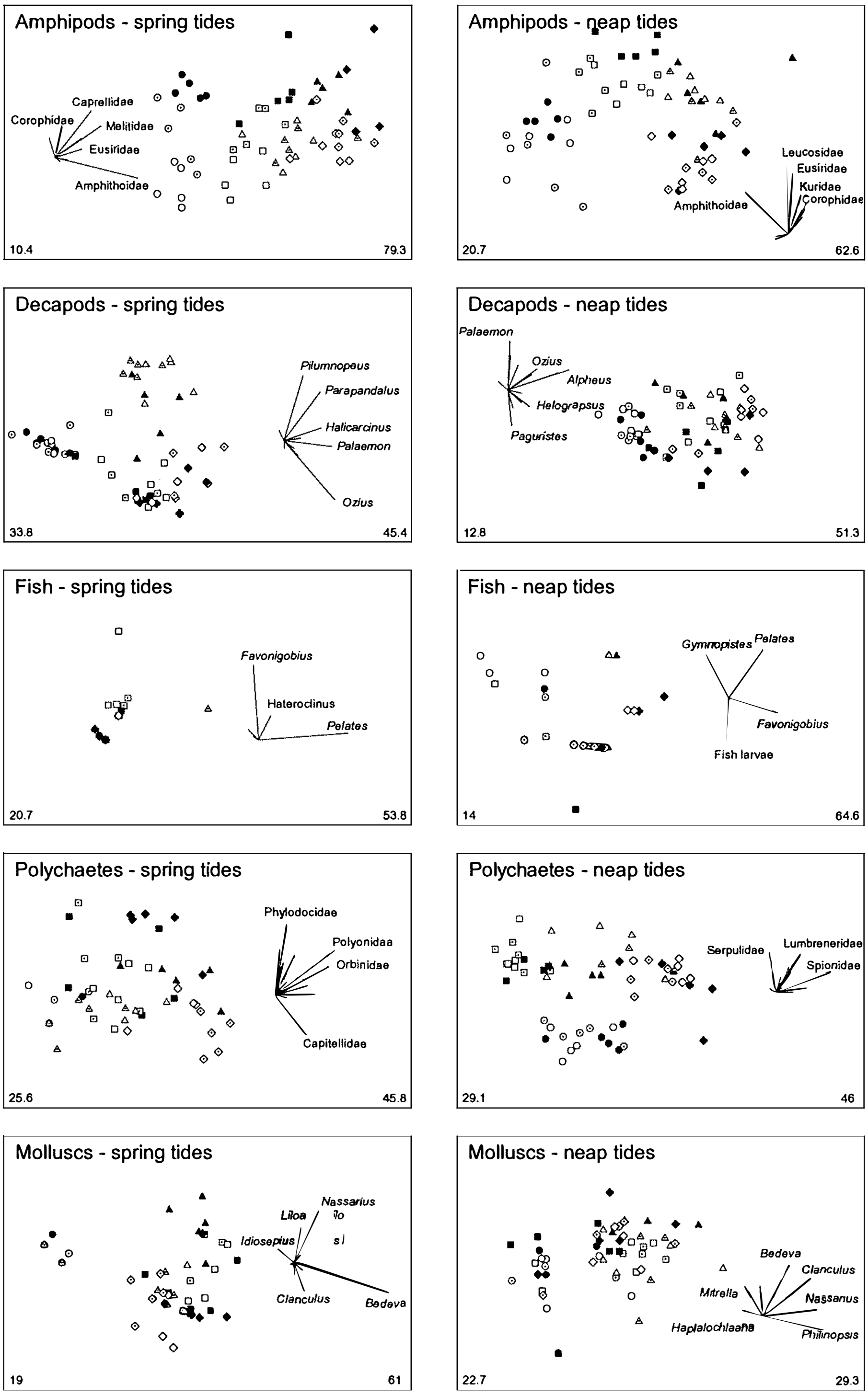

Figure 10.2. Canonical discriminant analysis showing the effect of patch shape/orientation on assemblage composition in artificial seagrass for the main higher level taxonomic groups present. While all plots show some separation between dates on the x-axis (○ - date 1; □ - date 2; △- date 3; ◇ - date 4), only amphipods during spring tides show consistent separation between patch types on the y-axis (hollow - parallel; solid - perpendicular; dotted - square). Numbers in the bottom right and left of each panel give the percentage of variation in the data represented by the x- and y-axes respectively. Biplots show taxa (families for amphipods and polychaetes, species for other taxa [only genus name given]) responsible for the greatest separation between samples. The length of each vector describes how important that taxon is in discriminating samples along the indicated direction.

Discussion:

Patch shape and orientation most clearly affected those groups with a high rate of movement over the spatial scale of the patches in this experiment. Thus amphipods, which have poor swimming ability, showed an orientation effect during spring tides but not neap. Fish also showed an orientation effect during spring tides, although this time it was related to movements between intertidal areas and subtidal refuges. During neap tides, this effect disappeared, and there is even a suggestion that fish movement is predominantly in the direction of the current when the tidal range is least.

Changes in the abundance of some species with changes in patch orientation could have flow-on effects to other species. Small seagrass patches act as refuges for juvenile American blue crabs (*Callinectes sapidus*) as they support lower abundances of conspecific adults, thus leading to reduced cannibalism (Hovel and Lipcius 2001). In another study (A Irving and JE Tanner unpublished data) we also show that there can be substantial priority effects in seagrasses, with early colonisation of a patch by some species altering the subsequent community structure of the patch. Thus, the responses of some taxa may not have been to patch orientation per se, but rather to changes in the abundance of other species.

The interaction between dispersal and patch orientation is not only important for marine animals. In a study of migrating birds, patches oriented across the migration pathway were found to support more species and higher nest abundances than patches oriented in other directions (Gutzwiller and Anderson 1992). Interestingly, patch shape per se had no influence, and neither shape nor orientation influenced resident species. Similarly, highly mobile millipedes are more abundant in elongate patches (regardless of orientation), presumably due to greater interception of animals moving in essentially random directions (Hamazaki 1996). In both of these studies, and that reported here, the importance of patch shape/orientation is related to the interception of highly mobile animals. Similarly, island orientation has been shown to be important for the interception of seaborne plant propagules (Buckley and Knedlhans 1986).

Spatial scale is likely to play an important role in determining how important patch orientation is for any given species. In all of the above studies, the patches studied were much smaller than the range of movement of the species of interest. If patches are larger than the movement range of a species, and there is little interpatch movement, then patch orientation will not influence interception and thus population size. In this case, other factors may come into play, such as edge effects, which could mean that compact patches have higher abundances than elongate patches (e.g. Bevers and Flather 1999, Helzer and Jelinski 1999, Golden and Crist 2000). Indeed Bevers and Flather (1999) found in their modelling study that elongate patches supported higher early population growth but smaller final population sizes than compact patches. Thus patch orientation will only be important when immigration plays a more important role than extinction in determining population sizes and community composition (Game 1980). The relationship of the patch to the surrounding landscape may also play an important role in determining how important orientation is. A single isolated patch may experience stronger effects than does a patch embedded within a mosaic of similar habitat where colonists are more likely to come from multiple directions.

