Final report to FIRDC committee on

the project 88/91

"Consequences for commercial fisheries of loss of seagrass beds in southern Australia".

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Executive summary

The effect of a substantial decline in seagrass cover on benthic invertebrate and fish communities in Western Port, Victoria, was assessed by sampling and comparing faunas associated with vegetated and unvegetated habitats. Many more invertebrate and fish species were collected from seagrass than from unvegetated habitats, with the faunas collected in shallow habitats being relatively homogeneous throughout Western Port, apart from at Cowes Bank near the entrance of the bay. Animals collected from deeper channel sites were more patchily distributed.

The production of the two major faunal components, animals buried in sediments (infauna) and animals associated with sediment and plant surfaces (epifauna), were studied separately because only epifaunal production plays a major role in trophic pathways leading to fishes. Total invertebrate production differed little between intertidal seagrass (79 $g.m^{-2}.yr^{-1}$) and unvegetated habitats (57 $g. m^{-2}.yr^{-1}$). Most of this production was concentrated in the infauna, a faunal component that did not differ between seagrass and bare habitats. By contrast, total epifaunal production was much higher in seagrass habitats (17.2 $g. m^{-2}.yr^{-1}$) than in unvegetated habitats (3.3 $g. m^{-2}.yr^{-1}$), and must have decreased sharply following seagrass dieback. Bay-wide declines in epifaunal production following seagrass loss are estimated to be ≈2,500 tonnes AFDW per year.

A high correlation was found between the production of small fishes at different sites and the production of epifauna, particularly crustaceans. We postulate that the production of small fishes was limited by food in the form of epifaunal crustaceans. This hypothesis is supported by seasonal data, which indicates that when the production of crustaceans was at its lowest during May, populations of small fishes were rapidly declining in Western Port, either by dying or emigrating. Because crustaceans were several times more abundant in vegetated than unvegetated habitats, seagrasses appear to have an important trophic role in supporting fish assemblages. Total production of small fishes in seagrass habitats (5.87 $g.m^{-2}.yr^{-1}$) was more than twice that found in unvegetated areas (2.31 $g.m^{-2}.yr^{-1}$). On a Bay-wide basis, these production rates indicate that the loss in small fish production associated with the decline in seagrass since the 1970s was ≈630 tonnes AFDW per year. However, falling numbers of only two commercial fishes, six-spined leatherjackets (*Meuschenia freycineti*) and blue rock whiting (*Haletta semifasciata*), were found to be directly associated with seagrass loss, with most of the loss of fish production being amongst the small non-commercial species, particularly pipefish, weedfish and soldierfish.

The flow-on effect of seagrass loss to the next level in the food chain, the larger commercial fishes, was difficult to quantify because many of the larger fishes fed on pelagic resources, most notably clupeoid fishes, and occurred in equal numbers in seagrass and unvegetated habitats. Overall, there was little apparent difference in abundance or species richness of the larger fishes between vegetated and unvegetated habitats, so no change in total catch of these

species could be directly attributed to the seagrass dieback.

A new technique for gut content analysis was developed during the study that allowed the biomass and size-structure of ingested prey to be quantified and directly compared with benthic invertebrate data. This technique also allowed large numbers of guts to be processed quickly. The diets of the great majority of the 88 fish species collected in Western Port were dominated by epifaunal crustaceans, with only six species (luderick, yellow-eye mullet, bridled leatherjackets and three species of goby) consuming large amounts of algal material, and only one species (sea garfish) ingesting seagrass in any quantity.

Crustaceans supplied over half the dietary intake for the fish communities at all sites, with molluscs and polychaetes also important but supplying >25% of food consumed at only two sites, Rhyll channel and Tooradin unvegetated. When daily rates of consumption were compared with daily production of food, most crustacean production was found to be cropped by fish. There was a large excess of production of the other major benthic groups. This result provides support for the hypothesis that the production of fish in Western Port is limited by the availability of high quality crustacean food.

An alternative hypothesis to the food limitation hypothesis is that fish production is dependent on the same environmental conditions to which crustaceans respond. Manipulative experiments using artificial seagrasses were set up at two locations, Western Port, Victoria, and Cloudy Lagoon, Tasmania, in order to test conflicting predictions arising from the different hypotheses. Epifauna was rapidly attracted in high densities to seagrass debris, and to a lesser extent to artificial seagrass leaves, indicating that food was a primary determinant of epifaunal production. Recruitment of fishes to all treatments was poor, preventing us from conducting statistical tests with sufficient power to separate the effect of environment from the effect of food on fish numbers. Fish production is apparently less strongly coupled with food than is the production of macrofauna (including crustaceans), possibly because of the lag between epifaunal food buildup and fish recruitment. Larger-scale experiments using artificial seagrasses with patch size >5 m^2 that are placed in the field for periods of 3-12 months are needed to provide a more conclusive indication of the degree to which fish production is related to crustacean production and seagrass biomass independent of other environmental factors.

We determined whether the relationships identified at Western Port between fishes, invertebrates and seagrasses were widespread in southern Australian coastal waters. Similar sampling techniques to those used in Western Port were applied on a reduced scale in seagrass and unvegetated habitats at 14 other locations in Western Australia, South Australia, Victoria, Tasmania and New South Wales.

In both the Western Port and the wider study, coastal seagrass beds were not found to have a substantive nursery function for commercial fishes, differing in this respect from estuarine seagrass beds. Seagrass beds supported more small fish than unvegetated habitats; however, species of goby, pipefish, hardyhead and weedfish were predominant at marine sites. The only common commercially-exploited species collected as juveniles in much higher numbers from vegetated than unvegetated habitats were six-spined leatherjackets (*Meuschenia freycineti*) and blue rock whiting (*Haletta semifaciata*).

While coastal seagrass beds were not found to act as nursery sites for many commercial species, they appear to play an important role to fisheries by enhancing fish production. The estimated production of crustaceans was highly correlated with the biomass of seagrass material and also with the silt/clay content of sediments across the range of sites in southern Australian. Fish production was highly correlated with crustacean production and seagrass biomass, and was negatively correlated with wave exposure (measured as fetch). The overall relationships between macrofaunal production (M; $mg.m^{-2}.d^{-1}$), macrocrustacean production (C; $mg.m^{-2}.d^{-1}$), demersal fish production (D; $mg.m^{-2}.d^{-1}$), fetch (F; km), seagrass biomass (L; $g.m^{-2}$) and silt/clay content of sediments (S; %) are:

$$\log M = 3.85 + 0.26.\ln F + 0.53.\ln S \; (R^2 = 0.56),$$
$$\log C = 1.77 + 0.27.\ln (L+1) + 0.35.\ln S \; (R^2 = 0.70),$$
$$\log D = 1.87 - 0.71.\ln F + 0.40.\ln (L+1) \; (R^2 = 0.50).$$

These regression equations allow the production of macrofauna, crustaceans and small fishes at unexamined sites to be predicted. The accuracy of these equations is high but could be further increased by expanding the data base used in their calculation, and by investigating the effects of such environmental parameters as turbidity, light, depth and nutrient concentration on fish production. Because these equations allow changes to small fish production to be estimated when a development is to occur that is expected to result in seagrass loss, they should prove an important tool for fishery management purposes.

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Section 1. General Introduction

A characteristic feature of shallow subtidal bays and inlets throughout temperate regions is the presence of dense beds of seagrasses. Because human coastal activity is generally concentrated in the same sheltered environments in which seagrasses flourish, and because seagrass beds are highly susceptible to increases in turbidity and nutrients (Silberstein et al., 1986; Shepherd et al., 1989), extensive seagrass loss has occurred in many areas. This loss of seagrass has far-reaching consequences to local ecosystems because of the variety of roles that seagrass beds play in coastal processes. Seagrasses (i) provide food and shelter for a great variety of plant and animal species, including juvenile commercial fish species, (ii) increase primary production of inshore waters, (iii) trap and recycle nutrients, and (iv) stabilize sediments and shorelines (Edgar and Kirkman, 1990). The first of these roles is widely cited but has surprisingly little empirical support. No model is available that allows quantitative predictions to be made about the consequences of seagrass loss to the fauna. When seagrass dieback does occur, the only general prediction which can be made from numerous studies worldwide where faunal differences between unvegetated and seagrass habitats are documented (see, e.g., Orth et al., 1984; Edgar, 1990b; Ferrell & Bell, 1991), and where these differences are related to physical and biotic variables (e.g., O'Gower & Wacasey, 1967; Lewis, 1984; Harrison, 1987), is that the abundance and species richness of benthic invertebrates and fishes will decline (Howard et al., 1989). This lack of predictive ability may be due to the fact that no general relationships exist between seagrasses and associated animals, or that techniques amongst seagrass workers differ so greatly that data collected at one site has little value when compared with data collected at another (see Lewis & Stoner, 1981).