The general trend emerging from empirical data is that patch shape and/or orientation can be extremely important in determining species abundances and community composition. Taxa responding to patch shape/orientation are usually highly mobile. Places where patch shape/orientation are important are those that intersect major dispersal pathways, or that are located in areas with a high degree of day to day movement. The times that patch shape/orientation are important are when dispersal is occurring and/or when there is a high degree of day-to-day movement between patches. Patch orientation can be particularly important when movement occurs predominantly in a single direction, such as exhibited by migrating birds or animals dispersing passively via water currents. So, in this study where colonisation was predominantly by adult individuals, orientation was most important for those taxa that enter the water column and have poor swimming ability, but only when currents were strong. Orientation was also important for more actively mobile species which do not rely on currents for dispersal (fish), but in this case it was patches oriented perpendicular to tidally induced movements that contained the highest densities.

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Chapter 11:Three decades of habitat change in Gulf St. Vincent, South Australia.

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Abstract:

Benthic habitats in Gulf St Vincent, South Australia, have changed considerably in the period between the 1960's and 2000/2001. Diver surveys in the 1960's indicated the presence of an extensive area of deep-water *Heterozostera* seagrass in Investigator Strait, and *Malleus-Pinna* assemblage in the south-eastern area of the gulf. Both of these habitat types were missing in remote video and diver surveys conducted in 2000/2001. In the central section of the gulf, the cover of bryozoans, and density of scallops, has also declined over the three decades between the two series of surveys. Further north, there have been fewer changes, with the original *Pinna* assemblages and seagrass meadows still being present. It is thought that these changes are primarily due to anthropogenic influences, with the two major candidates being increased turbidity (due to terrestrial inputs from sewage, stormwater runoff, agricultural runoff and dust storms), and direct damage from prawn trawling. As a consequence of these changes, the habitat complexity in Gulf St Vincent has been substantially decreased, with likely consequences for other fauna such as fish and mobile invertebrates.

Introduction:

While the effects of anthropogenic disturbance on many terrestrial systems are obvious and well documented, much less is known about what changes are occurring in marine systems, especially in waters deeper than a few metres. It is often thought that marine systems are stable, and little affected by change on a broad-scale, despite some well documented examples of change due to specific disturbances at smaller scales (e.g. Trawling: Jennings and Kaiser 1998; Hall 1999; Pollution: Neverauskas 1987; Lapointe *et al.* 1994; Sea Level Change: Seddon *et al.* 2000). This attitude is probably related to our inability to easily see what is happening on the ocean floor, and by the lack of long-term studies and baseline data on what systems looked like before human disturbance (or even in its early stages). While there is good evidence of change in some marine systems, such as seagrass loss (e.g. Walker and McComb 1992; Short and Wyllie-Echeverria 1996), including along the Adelaide metropolitan coast (Neverauskas 1987; Edyvane 1999), and changes in kelp abundance in the eastern North Pacific related to changes in otter abundance (e.g. Estes and Duggins 1995), there are few well documented studies that examine change in entire marine ecosystems over a period of decades. Most of those studies that have been done rely on the existence of earlier studies that utilised remote sampling techniques (such as benthic grabs) to examine infauna, or trawl gear to examine catches of fish and other macrofauna (e.g. Haedrich and Barnes 1997; Wilson *et al.* 1998; Frid *et al.* 1999, 2000).

Between 1964 and 1969, an extensive series of surveys of benthic habitats in Gulf St Vincent, South Australia, was carried out by divers who observed the intact habitat in situ, and recorded all the major components of the flora and fauna (Shepherd & Sprigg 1976). While these surveys were only qualitative, with few abundance estimates, a comprehensive map documenting the various community types in the gulf was published (reprinted here as Fig. 11.1). In this paper, I use this map to compare the major habitat features and benthic assemblages present in the 1960's, to those present in 2000/2001, with the aim being to determine if there have been any substantial changes in the intervening period. To do this I used an extensive series of remote video surveys, complemented by a number of spot dives to ensure that the information being obtained from the video was reliable. There have been no extensive benthic surveys carried out in Gulf St Vincent between these two studies, and thus it is only possible to speculate on the causes of any changes observed.

Gulf St Vincent is a large (~ 13000 km^2 including its approaches), relatively shallow, marine embayment located on the South Australian coast. It is an inverse estuary, with salinity being higher at the head of the gulf than at the mouth, due to high evaporation rates and low precipitation (Bye 1976). The location of Kangaroo Island across the mouth of the gulf also means that exchange of water with the open ocean is restricted, leading to long residence times of water within the gulf (de Silva Samarasinghe and Lennon 1987). This geography also means that the area is a low energy environment, especially in the northern section which as a consequence is slowly being filled in by sediment deposition. Most of the substrate is either sand or fine silt, with only a few areas of hard bottom (Shepherd and Sprigg 1976), although there are substantial areas of calcrete underlying much of the sand. The city of Adelaide (population > 1 million), is located on the eastern shore of the gulf, and is a source of considerable domestic and industrial pollution. There is considerable agricultural activity along the shores of the gulf, and in its catchment, which is a further source of pollution. The gulf also supports substantial recreational and commercial fisheries, including a small (10 boat) prawn fishing fleet which targets the western king prawn (*Melicertus latisulcatus*).