In order to address these problems, this project was initiated with three aims:

1. To quantify changes in the macroinvertebrate fauna and juvenile fish assemblages resulting from loss of seagrass beds.
2. To quantify changes in the trophic pathways to commercial fish species resulting from the loss of seagrass habitat.
3. To evaluate how seagrass loss influences the abundance and distributional patterns of commercial fish species.

We considered that the most appropriate way to achieve these aims was to subdivide the project into three major components:

Firstly, a detailed study of the relationships between commercial fish species, small non-commercial fish species, invertebrates and seagrasses was needed at one study site. The most suitable site was Western Port, Victoria, an area where seagrass loss has been particularly severe, with 178 km^2 of seagrass (70% of the total area) disappearing between 1973 and 1984 (Shepherd et al., 1989). During this period of rapid seagrass decline, several commercial fish species, particularly King George whiting, six-spined leatherjackets and blue rock whiting, decreased substantially in abundance (see Final Report of associated FIRDC-funded project by Jenkins et al., 1993). Western Port had additional advantages as a study site over other southern Australian bays where seagrass loss has occurred because some baseline data from the area were collected prior to the period of rapid seagrass decline (Coleman et al., 1979; Howard, 1984; Robertson, 1984; Watson et al., 1984).

The second component of the study was to assess whether the relationships detected between seagrasses, invertebrates and fishes in Western Port were of a general nature. To do this we needed to conduct similar studies, but on a less-intensive scale, at a variety of other sites in southern Australia. Consequently, seagrasses, invertebrates and small fishes were sampled in the Rottnest Island/Cockburn Sound and Albany regions of Western Australia, near Adelaide (South Australia), at Swansea and Bruny Island (Tasmania), in the Gippsland Lakes (Victoria), and in Jervis Bay (New South Wales).

In the final component of the study, manipulative field experiments involving artificial seagrass were set up to test hypotheses generated from the more descriptive field studies.

Section 2. Effects of seagrass loss on the species richness, size-distribution and production of benthos in Western Port, Victoria.

2.1 Summary

The effect of seagrass loss on benthic invertebrate communities in Western Port was assessed by comparing extant faunal differences between vegetated and unvegetated habitats over a 15 month period and identifying faunal differences between the two habitat types. Total infaunal production has probably changed little since seagrass loss began because comparable levels were recorded in intertidal seagrass (62 g. $m^{-2}.yr^{-1}$) and unvegetated habitats (54 g. $m^{-2}.yr^{-1}$). However, infaunal production was highly correlated with the amount of organic material in sediments, so long-term declines in infaunal production may occur due to lower production levels of seagrass detritus. Total production of epifauna, on the other hand, appears to have changed greatly following seagrass dieback; annual epifaunal production in intertidal seagrass habitats (17.2 g. $m^{-2}.yr^{-1}$) was much higher than in unvegetated habitats (3.3 g. $m^{-2}.yr^{-1}$). Bay-wide declines in epifaunal production following seagrass loss are estimated to be ≈2,500 tonnes AFDW per year.

Seagrass habitats in Western Port supported much higher numbers of macroinvertebrate species per core ($\bar{x}$ = 33) than unvegetated habitats ($\bar{x}$ = 15 species), with a mean of 17 species per core found in the deeper unvegetated channel habitats. The total number of species present in intertidal seagrass habitats in Western Port has nevertheless probably changed little since seagrass loss began because intertidal seagrass habitats possess a consistent fauna throughout much of the bay, hence the remaining beds should contain most of the original fauna. However, seagrass beds >2 m deep, a small but potentially species rich habitat type, have now disappeared, probably causing a substantial but unmeasurable decline in the total number of macrofaunal species in Western Port.

2.2 Introduction

The aims of this component of the study were to identify general relationships between sediment particle characteristics, seagrasses and benthic invertebrates for Western Port, and, using this information, to infer recent changes in the benthos which have occurred as a consequence of the massive decline in seagrass biomass over the past twenty years. Bulthuis (unpublished data cited in Shepherd et al., 1989) estimated that the area of macrobenthic plants in Western Port had declined from 250 km^2 in 1973 to 72 km^2 in 1984, and that most of the seagrass loss had occurred on the shallow tidal flats.

In contrast to previous studies, we have placed particular emphasis on documenting the size-distribution of the benthos in different habitats. This has the advantages that (i) major physical factors such as sediment particle size or seagrass biomass which affect the size-distribution of invertebrates can be identified, and (ii) data are expressed in a form which is largely independent of sampling protocol and can thus be directly compared with other studies. Moreover, if food does limit the population sizes of animals then general relationships are unlikely to be detected without reference to faunal size-distribution because the amount of food consumed by an animal depends as much on its size as on its species type.

In order to take into account the size-distribution of assemblages we have presented data in a novel way, by scaling the abundances of animals with respect to body mass raised to the power 0.78 (see Edgar, 1993). Data transformed in this way are not biased by either small or large species. They also provide an index of the metabolic rate of an assemblage that is approximately proportional to community processes such as total community production, respiration and consumption (Edgar, 1993). Metabolic-rate based indices, when shown for different sieve size-classes, can be readily converted to abundance and biomass data by dividing by the appropriate scaling factor.

2.3 Methods

Sites studied

Western Port is an extensive (≈30 km diameter), coastal embayment in central Victoria that arose following downfaulting in the Quaternary, with large islands in both the central (French Island) and southern (Phillip Island) sections of the bay (Fig. 2.1). Large expanses of intertidal mudflat are present throughout much of Western Port (≈40% of total area), with the dendritic channels (4-10 m deep) that drain the mudflats and three subtidal embayment plains also occupying considerable areas (Marsden & Mallett, 1975; Marsden et al., 1979). Water temperatures in Western Port range from ≈10 °C in winter to ≈22°C in summer, with salinities close to fully marine (≈33-38 ‰) throughout the year (Kimmerer & McKinnon, 1985). Tides are semi-diurnal with a daily range of 2-3 m. Because of the high tidal range, expansive mud flats and high levels of bioturbation, water is turbid through much of the bay (Shepherd et al., 1989), particularly in the areas furthest from oceanic influences.

Sampling was carried out at three primary localities, Rhyll (Phillip Island), Peck Point (French Island) and Tooradin (Fig. 2.1). At each of these localities, seagrass (intertidal to 0.5 m below MLWS), unvegetated mudflat (intertidal to 0.5 m depth) and channel (4-6 m depth) habitats, which were interspersed amongst each other, were sampled. All samples from unvegetated habitats at the primary localities were collected at distances >50 metres from seagrass beds. Seagrasses at these localities predominantly consisted of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog with lesser amounts of *Zostera muelleri* Irmisch ex Aschers. Figures mapping seagrass distribution in the 1970s (Marsden & Mallett, 1975; Wilk et al., 1979; Howard, 1981; Shepherd et al., 1989) indicated that the unvegetated sites at two of the three localities, Rhyll and Peck Point, occurred on substrata previously covered by seagrasses; this was also indicated by the presence in sediments of many old shells of *Diala suturalis*, the most common seagrass-associated mollusc. An additional two localities, Cowes Bank (adjacent to Observation Point) and Loelia Shoal, were sampled in order to include two other habitat types (sand bank and subtidal embayment plain) found within the bay. Shallow (0-1 m depth) sand flats and seagrass beds were sampled at Cowes Bank and the embayment plain (5 m depth) at Loelia Shoal. Two seagrass species, *Zostera muelleri* and *Halophila australis* Doty & Stone, were equally abundant at Cowes Bank. Seagrass and unvegetated habitats at one further locality, Crib Point, were sampled on a one-off basis on 14 August 1991 (see Section 5) because faunal density data were available for this site following studies by Watson et al. (1984) and Robertson (1984). This locality possessed similar features to the three primary localities.

Due to their proximity to large expanses of intertidal mudflats, the Tooradin and Rhyll localities were considerably more turbid than Cowes Bank and Peck Point. Light (PAR) levels recorded at 1 m depth at high tide on 27 November 1990 were 510, 790, 1100 and 1400 $\mu E.m^{-2}.s^{-1}$ at Tooradin, Rhyll, Cowes Bank and Peck Point, respectively (surface reading $\approx$2,800 $\mu E.m^{-2}.s^{-1}$). These readings represent close to the maximum transparency levels; at low tide on 1 December 1991, for example, PAR levels at 1 m depth at Rhyll were 10 $\mu E.m^{-2}.s^{-1}$ (surface reading 2,400 $\mu E.m^{-2}.s^{-1}$). The variation in light penetration between localiies was reflected in the maximum depth at which seagrasses survived. The maximum depths below low water mark at which *Heterozostera tasmanica* was recorded on 27 August 1990 at Peck Point, Cowes Bank, Rhyll and Tooradin were 1.6, 1.2, 0.4 and 0.4 m, respectively, while the corresponding values for the low-light tolerant species *Halophila ovalis* were 2.7, 1.2, 1.4 and 0.6 m.

Sampling and processing

Sampling was conducted at three-monthly intervals commencing on 22 August 1989 at Peck Point and Rhyll, and on 17 November 1989 at Tooradin, Cowes Bank and Loelia Shoal. Sampling concluded in August 1990 at the seven unvegetated sites excluding Cowes Bank and in November 1990 at the four seagrass sites and Cowes Bank. On the initial sampling date at Cowes Bank (30 November), no seagrass was detected. Seagrass patchily colonised this locality over the next twelve months; consequently, separate samples were collected from unvegetated and seagrass habitats (5 replicates each) at Cowes Bank on 13 February 1990 and subsequent occasions.

On each sampling occasion, benthic animals were collected using corers of two different diameters placed in close proximity at 5 haphazardly selected positions per site. [Note that in this study locality refers to a large geographic area ($\approx$ 500 m x 500 m) which includes several habitat types while site refers to a particular habitat within a locality]. Meiofauna were sampled using 50 mm diameter cores twisted into the substratum to a depth of 100 mm, and macrofauna were sampled using 150 mm diameter cores pushed to the same depth. Both corer types were constructed from PVC tubing with 125 μm mesh over the end caps. Core samples were transferred into plastic bags and preserved with formalin. In the laboratory, samples were washed through a stacked series of sieves (meiofauna - 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2 mm; macrofauna 1, 1.4, 2, 2.8, 4, 5.6, 8, 11.2, 16 mm) using the methods described by Edgar (1990a). Invertebrates collected on each sieve were then sorted into species (macrofauna) or larger taxonomic categories (meiofauna) and counted. Animals collected on the largest sieve were individually weighed after drying at 60 °C, and again after ashing at 550 °C, to determine their ash-free dry weight (AFDW). Because of the high densities of animals present on the smaller meiofaunal sieves, material present on the 0.355, 0.25, 0.178 and 0.125 sieves were subsampled using a Fulsom plankton splitter which reduced densities by factors of 2, 4, 8 and 16, respectively. The 0.178 and 0.125 mm sieves were used on one sampling occasion only, August 1990. All macrofaunal samples were sorted; however, in order to provide time for other aspects of the study, only three or four of the five replicate meiofaunal samples were processed for each sampling occasion, except for August 1990 when all five replicates were sorted.

The quantity of organic material and ash in sediments in each habitat was measured by amalgamating sediments from replicate meiofaunal cores collected in August 1990, and then weighing the sediments retained by different sieves (<0.063, 0.63, 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6, >8 mm sieve size-categories) after drying at 60°C for at least 2 d. Sediments were ashed at 550°C for 2 h after the dry weight had been measured, and reweighed to enable the percentage of ash and organic material to be determined. The biomass of live seagrass leaves, rhizomes and debris collected from macrofaunal core samples was also measured after drying at 60°C.

Data analyses

Estimates of the faunal biomass of benthic invertebrates in each sample were determined by multiplying the number of animals retained by sieves of different size with the mean weight of animals for each sieve size-class, as calculated from the regression equations listed in Table II of Edgar (1990a). Directly determined ash-free dry weights rather than estimates were used for animals collected in the 16 mm sieve. Estimates of the daily production of benthic invertebrates were determined using these mean weight estimates for each sieve size and the equation $P = 0.0049 * B^{0.80} T^{0.89}$ which relates daily production of macrobenthos P (μg/d) to ash-free dry weight B (μg) and water temperature T (°C) (Edgar, 1990a). Annual production estimates were made by calculating daily production in August 1989, November 1989, February 1990 and May 1990 using the above equation and mean water temperature data for these months at Rhyll (11 °C, 16 °C, 22 °C and 16 °C, respectively).

Data for animals collected on different sieves have also been analysed using an index P_{20} (Edgar, 1993), which was calculated using the production equation listed above at a constant water temperature of 20 °C. In practice, P_{20} is calculated simply by multiplying the abundances of animals collected on sieve sizes 1, 1.4, 2, 2.8, 4, 5.6 mm, etc., with the constants 3.94, 8.19, 17.0, 35.5, 73.8, 154 $\mu g.day^{-1}$, etc., the mean daily rates of production of animals of different sieve sizes at 20 °C. The chief reasons for using this index are to provide an index of community processes (Edgar, 1993), and also to allow data from a wide range of size-classes to be graphically presented without being dominated by either small or large animals (Edgar, 1994). While P_{20} is calculated and expressed in terms of production, it is best viewed as a general index of the metabolic rate of an assemblage, and as such is approximately proportional to community respiration and consumption as well as production.

For macrofauna (i.e., animals collected with the 150 mm cores), epifauna have been distinguished from infauna using the taxonomic criteria listed in Table I of Edgar (1994). Meiofauna have not been similarly assigned because infaunal species of nematodes and harpacticoid copepods were not separated from epifaunal species.

Plant biomass, faunal species richness and production data were compared using ANOVA. Hypotheses requiring a comparison between seagrass and other habitats were tested using data collected at the three primary localities on the four sampling occasions between November 1989 and August 1990. Habitats and seasons were considered fixed and localities a random factor in these analyses.

In order to determine whether the two types of corer produced similar abundance estimates for animals of a given size-class, invertebrate density estimates for 1, 1.4 and 2 mm size-classes were also analysed by ANOVA (factors: site and core size). In this analysis, data collected at all 12 sites were used, with sites considered a random factor.

The degree of heteroscedasticity in the different data sets were examined using box plots of means and variances of the different treatments and by investigating the distribution of residuals. In most cases data were log-transformed to make variances homogeneous. Analyses were run using SYSTAT (Wilkinson, 1987).

Qualitative faunistic relationships between sites were determined using presence/absence data for the 289 species found at more than one site, and by then calculating similarity levels between pairs of sites using the Jaccard coefficient (= a/b, where a is the number of species common to the two sites and b is the total number of species found at the two sites). Quantitative relationships between sites were also determined by computing the Spearman ρ coefficient between pairs of sites using information on the rank abundance of 54 common species.

2.4 Results

Seagrass biomass

Above-ground seagrass biomass varied between seasons in a different manner at the three primary localities (Fig. 2.2), as indicated by a significant site x habitat interaction term when the biomass of seagrass leaves collected in cores was analysed using two-way ANOVA (df = 6/47 [one missing value], F = 3.70, p < 0.01). Seagrass biomass varied significantly overall between sites (df = 2/47, F = 13.97, p < 0.001) and between seasons (df = 3/6, F = 4.85, p = 0.05), with seasonal influences explaining more of the total variation between samples (36%) than either site (19%) or site x season interaction (15%). Lowest levels of above-ground biomass occurred in May and August at the primary sites (Tukeys test, p<0.05), with seasonal trends at Peck Point much more obvious than elsewhere (see Fig. 2.2). Mean leaf biomass was significantly greater at Peck Point than at the other two sites (Tukeys test, p<0.05).

Seagrass biomass remained relatively constant during the study at Cowes Bank once seagrasses had become established in February 1990 (Fig. 2.2); however, following the conclusion of field work in 1991, seagrass had again disappeared from the site after being covered by mobile, longshore-drifting sand (G.Edgar & C.Shaw, pers. obs.).

Sediments

Sediment characteristics varied greatly between the different sites sampled (Fig. 2.3). Sediments collected at the three primary seagrass sites and Loelia Shoal were all dominated by the silt-clay fraction, with a high organic content. Sediments collected in the channel habitats were predominantly sands, but with a varying modal grain size of 125 μm at Peck Point, 250 μm at Tooradin and biomodal peaks at 250 μm and >8 mm at Rhyll. The latter peak was due to the presence of considerable quantities of large, calcareous bivalve fragments. Unvegetated habitats possessed sediments intermediate in characteristics between those found in adjacent seagrass and channel habitats. High amounts of both fine organic material and sand were present at the three primary unvegetated sites, with the sands having size-distributions similar to those found in adjacent channel habitats. The particle size-distribution of sands in the seagrass and unvegetated habitats at Cowes Bank were similar, with low amounts of organic material present.