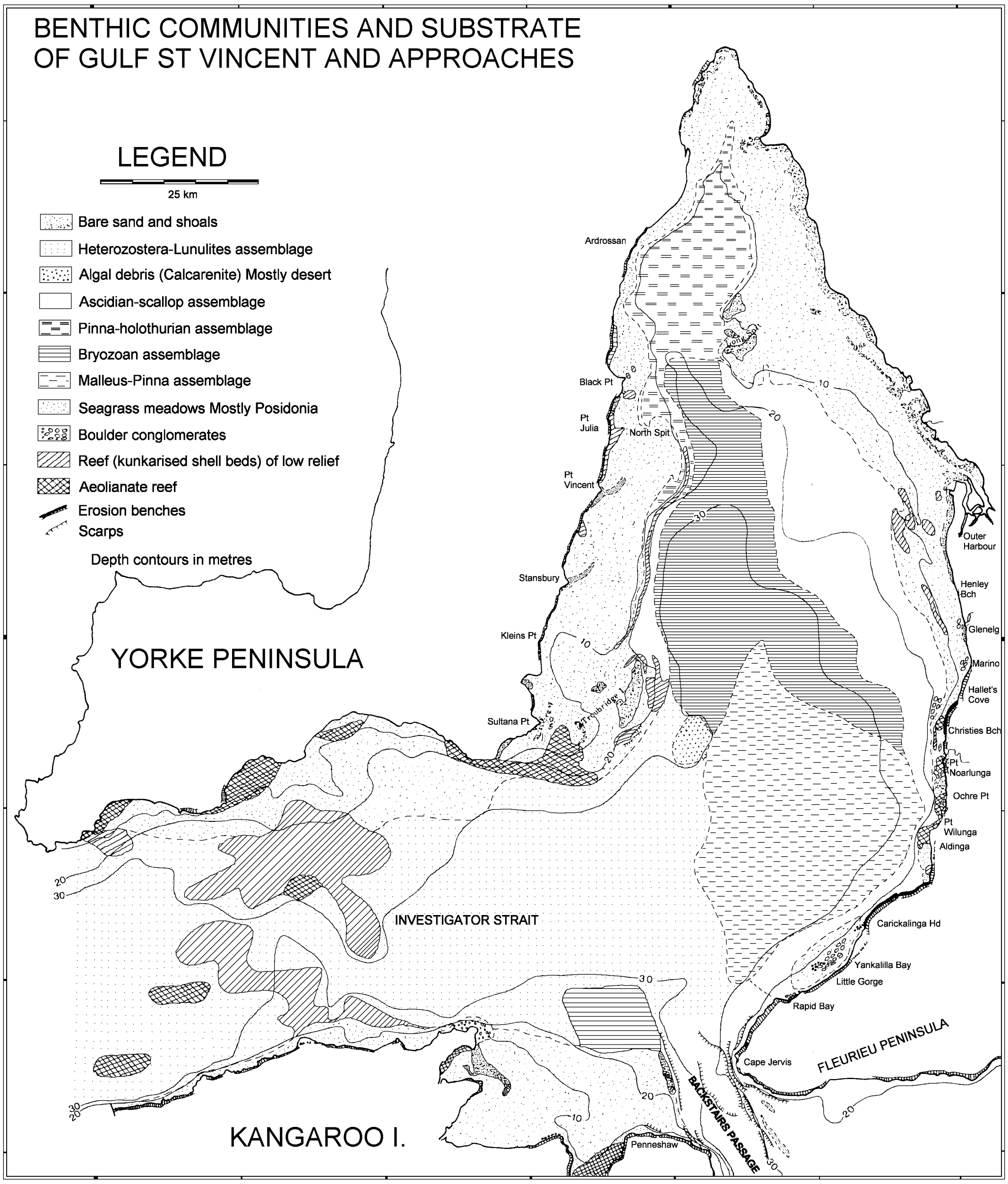

Figure 11.1. Benthic community composition in Gulf St Vincent in the 1960's as determined by diver spot surveys (reprinted with permission from Shepherd and Sprigg 1976, © Royal Society of South Australia).

The prawn fishery commenced in 1968/69, and effort reached a peak of 15200 hours of trawling in 1982/83, and a peak catch of 602 t in 1976/77, before dramatic declines in both catches (to 200-300 t yr^{-1}) and effort (~2000 hours yr^{-1}). During the early phase of the fishery, the northern portion of the gulf was heavily targeted (but south of $34^{o}30'$ S), but since the mid 1980's to early 1990's effort has predominantly focussed on more southern areas where the prawns tend to be larger (Morgan 1995). Due to the elimination of fishing from northern areas, there is concern in the industry that there has been a heavy build up of benthic invertebrates, especially bryozoans (known in the industry as "coral"). It has been suggested that this has caused a reduction in suitable habitat for prawns (which require areas of bare sand in which to burrow during the day), leading to a reduced population size and hence decreased catches. Thus a secondary objective of this study was to determine whether a build up of bryozoans has occurred, and if so whether there are likely to be any detrimental affects for the prawn population.

Methods:

To quantify the distribution, abundance and composition of benthic habitats throughout Gulf St Vincent, an extensive series of remote video surveys was conducted between June 2000 and June 2001. Survey sites were located every 2 nm on east-west transects across the gulf spaced every 5 nm (18 transects between $34^{0}15'$S and $35^{0}40'$S). Transects extended from the eastern to the western edge of the gulf (although areas less than approximately 5 m deep were inaccessible to the vessel used and therefore excluded). The western extremity of the survey area was $137^{0}40'$, and the easternmost point was $138^{0}30'$E. In total, data were obtained for 294 stations, with an additional three sites excluded from analysis because of poor image quality (see Fig. 11.2 for site locations). At each site, a digital video camera was lowered to within 1 m of the bottom, and left to record for 10 min while the boat drifted. To determine the linear distance moved during this time, a GPS was used to record the location (±10m) when a clear image of the bottom was first obtained, and again when it was lifted off the bottom. The mean distance covered per 10 min survey was 141±1 m (se).

Animal taxa visible in the video footage were enumerated, with total abundance standardised to the mean distance covered in a 10 min survey (141 m). Counts were only made for segments of the footage that were clear, and standardised counts were also adjusted for the proportion of the video that could not be used reliably. The actual area covered could not be calculated, as there was some variation in the height of the camera from the substrate, and the camera was not directed straight down, but rather faced forward with a downwards tilt of approximately 10^{0}. For those taxa for which individuals could not be distinguished (seagrasses, algae and bryozoans), as well as bare substrate, the video was frozen approximately every 1 min, and percent cover recorded with the aid of a grid overlying the image. The mean percent cover for all recorded frames was then calculated for each site. To ensure that the video provided a reliable record of the benthos, spot dives were made at 53 sites to examine the benthos in more detail, and a series of photographs taken of 0.25 m^2 quadrats for a later comparison with the video footage. Dives were conducted on most of the defined habitat types, although depth constraints prevented stations > 24 m in depth from being surveyed in this way.

To objectively determine the community type at each site, cluster analysis was used on the raw data. As the objective was to produce a map that could be compared to that produced by Shepherd and Sprigg (1976), taxa were grouped at the same level as they used, and minor taxa were removed from the analysis. The clustering technique used was Wards Flexible β, with $\beta = -0.25$ (Seber 1984). This technique was chosen as it did not produce any chaining, unlike more commonly used methods such as group-average and centroid. Initially, 15 groups were chosen for further investigation, and these were manually merged on the basis of their dominant taxa to achieve similar groupings to those used by Shepherd & Sprigg (1976).

Results:

There have been some substantial changes in the epibenthos of Gulf St Vincent since the surveys of the mid to late 1960's by Shepherd & Sprigg (1976) (compare Fig. 11.1 to Fig. 11.2). Particularly noticeable is the absence of the seagrass *Heterozostera*, which covered extensive areas of deep sand plains in the southern gulf and Investigator Strait. While there was previously only a sparse cover of *Heterozostera*, this area is now completely devoid of seagrass, with none being seen either in the remote video footage or on the spot dives. Also missing is the *Malleus-Pinna* assemblage that Shepherd & Sprigg (1976) documented in the south-eastern section of the gulf. While this area still contains some scattered *Pinna*, there was no evidence of any *Malleus*. It is possible in this case that individual animals would not have been detected in the remote video footage because of their size, whilst the depth precluded diving to check for them. Nevertheless, the clumps that existed previously would have been detectable with the video sampling, and can thus be regarded as missing.

There is no evidence that new types of assemblage dominated by large macrofauna have established in the place of the *Heterozostera* and *Malleus-Pinna* assemblages that have disappeared. Instead, these areas now appear to be predominantly bare sand (Fig. 11.5), with scattered invertebrates, including ascidians, bryozoans, sponges and some *Pinna*. There are extensive areas (mostly in water greater than 30 m deep, see Figure 11.1 for coarse bathymetry) that are very depauperate in large macrofauna, however, and appear to be barren sand plains.

The other substantial changes are an apparent decrease in the area dominated by bryozoans in the central part of the gulf, and a reduction in the abundance of scallops in the central eastern section. In most of the areas where scallops were formerly a noticeable part of the benthic assemblage (with densities of 0.5 - 4 m^{-2}) they now only occur in low abundance (assuming a 0.5 m wide transect average density at sites with scallops in 0.21 m^{-2}). In 2000/2001, only three stations on the western side of the gulf had substantial numbers of scallops (Fig. 11.2), whereas in the 1960's there were

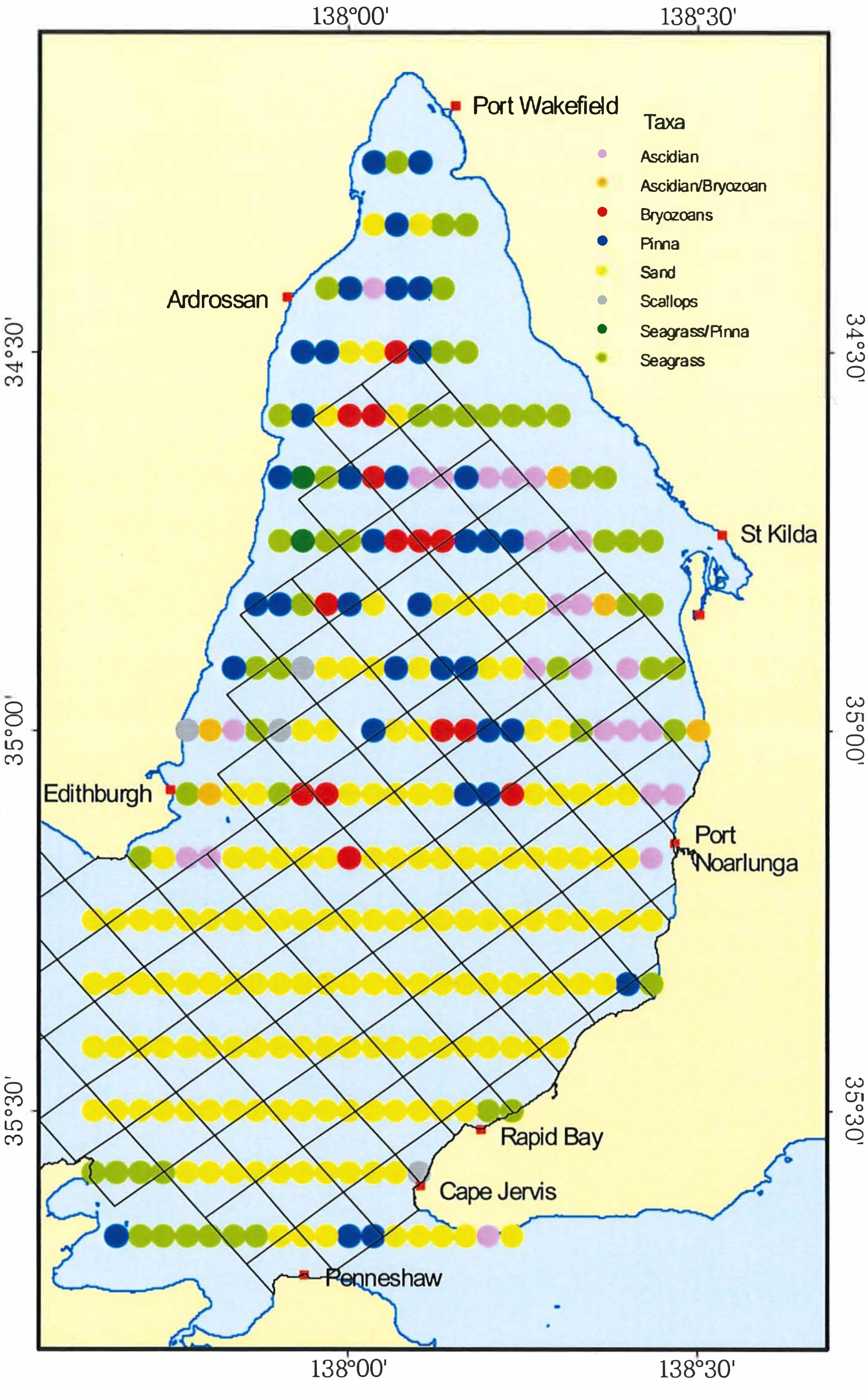

Figure 11.2. Benthic community composition in Gulf St Vincent in 2000/2001 as determined from remote video surveys. The diamond grid represents the prawn fishing blocks.