Macrofaunal distribution patterns

A total of 483 species was recorded during the study, of which 39% were crustaceans, 33% were polychaetes, 18% were molluscs and 10% other taxa. These numbers are probably conservative, due to the likelihood that some mistakes occurred in the recognition of species groups and that undescribed species were more likely to be lumped rather than split. Such errors probably occurred most often when identifying polychaetes where sibling species are particularly common.

The number of macrofaunal species collected per core differed substantially between different habitats and between different localities, with a significant locality x habitat interaction also detected by ANOVA (Table 2.1). Differences in species richness between habitats explained more of the total variance between samples (51%) than all other factors together, with locality x habitat interaction explaining a further 11% of total variance. Tukeys mean comparison tests indicated that significantly ($p<0.001$) more species were collected in cores from seagrass ($\bar{x} = 33.4$) than from unvegetated ($\bar{x} = 15.4$) or channel ($\bar{x} = 16.8$) habitats, and from Peck Point ($\bar{x} = 26.9$) than from Rhyll ($\bar{x} = 20.0$) or Tooradin ($\bar{x} = 18.7$). Month had no clear effect on the number of species collected per core, either directly or interactively (Table 2.1).

The patterns of species richness found at the scale of individual cores changed at larger scales. Considerably more species were collected in channel habitats than in unvegetated habitats at each of the sites (Fig. 2.4). Moreover, when the total number of species collected from the three primary localities is considered, no clear differences were evident between the number of species collected from seagrass habitat (300 species collected over six sampling months) and from channel habitat (265 species collected over five sampling months). At this larger scale, the total number of species collected from unvegetated habitats remained comparatively low (185 species).

At most sites, similar numbers of crustacean and polychaete species were collected, with lower numbers of molluscs and much lower numbers of other groups (Fig. 2.4). By contrast, in the unvegetated habitats at Rhyll and Tooradin many more polychaete species were collected than crustaceans, with more crustaceans than polychaetes collected from the seagrass habitat at Cowes Bank.

Abundances of the most common species at each of the sites are shown in Table 2.2. The most common species was a capitellid polychaete, *?Barantolla* sp., which was collected at all sites. Polychaetes were much more abundant than other faunal groups at all sites other than Peck Point seagrass, where the gastropod *Diala suturalis* was prevalent, and in the sand at Cowes Bank where an undescribed species of amphipod, *Urohaustorius* sp., was the most common species.

Faunal relationships between pairs of sites were found to depend partly on whether quantitative or qualitative data were used (Table 2.3). For example, the two sites showing poorest faunal relationship using Spearman ρ, Tooradin channel and Peck Point seagrass, were found to have a greater percentage of species in common than most other site pairs. In general, Jaccard's coefficient produced relatively poor discrimination between sites, with most pairs of sites having similarity levels between 0.2 and 0.4.

The three primary seagrass sites showed a high degree of faunal similarity using both classification methods, with the quantitative data showing better separation of primary seagrass sites from other sites, and a next closest relationship to Cowes Bank seagrass (Table 2.3). Amongst the unvegetated and channel sites, there was no clear trend for sites to link primarily on either a locality or habitat basis. Rhyll unvegetated showed a close faunal relationship with both Tooradin unvegetated and Tooradin channel, while Rhyll channel showed highest faunal similarity with Peck Point unvegetated and Peck Point channel.

Comparison of macrofaunal data collected from seagrass habitats during this study with data collected by Watson et al. (1984) in 1974 and 1975 at Crib Point and Rhyll, respectively (Table 2.4), provides no indication that the seagrass fauna has changed greatly since that time. The larger macroinvertebrates occurred in similar densities during the two studies; however, densities of the smaller macrofaunal species, particularly polychaetes, were much greater during the present survey. This difference is probably more a consequence of different sorting techniques used rather than changes in the fauna because invertebrates collected by Watson et al. (1984) were sorted under an illuminated magnifier, resulting in many of the small, thin animals being overlooked. Watson et al. (1984) mention that many small epifaunal taxa were not collected. They also collected relatively high numbers of callianassid shrimps, presumably because their data include samples from unvegetated as well as seagrass habitats.

Data are also available on the numbers of macrobenthos collected with a Smith-MacIntyre grab at a variety of sites in Western Port during the 1973/74 summer. Coleman et al. (1978) summarised this information but unfortunately did not separate samples containing seagrass nor discuss faunal differences between vegetated and unvegetated habitats. High abundances of seagrass-associated shrimps and crabs at three stations in their original data set nevertheless clearly indicate that two of their sites adjacent to our Tooradin locality (Stations 1706 and 1708) and one site near Peck Point (Station 1716) were on seagrass beds. The two Tooradin stations have since lost seagrass cover.

As with the data of Watson et al. (1984), it is now impossible to compare the changes in abundances of all species between the study of Coleman et al. (1978) and the present because a large proportion of taxa are undescribed and hence are listed by genus or family. Nevertheless, many species can be confidently referred between Western Port studies, and the abundances of 21 common species at seagrass sites adjacent to Peck Point and Tooradin are shown in Table 2.5. The composition of the seagrass-associated fauna in the Bay appears to have changed during the past 20 years, with a number of epifaunal molluscs common now that were formerly rare. This change is unlikely to be solely due to the substantial differences in sampling equipment used in the two studies because several molluscs now abundant throughout Western Port (including *Diala suturalis, Styliferina translucida* and *Pseudoliotia micans*) were not collected at all during the earlier survey (N.

Coleman, unpublished data).

Macrofaunal biomass and production

Total estimated biomass and annual production of macrofauna >1mm sieve size at each of the sites is shown in Table 2.6, with the biomass and annual production of infauna and epifauna shown in Figs 2.5 and 2.6, respectively. With the exception of the Peck Point channel site, epifaunal biomass was higher in the primary seagrass sites than the unvegetated or channel sites. The biomass of epifauna in Peck Point channels was unusually high because seagrass debris (with associated animals) was sometimes collected in cores, and because eight large filter-feeding brachiopods were collected on one occasion (producing a very large standard error). No clear differences in the biomass of infauna were found between habitats, although sites with mud had much higher infaunal biomass than the sandy Cowes Bank sites. Crustaceans were the major contributors to epifaunal biomass at most of the sites, but provided negligible infaunal production, apart from at Loelia Shoal where callianassid shrimps were abundant. Macrofaunal biomass at all primary sites other than the Tooradin unvegetated and Tooradin channel sites was concentrated in a few large bivalve species. The importance of particular bivalves differed between sites with *Anadara trapezia* and *Tellina* spp. the biomass dominants at the primary seagrass sites, *Barnea australasiae* dominating at Peck Point unvegetated, *Neotrigonia margaritacea* dominating at Rhyll channel, and *Notospisula trigonella* at Rhyll unvegetated. Faunal biomass data were not statistically analysed using ANOVA because variances were heterogeneous.

Trends in estimated annual production of epifauna and infauna were similar to trends in macrofaunal biomass (Fig. 2.6). Highest epifaunal production was found at the site with highest plant biomass, Peck Point seagrass; at this site grazing molluscs, particularly *Diala suturalis*, and amphipods were especially productive. The production of epifauna at all seagrass sites was several times greater than epifaunal production at adjacent unvegetated sites. Infaunal production, on the other hand, showed no consistent variation between seagrass and unvegetated sites. Infaunal production was, however, much higher at sites with organically enriched sediments, with infaunal production (I; $g.m^{-2}.yr^{-1}$) significantly correlated with the percentage of organic material in sediment cores (M; g): $M = 3.46 + 1.28*I$ ($r=0.63$, $n=12$, $p = 0.01$).

Macrobenthic community P/B ratios were close to 2.5 at all primary seagrass sites, and were slightly higher in the adjacent unvegetated habitats (Table 2.6). The lowest P/B ratio was recorded at the Peck Point channel site (P/B =1.71), where many large molluscs were encountered, and was highest at Loelia Shoal (P/B =4.56), where no large animals were collected, and Cowes Bank seagrass (P/B =4.09), where the epifauna was disproportionately important.