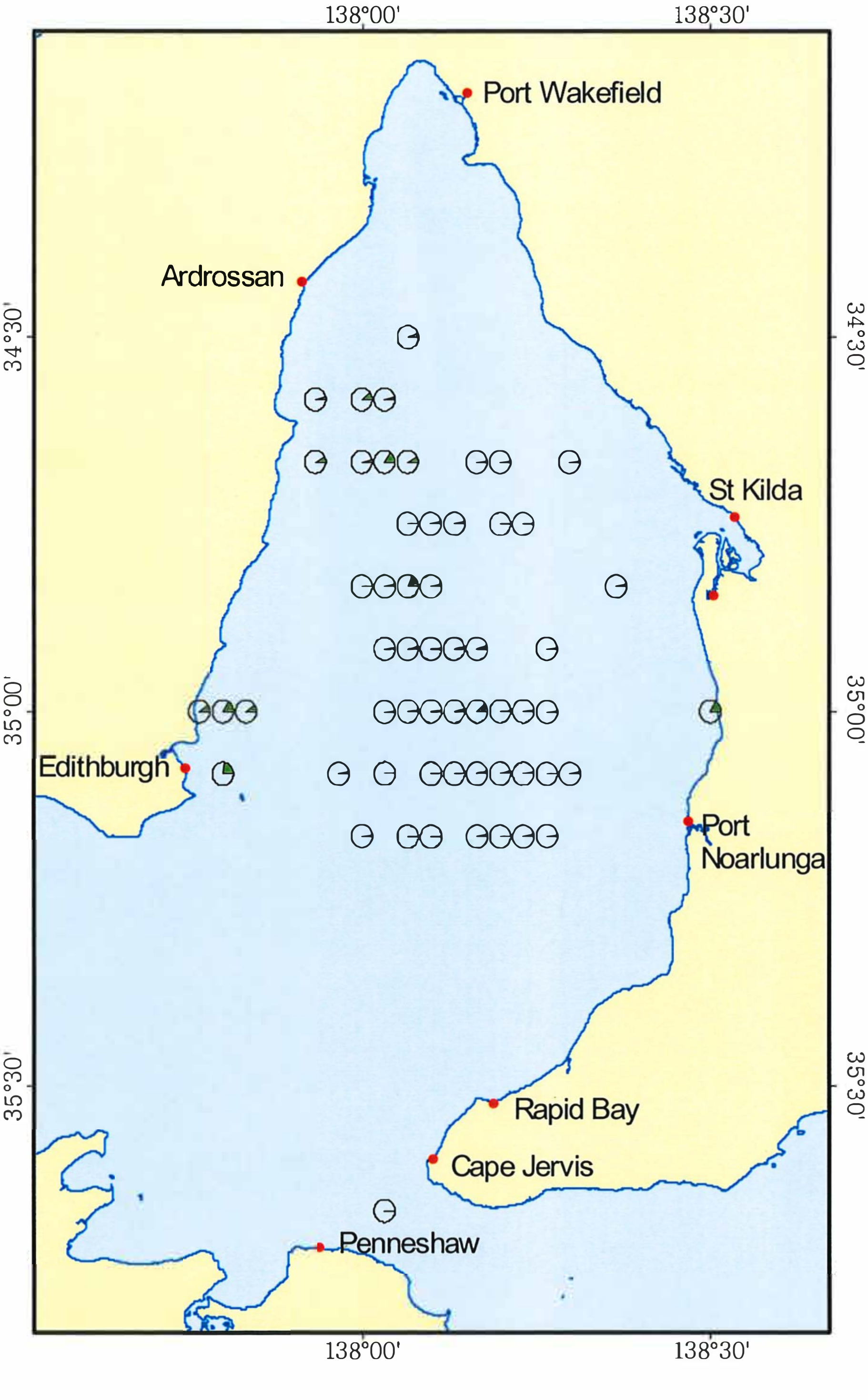

Figure 11.3. Distribution of bryozoans in Gulf St Vincent in 2000/2001. Pie charts at each survey location indicate the percent cover of bryozoans.

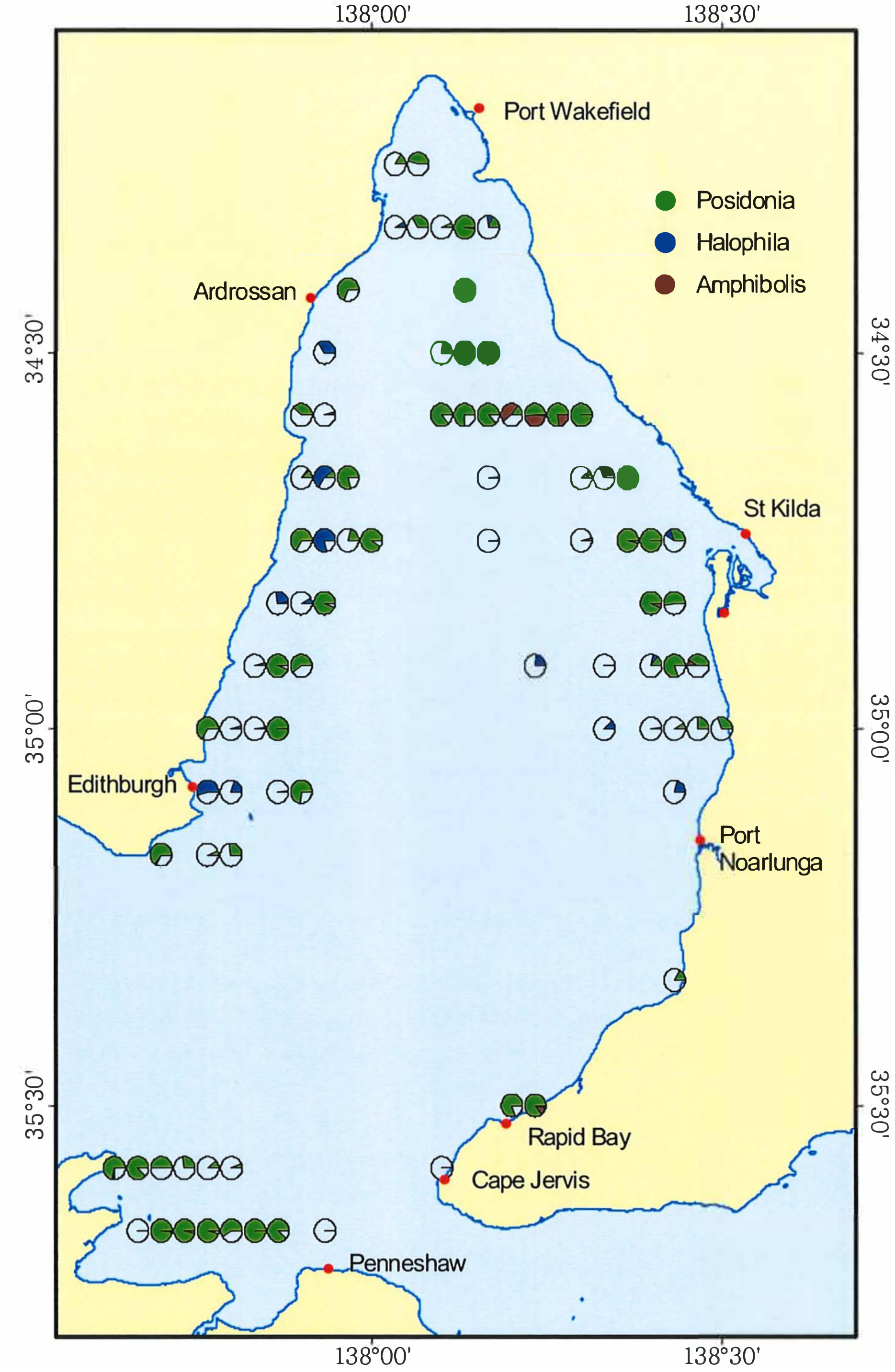

Figure 11. 4. Distribution of the three abundant subtidal seagrass genera in Gulf St Vincent in 2000/2001. Pie charts at each survey location indicate the percent cover of each genus.

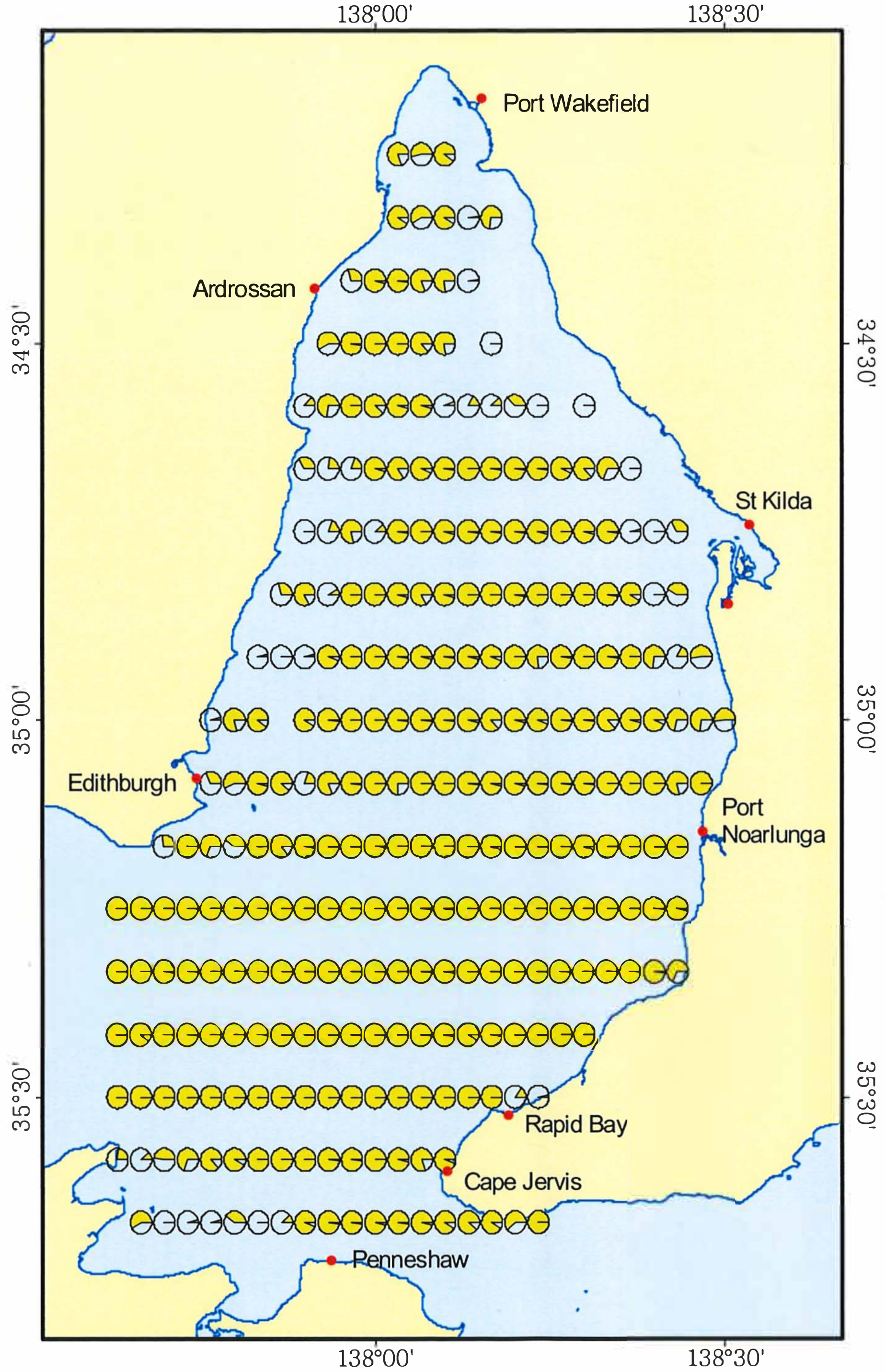

Figure 11.5. Distribution of bare sand in Gulf St Vincent in 2000/2001. Pie charts at each survey location indicate the percent cover of sand.

also large areas on the eastern side where they dominated (Fig. 11.1). Of particular interest is the distribution and abundance of bryozoans (Fig. 11.3). This group of animals now only occurs in low abundance, mostly in the central part of the gulf. Only 12 of the 294 sites surveyed had a bryozoan cover of greater than 5%, with none greater than 25%. This compares to the 1960's, when bryozoans dominated a substantial portion of the central gulf (Fig. 11.1).

As was the case in the 1960's, seagrasses still dominate many of the shallower areas both in the gulf and along the northern shore of Kangaroo Island (Fig. 11.4). The dominant seagrass genus remains *Posidonia*, with only a few areas of *Amphibolis*, and *Halophila* occurring predominantly on the western side of the gulf. There is also some *Halophila* in deeper waters, which appears to be ephemeral as it was only detected at sites surveyed during the summer. *Pinna* in the northern section of the gulf remained relatively unchanged, with this area being the most similar between the two sampling occasions.

Discussion:

There have been some obvious changes in the benthic assemblages present in Gulf St Vincent in the period between this study and that of Shepherd & Sprigg (1976), especially in the southern part of the gulf and in Investigator Strait. The main changes are the loss of extensive deep-water *Heterozostera* meadows and *Malleus-Pinna* assemblages in the southern region, and a reduction in the cover of bryozoans and density of scallops in the central and eastern parts of the gulf. There are several significant anthropogenic influences that may have contributed to these changes, although natural processes may also have played a role. The city of Adelaide discharges a large amount of pollution into the gulf, in addition to that coming from agricultural runoff, and this is likely to have imposed a substantial stress on many organisms (Miller 1982; Neverauskas 1987; Edyvane 1999). There were also several severe dust-storms in the 1980's which removed large amounts of top-soil from the Yorke Peninsula and deposited it into gulf waters (G.K. Jones, pers. comm.). The long flushing time of the gulf (Bye 1976; de Silva Samarsinghe and Lennon 1987) will have exacerbated any effects due to increased terrestrial inputs, as they are only slowly removed from the system. Prawn trawling has also been extensive (Morgan 1995), and although now carried out in a much more sustainable manner, damage from the previously intensive fishery may take many decades to be reversed.