When the effects of temperature were not included in calculations of production (i.e., the parameter P_{20} was examined), month was found to have little influence on production (Table 2.7). P_{20} values for the total macrofauna, infauna and epifauna all showed significant habitat x locality interaction, and for total macrofauna and epifauna there was significant overall differences in production between habitats. General differences between habitats explained a greater proportion of the total variance in P_{20} than other factors (Table 2.7). Macrofauna in channel habitats ($\bar{x}$ = 118 $mg.m^{-2}.d^{-1}$) had significantly lower total production rates than macrofauna in seagrass ($\bar{x}$ =257 $mg.m^{-2}.d^{-1}$) and unvegetated habitats ($\bar{x}$ = 197 $mg.m^{-2}.d^{-1}$), while epifauna in seagrass habitats ($\bar{x}$ = 57 $mg.m^{-2}.d^{-1}$) had much higher production rates than in channel ($\bar{x}$ = 20 $mg.m^{-2}.d^{-1}$) or unvegetated ($\bar{x}$ = 10 $mg.m^{-2}.d^{-1}$) habitats (Tukey mean comparison tests; $p<0.05$). Infauna were more patchily distributed than epifauna, resulting in a high level of variation in P_{20} between individual replicates and large error term shown in Table 2.7.

Invertebrate size-distribution patterns

The results of the two-way ANOVAs, using invertebrate density estimates for 1, 1.4 and 2 mm size-class animals (Fig. 2.7) obtained from the two types of corer and from different sites, indicated that the 50 mm corer produced significantly higher density estimates of 1 and 1.4 mm size-class animals than the 150 mm corer (Table 2.8). However, in these ANOVAs, data could not be transformed to make sample variances for the different treatments homogeneous because variances both increased with the mean and were lower for the 150 mm corer than the 50 mm corer (due to fewer animals sampled using the 50 mm corer). Significance levels associated with these ANOVAs should therefore be treated with caution (Day and Quinn, 1989), although the high levels of significance make it unlikely that a Type I error has occurred. A significant corer x site interaction was also found using ANOVA for 2 mm sieve-size animals. In the primary seagrass and Loelia Shoal sites, 150 mm corers appeared to be more efficient than 50 mm corers at collecting 2 mm sieve-size animals, while in the channel and sand habitats, 50 mm corers were slightly more effective (Fig. 2.7).

Because the 150 mm corers produced underestimated densities of 1 and 1.4 mm animals, densities of animals in different habitats were calculated using data from the 50mm corers for animals ≤1.4 mm sieve size. Data from the 150 mm cores were used to estimate densities of animals ≥2.8 mm sieve size, and, in order to smooth any discontinuities between the two methods, the densities of animals at 2 mm sieve-size were calculated as the mean of data from the two corer types.

No general trends were apparent for different habitats when the densities of animals were scaled with respect to production-rates and plotted against sieve-size class (Fig. 2.8). P_{20} was concentrated at the Rhyll sites in the largest size-classes, at Tooradin seagrass and Cowes Bank unvegetated in the smallest size-classes, and at other sites there was little overall difference between the smaller and larger size-classes. Faunal size-distribution patterns were polymodal at a number of sites. Low P_{20} levels were evident at 355 μm sieve size at Peck Point channel and the Rhyll sites, whereas relatively low levels occurred at 1.4 mm sieve size at Loelia Shoal. Several sites with bimodal patterns (Peck Point unvegetated, Peck Point channel, Tooradin seagrass, Tooradin channel, Loelia Shoal) had maxima at 4 or 5.6 mm sieve size.

Size-distribution patterns for crustaceans have been shown separately (Fig. 2.9) because these patterns differed slightly from the overall patterns and because fishes predominantly consumed this group (see Section 4). Modes in P_{20} were generally more clearly defined for crustaceans than for the total fauna. Although the patterns at the three primary seagrass and unvegetated sites, and Tooradin channel, showed reasonable similarity, the positions of modes at other sites were highly variable. Peaks at Rhyll channel broadly corresponded with troughs at Loelia Shoal, with similar complementary patterns occurring at the Cowes Bank seagrass and Rhyll unvegetated sites.

Seasonal changes in faunal size-distribution patterns were not consistent in different habitats (Fig. 2.10). Most faunal recruitment at the primary seagrass sites occurred in winter and spring, with the modal size of these newly recruited animals reaching ≈4 mm in February and ≈8 mm in May. P_{20} in the small macrofaunal size range (0.5-2 mm sieve size) was extremely low in May. Similar trends were also found in the unvegetated habitat; however, at the channel sites, considerable recruitment has occurred prior to the February sampling dates. Much of this channel production has been consistently lost from all size-classes ≥1.0 mm by May, thereby causing very low production in the 2-8 mm size range at this time.

Seasonal changes in crustacean size-distribution patterns differed from patterns for the total fauna, although production of crustaceans in the 0.5-4 mm size range was also extremely low in all habitats in May (Fig. 2.11). In the channel habitat, crustacean production was fairly evenly distributed across size-classes, unlike total production which was concentrated in the meiofaunal size classes. Production in the unvegetated habitat was very low at ≈1.4 mm sieve size, with this trough being partly obscured in February when the annual recruitment mode passed through that size.

2.5 Discussion

Measurement of density and production

By using corers of two different sizes, we found that relatively slight changes in sampling gear can result in substantial systematic errors in faunal density estimates. Although such sampling biases have been discussed before (Lewis & Stoner, 1981), they are not widely recognized. Our results indicate that it may not only be misleading to compare densities in studies with different sampling techniques, but also abundances of animals in different habitats sampled using the same method.

Systematic errors were of two types. Firstly, the 150 mm corer produced significantly lower density estimates than the 50 mm corer for 1 and 1.4 mm sieve size animals (and therefore total numbers because these two size classes contribute ≈70% of total macrofauna). In an associated study made using similar techniques, density estimates were found to be lower using the 150 mm corer at 1 mm sieve size but not at 1.4 mm sieve size (Edgar & Shaw, 1993). The most likely reason for the small corer being more efficient at collecting small animals was that the large corer did not hold sediment as well as the small corer when being withdrawn from the substratum. This problem occurred most frequently on well-sorted sands where it was necessary to dig around the corer while it was still embedded in the sediment, and then place an endcap on to hold in the sediment.

The second systematic error was that the two corer types had different efficiencies relative to each other when sampling 2 mm sieve size animals in different habitats. The 150 mm corer appeared to disproportionately undersample animals in the soft sediment substrata, while the 50 mm corer produced underestimates of numbers when used in the seagrass habitat. The poor efficiency of the 50 mm corer in seagrass beds probably has two causes; when the corer is pushed through the above-ground seagrass layer it moves leaves and stems aside, thereby undersampling leaf-associated animals, and when it is pushed below ground the seagrass stems falling across the face of the corer cause muds to be compressed, reducing the amount of sediment which enters the core. These problems in sampling methodology are not confined to hand-held corers but will, if anything, be more acute when remote grabs are used because grabs penetrate into the sediment to a variable depth, depending on the type of grab and hardness of the substratum. Problems sampling seagrass habitats may nevertheless be largely remedied by sampling the above ground vegetation separately from the sediment and rhizomes.

Prior to the commencement of the study, we expected that the 150 mm corer would be more efficient than the 50 mm corer at collecting large animals because mobile animals could more easily swim out of the path of the small corer on its approach (Kajak, 1963). While we did not collect sufficient numbers of large sized-animals with the small corer to statistically test differences between corers, we now do not consider faunal escapement to have been a major problem. Both corers collected benthic fishes, with 150 mm cores sampling six fish species during the study and 50 mm cores two species.

Any errors in density measurements have also been incorporated into production estimates, as were errors caused by the use of constants to convert abundance data to biomass data and biomass data to production data. Errors in the conversion of abundance to biomass data should be relatively minor (<10%) because the larger bivalves which contribute most biomass at the primary sites were measured directly, and because the mean weight of animals retained per sieve has a small standard error when >5 animals are collected (Edgar, 1990a).

The major source of inaccuracy in production estimates was probably introduced when biomass data were converted to production rates. Edgar (1990a) cautioned against the use of production/biomass equations when communities are dominated by one or two species, as is the case here for infaunal assemblages, because the dominant species may have atypically high or low production levels which introduce a large error into the community estimates. While keeping this warning in mind, we have nevertheless calculated production rates using this method as it was the only method practicable. Errors in production introduced in this way would be higher for infauna than for epifauna. They are also more likely to have caused annual production of infauna to be overestimated rather than underestimated because old animals, such as large individuals of the bivalves *Anadara trapezia* and *Tellina deltoidalis,* which contribute substantially to total production at the primary seagrass sites, generally have lower P/B ratios than young animals of the same body size (Edgar, 1990a).