The loss of *Heterozostera* is most likely a result of increased water turbidity, and a subsequent decline in the amount of light reaching the bottom. Given that this species occurred predominantly in deep (> 30 m) water, it was probably at its lower depth limit, and it would only have required a small decrease in light penetration for *Heterozostera* to be unable to survive. An increase in turbidity could have come about through several different mechanisms. Firstly, increased coastal discharge, both from the city of Adelaide and from agricultural areas, may have resulted in an increase in the amount of fine sediment in the water column. It would thus be of interest to examine the sediments of these and other areas of the gulf to see if an increase in the amount of terrigenous material can be detected over the last several decades. Secondly, there has been a substantial loss of seagrass along the metropolitan coast, connected predominantly to sewage discharge (Neverauskas 1987; Shepherd *et al.* 1989), resulting in a substantial increase in the rate of sediment resuspension in shallow waters. Although this increase in sediment resuspension has not been reliably quantified, there is now a consistent band of dirty brown water inshore of the seagrass line, which numerous anecdotal reports suggest is a relatively recent phenomenon (occurring since the loss of seagrasses). If these resuspended sediments include a substantial proportion of very fine material that can stay in suspension for long periods of time, it is possible that they may have been distributed throughout the gulf, resulting in a system-wide increase in turbidity. Finally, heavy trawling activity is well known to result in sediment resuspension (Churchill 1989; Pilskaln *et al.* 1998; Palanques *et al.* 2001), and this may have increased the amount of suspended material. Trawling may also have had a direct impact on *Heterozostera*, causing more damage than could be sustained in areas where it could only just survive. The area formerly covered by *Heterozostera* has experienced substantial trawling pressure throughout the lifetime of the fishery (Morgan 1995), and despite the substantial decline in effort over the last decade, the system may have experienced a state change that cannot easily be reversed.

The former *Malleus*-*Pinna* assemblage that existed in the south-eastern portion of the gulf coincides very closely to the current main trawl grounds for the prawn fishery. It is thus likely that this assemblage experienced substantial direct damage from the trawl gear, as well as possible negative effects from increases in turbidity, whether due to trawling or coastal activities. While most of this area could not be examined by divers because of the depth, no *Malleus* were seen either in the video footage, or in the shallower areas that were accessible to divers. Further north, the bryozoan assemblages would also have been susceptible to trawl activity, as they are fragile and not adapted to cope with extensive physical disturbance (Bradstock and Gordon 1983). At its peak, the prawn fishery trawled in excess of 1600 km^2 yr^{-1} (assuming a trawl speed of 3 kn, and that the nets sweep a 20 m wide path), and thus would have had a direct effect on a large proportion of the gulf, although currently a much smaller area is trawled (200-450 km^2 yr^{-1} in the 1990's). While there are many well documented cases of trawling having a negative impact on benthic organisms (e.g. Auster *et al.* 1996; Engel and Kvitek 1998; Kaiser *et al.* 1998; Collie *et al.* 2000), there is considerable controversy over how great the real impact is. This controversy arises as many studies have failed to show that trawling affects the benthic community (e.g. Gibbs *et al.* 1980; Van Dolah *et al.* 1991; Hall *et al.* 1993; Hannson *et al.* 2000; Lindegarth *et al.* 2000). In Gulf St Vincent, the current trawling practices seem to have little impact on infauna over the short term, at least in the habitats that have been studied (Drabsch et al. 2001, Chapter 2), although approximately 36% of epifauna is removed or dies subsequently (Chapter 1). This suggests that previous periods of intense trawling may well have had a substantial negative effect on benthic communities in the gulf.

The loss of these macro-faunal and floral assemblages has potentially important ecosystem level consequences. As it has been the species that formed most of the structure in these otherwise relatively homogenous sand plains that have been lost, there are likely to be important implications for species that require complex habitat-structure to survive. For example, in New Zealand, bryozoan beds have been protected from destructive fishing practices as they form an important habitat for juvenile snapper and other commercially fished species (Bradstock and Gordon 1983). Given that other habitat-forming species have not replaced those that have been lost, the physical complexity of these habitats has been greatly reduced, and there has likely been concomitant losses or reductions in other species. It has been well established, for example, that shallow-water seagrasses provide important habitats for many fish and invertebrate species (e.g. Bell and Westoby 1986; Edgar 1990; Connolly 1994; Perkins-Visser *et al.* 1996), and while much less is known about deep-water seagrasses, they are likely to serve a similar function. These habitat-forming species may also have provided an important food source for other species, and so their loss may have disrupted food-webs. For example, snapper (*Pagrus auratus*) are important predators of *Malleus*, and the loss of the latter species may have played a role in the decline of snapper stocks in Gulf St Vincent.

Given that the bryozoan communities documented by Shepherd & Sprigg (1976) have declined in extent, and that bryozoan abundance is now low at all survey sites, it is obvious that they have not increased in abundance over large areas of the northern section of the gulf as has been previously hypothesised. Given the low abundance at nearly all sites, it is also very unlikely that they are having a negative effect on prawn stocks, as at no site do they occupy more than 25% of the substrate. If these areas are subjected to trawling, however, the presence of bryozoans could still have a negative effect on fishing activity. The growth form of these animals means that they are particularly susceptible to being caught in the trawl, and thus they can cause significant damage to the catch (and also appear to be more abundant than they are).

In conclusion, there have been substantial changes to the benthic habitats present in Gulf St Vincent between the 1960's and 2000/2001, especially in the central and southern regions. Potential causes include increases in turbidity due to terrestrial runoff (including sewage discharge, stormwater and agricultural runoff) and dust-storms, and the direct effects of trawling. The northern (most inland) portion of the gulf seems to have experienced the least degradation, possibly due to the very limited terrestrial runoff associated with South Australia's arid climate, and the lack of a history of trawling. The changes documented predominantly involve the loss of important structure-forming species, and thus could potentially have substantial implications for many associated species which rely on physically complex habitats for their survival.

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Benefits:

The prawn industry has benefited from this project through an enhanced understanding of the consequences or trawling activity for benthic assemblages and habitats. There is increasing community concern about these consequences, and an essential first step in alleviating this concern is to obtain good quantitative data on what damage trawling is doing, which this project has done. Substantial recruitment in the trawled areas was also documented in the short-term, suggesting that recovery may be fairly rapid, which will further help to alleviate public concern about destructive trawling practices. This information is also an essential component of the industry's submission to Environment Australia for assessment on the fishery's ecological sustainability, as required for renewal of the industries export license.