Estimates of macrofaunal production determined in this study are comparable to those reported elsewhere, although it should be noted that few new production estimates would fall outside the large range reported in the literature for unvegetated sites of 1.7 $g.m^{-2}.yr^{-1}$ (Buchanan & Warwick, 1974) to 345 $g.m^{-2}.yr^{-1}$ (Möller & Rosenberg, 1983). Möller et al. (1985) summarised data on the annual production and biomass of infaunal communities at sites studied prior to that time. Most community P/B ratios fell between 1 and 5, with the two most comparable sites to our primary localities being the intertidal mudflat sites studied by Warwick & Price (1975) (P/B = 1) and Nichols (1977) (P/B = 4.5). Our P/B ratios for unvegetated habitats (P/B = 2.5 to 3.0) are intermediate between these values.

Robertson (1984) estimated annual production rates for macrofauna at Crib Point, Western Port in 1975/76 by determining the growth of cohorts of the three dominant species and using approximate production/biomass ratios to estimate the production of other animals. Total production at Crib Point was estimated to be ≈38 $g.m^{-2}.yr^{-1}$ in dense seagrass beds and ≈23 $g.m^{-2}.yr^{-1}$ in areas with no seagrass or a very light seagrass cover. While these values appear considerably lower than the values reported for our primary sites, Robertson (1984) sampled few large molluscs at Crib Point, so his faunal biomass values (8.98 $g.m^{-2}$ in bare or nearly bare areas, ≈13 $g.m^{-2}$ in the dense bed) are also correspondingly low. Data provided in his paper indicates community P/B ratios of 2.6 and 2.9 in the bare and dense seagrass areas, virtually identical to the P/B ratios calculated here for our primary localities. In a study of Western Australian seagrass communities that used similar sampling protocol to that used here (Edgar, 1990b), the P/B ratios in *Heterozostera* habitats where few large molluscs were collected were much higher (≈5) than at Western Port. Extremely high annual rates of benthic production (>100 g $AFDW.m^{-2}.yr^{-1}$) and community P/B values (>10) evidently occur in some seagrass beds, as was found by Fredette et al. (1990) in the Lower Chesapeake Bay.

Faunal size-distribution patterns

In Western Port, the shape of the relationship between log body-size and production varied considerably between different sites, with no consistent depression in the relationship occurring at any body size. This differs from the results of several studies in the Northern Hemisphere where animals at ≈1 mm body size have low community biomass (and therefore production) relative to both smaller- and larger-sized animals (Fenchel, 1967; Schwinghamer, 1981; Gerlach et al., 1985). The most frequently cited hypothesis to explain these observations is that energetic inefficiencies hinder animals of 1 mm body size passing through the sediment; smaller animals move through interstitial spaces while larger animals are able to push sand grains aside (Fenchel, 1967; Schwinghamer, 1985). If this hypothesis is correct then one would predict that differences between sites in sediment particle sizes would be reflected in benthos size-structure. Our data do not support this prediction as there was no apparent trend for faunal size-distribution patterns to vary with changes in particle size-distributions. For example, faunal size-distribution patterns in the Rhyll unvegetated habitat were similar to those found in the Tooradin unvegetated habitat (Fig. 2.8), despite muds predominating at Rhyll and sands at Tooradin (Fig. 2.3).

Consequences of seagrass loss

Three different approaches can be used to determine the effect of seagrass loss on associated faunas: (i) comparison can be made between faunas in adjacent vegetated and unvegetated patches, (ii) natural fluctuations in faunas before and after seagrass change can be investigated, and (iii) seagrass can be added or removed from patches, with a comparison then made of manipulated treatments versus controls. All methods possess particular advantages and disadvantages, hence none of these methods are likely to answer all questions concerning the effects of seagrass decline.

The chief disadvantage with investigations of natural patterns is in the assumptions that need to be made. If differences between adjacent seagrass and unvegetated patches are studied, as is the case with the primary localities here, then it is necessary to assume that the physical processes which have caused seagrass loss in the unvegetated sites or seagrass colonisation in the seagrass sites do not also directly influence the fauna. Similarly, if an area is studied before and after seagrass decline, as is the case with the Crib Point data, then it is necessary to assume that general environmental conditions are similar at the times of the different samplings. Ideally, samples should be collected from unvegetated patches before and after the period of seagrass change and from adjacent seagrass and unvegetated patches, as is the case with the Cowes Bank data, although this method does not preclude the possibility that interactive changes between habitats and long-term conditions occur which will confound the interpretation of results. Because changes in seagrass distribution occur unpredictably, data collected using this method could not be replicated at a second locality during our study, and, unfortunately, the Cowes Bank data were not representative of the majority of habitats bay-wide because sediments consisted of mobile sands with little organic matter rather than the more typical muds.

While it is possible that our data for the primary localities are confounded by environmental parameters, independent of seagrass structure, acting differently on macrofaunas associated with vegetated and unvegetated habitats, we consider that differences between these habitats can principally be attributed to the effects of seagrass because vegetated and unvegetated habitats were interspersed within locality. Differences between habitats in the major physical parameters (temperature, salinity, light, nutrients) were therefore slight compared to the direct and indirect differences caused by vegetation structure. The advantage of using this 'natural experiment' approach is that bay-wide patterns can then be studied.

By contrast, manipulative experiments can be designed without the problems of spatial or temporal confounding that are inherent in natural experiments (Homziak et al., 1982). Economic and ethical considerations nevertheless make it impracticable for seagrass patches >10 m diameter to be either removed or established with sufficient replication for powerful statistical tests to be used (see Fonseca et al., 1990). Thus, manipulative methods are particularly appropriate when addressing processes on a small scale but are not so useful at larger ones. Densities of fishes and some invertebrates, for example, are very high on unvegetated habitats immediately adjacent to seagrasses (Thistle et al., 1984; Ferrell & Bell, 1991). The creation of small scale (e.g., 2 m diameter) patches of bare substrata in seagrass beds may consequently cause little change to animal abundances whereas the loss of large beds (>100 m^2) may result in precipitous faunal declines.

Species richness and faunal composition

Of the faunal parameters investigated here, scale is of particular relevance when the consequences of seagrass decline to invertebrate species richness are discussed. On the smallest scale studied, the scale of individual cores, seagrass habitats possessed approximately twice the species richness of unvegetated and channel habitats. However, channel habitats had lower levels of similarity between sites than other habitats, with the consequence that the total number of species collected from channel habitat in the three primary localities was similar to the number of species collected from seagrass habitat.

A trend existed for species richness to be greater in seagrass than adjacent unvegetated habitats, as well as a trend for species richness to increase between low water mark and shallow (≈5m), subtidal depths in unvegetated habitats. The first trend was presumably a consequence of the structural heterogeneity of seagrasses providing a habitat for epifaunal species which cannot survive on bare substrata (see, e.g., Lewis, 1984; Edgar, 1990b), while the second trend may have been caused by differences in substrata or in water flow between sites providing microhabitats for different species (O'Gower & Wacasey, 1967), or by greater environmental stability at depth (Sanders, 1968). If both trends do not interact strongly, then we would predict that macrofaunal species richness of subtidal seagrass beds would be considerably higher than that of any of the habitats studied. The extent of any interaction between depth and seagrass structure in their effect on species richness cannot be assessed now because all beds >2 m depth have been lost from Western Port. Seagrasses once extended to 5 m depth in many parts of the Bay (Shepherd et al., 1989), but, because of increases in turbidity, have been lost from subtidal areas during the past 15 years. While the effect of this loss on total numbers of species in Western Port cannot now be determined, potentially it was considerable. Coleman et al. (1978) recognized 572 species amongst the 19,600 individuals collected during their study, albeit from 41 sampling stations, compared to 483 species among 20,160 individuals collected from 12 sites here.

No major changes in the species composition of shallow communities can be attributed to seagrass loss in Western Port since the 1970s. Of the species considered common in the study by Coleman et al. (1978), only two species were rare (fewer than five specimens collected) in our study. These bivalve species, *Notocallista diemenensis* and *Katelysia rhytiphora*, were infaunal species associated with bare sediments so were unlikely to be directly associated with seagrass loss. Rather than a loss of species, there is some evidence that particular molluscs have increased in abundance in seagrass habitats in 1989/90. *Diala suturalis, Styliferina translucida, Cantharidella tiberiana* and *Pseudoliotia micans* (see Table 2.2) were not recorded in the earlier surveys; *Diala suturalis* (= *Diala varia*), *Styliferina translucida* (= *Alba translucida*) and *Cantharidella tiberiana* were, however, common at Crib Point in 1977 (Daly, 1977), and *Diala suturalis* (as *Diala varia*) was recorded in 1965 from the same site (Coleman, 1976).

Faunal production and biomass

Seagrass loss in Western Port has resulted in little, if any, immediate loss of macroinfaunal production. However, assuming that extant seagrass beds had similar macrofaunal production levels to pre-existing beds, epifaunal production declined from ≈17.2 to 3.3 g AFDW.$m^{-2}.yr^{-1}$ in the areas of seagrass loss. Given that 178 km^2 of former seagrass habitat is now unvegetated and that most of the seagrass loss has occurred on the shallow tidal flats studied at the primary sites (Shepherd et al., 1989), total epifaunal production throughout Western Port is estimated to have annually declined by ≈2,500 tonnes AFDW. This estimate does not take into account animals smaller than 1 mm sieve size, and so is conservative. The size-distribution of animals has also changed following seagrass loss because production in the meiofaunal and lower macrofaunal size-range (i.e., 0.125-8 mm sieve size) in unvegetated habitats is about half the corresponding levels in seagrass beds (see Figs 2.8 and 2.10), while the production of larger animals is similar in the two habitats.

Both the size-distribution shift and the decline in epifaunal production following seagrass loss may well produce flow-on effects to epibenthic carnivores. Fish and predatory decapods prefer to consume epifauna rather than infauna (Virnstein, 1977; Nelson, 1979; Orth et al., 1984), and the juvenile fishes that settle in shallow habitats in high numbers predominantly consume prey in the 0.25 mm to 2 mm sieve size range. Following seagrass loss, there is thus a considerable decline in the availability of food to juvenile fishes.

In addition to the direct effects of seagrass beds on macrofauna, the presence of seagrasses may indirectly enhance benthic production by fueling the detritivorous food web through the input of decaying plant material. The trophic importance of seagrass detritus to infaunal species inhabiting unvegetated habitats has not been assessed in this study. The significant correlation found between infaunal production and the amount of organic material in sediments nevertheless indicates that production of infauna may be partly dependent on seagrass detritus bound in sediment, although the meagre evidence available provides no indication that the densities of detritivores have changed substantially between the earlier studies and the present.

Table 2.1. Results of three-way ANOVA (fixed factors: month and habitat, random factor: locality) using data on the number of macrofaunal species collected per core.

Factor	Hypothesis	DF	SS	F
Month (M)	M/ML	3	460	2.05
Habitat (H)	H/HL	2	12100	9.20*
Locality (L)	L/E	2	2320	33.10***
Month*habitat (MH)	MH/MHL	6	114	0.68
Month*locality (ML)	ML/E	6	449	2.14
Habitat*locality (HL)	HL/E	4	2630	18.80***
Month*habitat*locality (MHL)	MHL/E	12	336	0.80
Error (E)		144	5040	

Table 2.2. Total numbers of dominant species in terms of abundance and biomass collected at different sites - Peck Point seagrass (PPS), Rhyll seagrass (RS), Tooradin seagrass (TS), Peck Point unvegetated (PPU), Rhyll unvegetated (RU), Tooradin unvegetated (TU), Peck Point channel (PPC), Rhyll channel (RC), Tooradin channel (TC), Cowes Bank seagrass (CBS), Cowes Bank unvegetated (CBU), Loelia Shoal (LS).

Species	Sites											
	PPS	RS	TS	PPU	RU	TU	PPC	RC	TC	CBS	CBU	LS
Paradexamine churinga Barnard	120	165	105	8	0	3	0	2	0	156	1	0
Tethygeneia sp.	88	44	180	2	0	5	1	2	4	98	0	0
Maera mastersi (Haswell)	1	0	2	3	5	3	34	77	1	0	0	0
Ceradocus rubromaculatus (Haswell)	0	0	0	0	0	0	64	12	0	0	0	0
Urohaustorius sp.	0	0	0	0	0	0	17	0	0	1	70	0
Byblis sp.	0	0	0	0	0	0	0	0	0	1	41	0
Leptochelia sp.	25	53	6	0	4	2	7	2	2	0	0	0
Halicarcinus ovatus Stimpson	27	47	34	1	0	0	9	1	4	24	0	0
Macrophthalmus latifrons (Haswell)	0	0	0	0	11	10	0	0	1	0	0	0
Halicarcinus rostratus (Stimpson)	7	1	3	1	0	0	11	0	4	3	1	0
Alpheus euphrosyne De Mann	1	3	13	0	5	3	0	0	2	0	0	0
Callianassa spp.	4	5	36	25	7	40	19	17	27	14	5	41
Nebalia sp.	0	0	0	0	0	0	42	0	0	0	0	0
Nassarius pyrrhus (Menke)	77	68	40	2	42	11	32	0	10	13	3	1
Diala suturalis (Adams)	675	2	23	2	0	0	35	0	0	0	0	0
Styliferina translucida (Hedley)	158	5	23	0	0	0	0	0	0	0	0	1
Pseudoliotia micans Adams	175	120	173	0	40	73	4	0	8	0	0	0
Cantharidella tiberiana (Crosse)	254	29	1	0	0	0	0	0	0	0	0	0
Rissoidae sp.	6	19	137	24	5	9	6	1	17	15	2	27
Theora lubrica (Adams)	0	0	6	0	0	4	0	0	4	0	0	112
Tellina spp.	51	127	57	1	33	35	59	0	10	0	0	0
Laternula gracilis (Reeve)	12	24	1	0	19	1	0	0	3	0	0	0
Anadara trapezia (Deshayes)	13	69	3	0	3	9	0	0	0	0	0	0
Pecten fumata Reeve	105	14	0	0	0	0	1	0	0	0	0	0
Neotrigonia margaritacea Lamarck	0	0	0	0	0	0	7	32	2	3	0	0
Notospisula trigonella (Lamarck)	0	0	1	0	119	27	1	0	73	0	0	0
Mysella donaciformis Angas	9	2	1	13	4	20	19	0	39	78	9	4
Barnea australasiae (Sowerby)	0	0	0	40	0	0	0	0	0	0	0	0
Nephtys australiensis (Fauchald)	110	233	70	17	103	67	64	15	43	88	26	26
Armandia sp.	14	0	3	10	2	0	72	56	0	0	16	1
Lumbrineris sp.	39	46	15	40	36	29	46	32	16	63	23	4
Phyllodocidae sp.	29	12	3	5	29	25	9	4	12	6	4	20
Harmothoe sp.	93	72	57	4	6	2	16	20	12	5	0	0
?*Leitoscoloplos* sp.	4	6	24	61	10	35	18	24	24	15	24	0
Terebellides sp.	377	346	118	0	2	4	18	1	1	6	0	0
?*Isolda* sp.	0	0	0	2	3	103	0	3	24	0	0	0
Pherusa sp.	157	58	16	0	0	2	56	0	0	0	0	2
Cirratulidae sp.	52	16	16	3	18	11	37	11	30	15	2	11
Spionidae sp.	99	127	90	5	273	84	14	3	1	7	0	8
?*Barantolla* sp.	241	1433	184	69	424	267	106	108	43	197	23	167
Number of cores collected	30	30	25	25	25	20	25	25	20	20	25	20

Table 2.3. Faunal similarities between pairs of sites as calculated using Jaccard (below diagonal) and Spearman ρ (above diagonal) coefficients.

	Sites											
Sites	PPS	RS	TS	PPU	RU	TU	PPC	RC	TC	CBS	CBU	LS
Peck Pt seagrass (PPS)	1	0.76	0.61	0	0.07	0.08	0.13	0	-0.07	0.23	-0.05	0.12
Rhyll seagrass (RS)	0.59	1	0.77	0.3	0.36	0.39	0.42	0.05	0.24	0.38	0.06	0.19
Tooradin seagrass (TS)	0.49	0.51	1	0.25	0.31	0.47	0.34	0.22	0.4	0.5	0.14	0.34
Peck Pt unvegetated (PPU)	0.27	0.15	0.3	1	0.34	0.43	0.35	0.48	0.47	0.4	0.56	0.53
Rhyll unvegetated (RU)	0.32	0.32	0.38	0.3	1	0.79	0.34	0.29	0.72	0.18	0.26	0.37
Tooradin unvegetated (TU)	0.27	0.32	0.34	0.3	0.42	1	0.28	0.2	0.73	0.28	0.29	0.47
Peck Pt channel (PPC)	0.42	0.15	0.28	0.32	0.36	0.22	1	0.47	0.33	0.3	0.36	0.38
Rhyll channel (RC)	0.29	0.31	0.23	0.34	0.23	0.21	0.36	1	0.31	0.43	0.27	0.26
Tooradin channel (TC)	0.3	0.29	0.31	0.27	0.38	0.4	0.34	0.23	1	0.41	0.36	0.46
Cowes Bank seagrass (CBS)	0.36	0.35	0.32	0.27	0.25	0.24	0.34	0.27	0.27	1	0.5	0.15
Cowes Bank unvegetated (CBU)	0.16	0.14	0.17	0.22	0.2	0.21	0.21	0.17	0.22	0.24	1	0.22
Loelia Shoal (LS)	0.1	0.14	0.15	0.21	0.17	0.19	0.14	0.18	0.17	0.4	0.53	1

Table 2.4. Mean abundances (m^{-2}) of invertebrates collected using spade corers from Crib Point on 22 June 1974 and Rhyll on 16 June 1975 (see Table I in Watson et al., 1984). Mean densities (m^{-2}; ±95% confidence intervals) of invertebrates recorded during the present study from seagrass and unvegetated habitats at Crib Point on 29 August 1990 and Rhyll on 14 August 1991 are also shown.