The results of the modelling component of the study provide further support to the current management strategy for the prawn fishery, that limits total number of hours fishing such that only a small proportion of Gulf St Vincent is fished in any one year. Such independent support of the current strategy should increase the confidence of all involved that the current strategy is in fact approriate. In addition, the incorporation of stochastic variation to the model suggests that in this fishery, environmental variation in population dynamics from year to year will have little consequence for how the stock is fished. In a number of other fisheries, including many of those that have unexplainably collapsed, it is thought that such variation has played an important role in the collapse. It appears that this will be unlikely to occur in the Gulf St Vincent prawn fishery, although this conclusion should not be regarded as absolute.

The suite of experiments on habitat use by juvenile prawns and blue crabs, as well as the assemblage of organisms that they prey on, provides important information to management on how both species are likely to respond to habitat degradation and fragmentation. While sewage discharge has a definite negative effect on both species, this effect seems to be fairly localised, and may even be reversed at moderate distances from outfalls due to habitat change (loss of seagrass) that benefits juvenile prawns. Fragmentation of seagrass beds is likely to have substantial negative consequences for juvenile blue crabs, however, as their predation rates increase and the abundance of epifaunal prey decreases.

Finally, by incorporating the first comprehensive survey of benthic assemblages in Gulf St Vincent for over 30 years, this study provides extremely valuable information on how the gulf has changed. This has allowed some theories on how habitat change has negatively affected commercial fisheries to be dismissed (for example the idea that bryozoans have choked the northern section of the gulf, preventing prawns from inhabiting the area), allowing attention to be focussed on other theories that may still be important (such as the decrease in snapper stocks being due to a decrease in the physical complexity of habitats).

Further Development:

While this project has provided important information on the effects of trawling on the benthic habitats in Gulf St Vincent, there are still a number of important questions that need to be answered. Firstly, it remains to be determined how frequently any given area of seabed is trawled. The work done here utilised only a single episode of trawling, whereas if specific areas are trawled repeatedly over a number of years, then the potential for recovery will be substantially reduced, and damage will be greater than suggested here (although concentrated in a small area). If repeated trawling does occur, then the consequences of this need to be examined. In concert with this, recovery rates need to be followed, as well as the dynamics of individual species, to ensure that the increased recruitment seen after trawling does in fact translate into rapid recovery of the assemblage.

The large scale changes detected in benthic habitats in deeper areas of the gulf point out a need for a better understanding of how different fish species use their habitat, and how habitat change might be affecting fisheries. For example, it is currently thought that a decrease in the physical complexity of the habitats available in Gulf St Vincent may have been an important contributor to the collapse of the snapper fishery. While I have documented that the suggested habitat changes have in fact occurred, we still do not properly understand how snapper use the habitats that have been lost (or those that are still present), and consequently how they may have been affected by the loss of habitat.

Conclusions:

Objective 1. To determine and correlate the distribution and relative abundance of prawns, crabs, and encrusting epibiota in the vicinity of prawn and crab grounds in relation to coastal discharge sites in Gulf St Vincent.

The abundance of juvenile prawns and blue crabs is reduced in the immediate vicinity of the Bolivar sewage outfall, however, this reduction only occurs in a localised area (within 2 km of the outfall), suggesting that the individual effect of the outfall is relatively minimal. It is still possible, however, that increased nutrient inputs to the gulf as a whole could have a negative effect on both species over a larger spatial scale. Due to the patchy nature of adult prawns and crabs, and the spatially diffuse nature of pollution discharge sites along almost the entire eastern side of the gulf, it was not possible to correlate the abundance of adults with proximity to discharge sites. The low abundance of bryozoans (which have decreased since the last survey in the 1960's), and their concentration in the centre of the gulf, also meant that their abundance could not be correlated to distance from point sources of pollution. This low abundance, however, means that bryozoans are very unlikely to be having any negative impact on the prawn population, as even in areas with high cover of benthic epifauna there were still substantial amounts of bare sand present. The only organisms likely to be restricting the abundance of adult prawns through pre-emption of space are seagrasses, which occur predominantly in shallow water whereas prawns tend to prefer deeper water.

Objective 2: To measure and compare the outcome of controlled trawling on epifaunal composition of prawn/crab habitats & bryozoan dominated habitats.

Trawling in Gulf St Vincent has a substantial affect on epifauna, with approximately 36% of large epifaunal animals either being directly removed by the trawl, or dying in the following 2-3 months. This is despite the fact that the trawling regime used was relatively light, and that the impact of the trawl boards was not examined. Commercial trawl shots last for 1-2 hrs (compared to 10 mins used here), and the action of a full cod-end dragging along the substrate is likely to destroy more animals than was found in this experiment. It is also important to determine what the return time between trawls is for any given unit of bottom. If return times are short, then the benthic assemblage will not have time to recover between disturbances, and damage will accumulate over time. This will be particularly relevant for areas that are visited on a regular basis because of consistent high catch rates, or if the same line is trawled repeatedly on a single night, as occurs in some fisheries. On the other hand, if return times are long, recovery can occur. At the small spatial scale of this study, trawling did not negatively affect subsequent catch rates of either prawns or blue crabs, and given that neither of these species rely on the presence of substantial habitat structure, it is unlikely that trawling will negatively affect them through a reduction in habitat quality.

Objective 3: To provide an understanding of the consequences of habitat modification on productivity of important commercial & recreational fisheries.

Substantial changes in benthic habitats over a period of three decade were recorded in Gulf St Vincent. In particular, there has been a large decline in the abundance of structural species (seagrasses, *Pinna*, *Malleus* etc) in the southern part of the gulf, either due to an increase in terrigenous inputs or due to trawling. These change in biotic habitat are likely to have substantial negative implications for a number of finfish species, although they may not have much effect on either prawns or blue crabs. Species such as snapper, which rely on habitat structure provided by benthic organisms, are likely to be particularly affected. Indeed, the snapper stock in Gulf St Vincent has experienced a major decline in the intervening period, which may be related to loss of habitat.

In shallower water, there has been a well documented decline in seagrass abundance, which is also likely to have negative consequences for a number of important fishery species. While prawns may be little affected, as they tend to inhabit areas of bare sand, juvenile blue crabs are often found in areas of seagrass. As seagrass meadows become fragmented, the proportion of seagrass in close proximity to a seagrass/sand boundary increases, and this study show that crustaceans in these areas experience increased rates of mortality compared to those that inhabit seagrass interior. As seagrass is lost, there is also a substantial decline in the abundance of small epifaunal species, such as amphipods, which also are likely to be an important food source for a number of species, including both prawns and crabs. Other food sources such as infauna, however, appear to be little affected by small-scale loss of seagrass. There are also likely to be direct effects of seagrass loss on many finfish species, which as juveniles rely on seagrass as a nursery habitat, although this was not examined in this study.

Appendix 1: Intellectual Property.

The FRDC's share of intellectual property, based on inputs, is 47.01%.

Appendix 2: Project Staff.

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