	Crib Point			Rhyll		
	Watson et al.	Present study		Watson et al.	Present study	
Species		Seagrass	Unvegetated		Seagrass	Unvegetated
Nemertinea	5.0	102±42	0	23.1	11.3±22.2	0
Haploscoloplos	0.6	22.6±27.2	34.0±27.2	26.2	0	0
Barantolla	73.9	1109±455	113±168	644.4	2990±1430	792±405
Armandia	173.9	169±78	0	67.0	11.3±22.2	0
Cirratulidae	3.3	79.2±56.6	0	65.0	56.6±85.9	125±190
Dorvillea	17.2	67.9±81.5	0	25.7	125±158	0
Lumbrineris	17.8	11.3±22.2	22.6±27.2	40.7	272±197	102±95
Glycinde	0.6	0	0	35.1	56.6±70.1	34.0±44.4
Nephtys	350.0	577±200	22.6±27.2	203.8	577±430	215±82
Platynereis	52.8	158±108	0	8.3	374±599	0
Phyllodoce	4.4	57±111	56.6±35.1	36.5	45.3±22.2	67.9±81.5
Syllidae	1.1	453±161	0	11.0	283±235	56.6±70.1
Spionidae	13.9	147±134	306±354	22.4	407±334	0
Terebellidae	163.4	260±114	0	59.0	487±413	22.6±27.2
Tellina deltoidalis	15.6	181±95	11.3±22.2	91.9	340±213	272±346
Callianassa	56.1	11.3±22.2	136±103	156.1	11.3±22.2	0
Litocheira bispinosa	20.6	11.3±22.2	0	0	11.3±22.2	0
Halicarcinus ovatus	11.1	11.3±22.2	0	15.1	45.3±41.5	0
Halicarcinus rostratus	32.8	0	0	8.4	0	0
Macrophthalmus latifrons	18.3	0	34.0±44.4	17.5	0	22.6±27.2
Alpheus	30.6	34.0±27.2	0	12.7	0	11.3±22.2
Gammaridea	845.0	498±197	34.0±44.4	256.6	781±388	0
Paratanais (= *Leptochelia*)	98.3	125±95	11.3±22.2	2.8	204±181	22.6±27.2
Anthuridae	0	249±134	0	0.6	113±172	0
Mysidacea	0.6	521±266	0	1.7	0	0

Table 2.5. Mean numbers (±SE) of invertebrates recorded by Coleman et al. (unpublished data) in 0.1 m^2 Smith-McIntyre benthic grab samples from seagrass habitat near Peck Point (Station 1716) and near Tooradin (Stations 1706 and 1708) during January 1974 (see Coleman et al., 1978). Mean densities (±SE) of invertebrates (expressed per 0.1 m^2 area of substratum) recorded during the present study on November and February sampling dates are also shown.

	Coleman et al.		Present study	
Species	Peck Pt	Tooradin	Peck Pt	Tooradin
Paradexamine churinga	0	3.3±1.8	18.3±12.9	23.6±7.4
Tethygeneia sp.	7.0±5.5	2.8±1.3	16.5±10.7	53.1±15.8
Cymadusa sp.	2.0±0.6	4.0±1.8	2.4±2.4	3.1±1.5
Corophium sp.	0	4.8±2.1	0	0
Leptochelia sp.	5.0±3.1	2.2±1.3	7.4±3.4	1.5±1.4
Pontophilus intermedius	0	1.8±0.7	1.7±2.2	1.1±1.0
Litocheira bispinosa	1.3±0.9	7.5±1.5	0	1.1±0.7
Halicarcinus ovatus	1.0±0.6	4.2±1.3	8.0±3.8	12.5±4.9
Nassarius pyrrhus	0	0	14.3±5.3	8.0±2.0
Diala suturalis	0	0	122.4±57.0	6.5±4.2
Styliferina translucida	0	0	42.1±21.6	8.0±4.2
Pseudoliotia micans	0	0	59.9±37.4	58.0±20.0
Tellina spp.	1±1	6.0±2.4	10.3±4.0	19.0±4.9
Nephtys australiensis	50.0±20.0	51.0±15.0	16.0±5.3	17.1±3.3
Armandia sp.	3.7±2	0.8±0.3	3.4±2.4	0.4±0.5
Lumbrineris sp.	0	0	5.6±3.1	5.3±1.8
Harmothoe sp.	0	0	21.0±5.4	18.7±4.4
Exogone sp.	0.3±0.3	4.7±2.1	6.3±6.2	1.5±0.8
Terebellides sp.	4.7±2.6	4.0±1.7	83.8±30.7	19.8±4.9
Pherusa sp.	8.0±3.0	0	48.4±10.5	2.7±1.7

Table 2.6. Total annual production ($g.m^{-2}.yr^{-1}$), mean annual biomass ($g.m^{-2}$) and annual production/biomass (P/B) ratios for macrofauna at the sites studied.

Habitat	Annual Production ($g.m^{-2}.yr^{-1}$)	Mean Biomass ($g.m^{-2}$)	P/B
Peck Point seagrass	79.8	29.7	2.69
Rhyll seagrass	106	43.1	2.46
Tooradin seagrass	50.7	19.6	2.59
Peck Point unvegetated	58.9	20.4	2.88
Rhyll unvegetated	82.5	32.7	2.53
Tooradin unvegetated	29.8	9.8	3.04
Peck Point channel	40.7	23.8	1.71
Rhyll channel	52.5	21.4	2.45
Tooradin channel	23.4	7.47	3.13
Cowes Bank seagrass	15.3	3.73	4.09
Cowes Bank unvegetated	5.30	1.55	3.42
Loelia Shoal	7.78	1.70	4.56

Table 2.7. Results of three-way ANOVAs (fixed factors: month and habitat, random factor: locality) using P_{20} data for epifauna, infauna and the total fauna from different habitats at the primary localities.

		Total fauna			Epifauna			Infauna		
Factor	df	SS	MS	F	SS	MS	F	SS	MS	F
Month	3	1.71	0.57	0.66	1.93	0.64	0.50	2.77	0.92	0.71
Habitat	2	25.5	12.7	7.22*	122.0	61.0	7.06*	17.9	8.93	6.48
Locality	2	14.5	7.24	12.9***	3.02	1.51	1.63	17.0	8.48	12.9***
Month*habitat	6	2.52	0.42	0.39	6.91	1.15	3.60*	2.67	0.45	0.36
Month*locality	6	5.19	0.87	1.54	7.73	1.29	1.39	7.83	1.31	1.99
Habitat*locality	4	7.05	1.76	3.14**	34.6	8.64	9.31***	5.51	1.38	2.10
Month*habitat*locality	12	12.9	1.07	1.91*	3.84	0.32	0.34	14.7	1.22	1.86*
Error	144	80.9	0.56		134	0.93		94.6	0.66	

Table 2.8. Results of two-way ANOVAS (fixed factor: core size, random factor: site) using density data for animals of 2 mm, 1.4 mm and 1 mm sieve size.

		Sieve size								
		2 mm			1.4 mm			1 mm		
Source	df	SS	MS	F	SS	MS	F	SS	MS	F
Corer	1	185	185	0.58	6,060	6,060	12.1**	46,400	46,400	69.0***
Site	11	26,200	2380	20.2***	94,700	8,620	25.9***	196,000	17,800	28.7***
Corer*site	11	3,530	321	2.71**	5,520	502	1.51	7,410	673	1.08
Error	454	53,700	118		151,000	332		282,000	621	

Fig. 2.1. Western Port, showing locations of sampling sites.

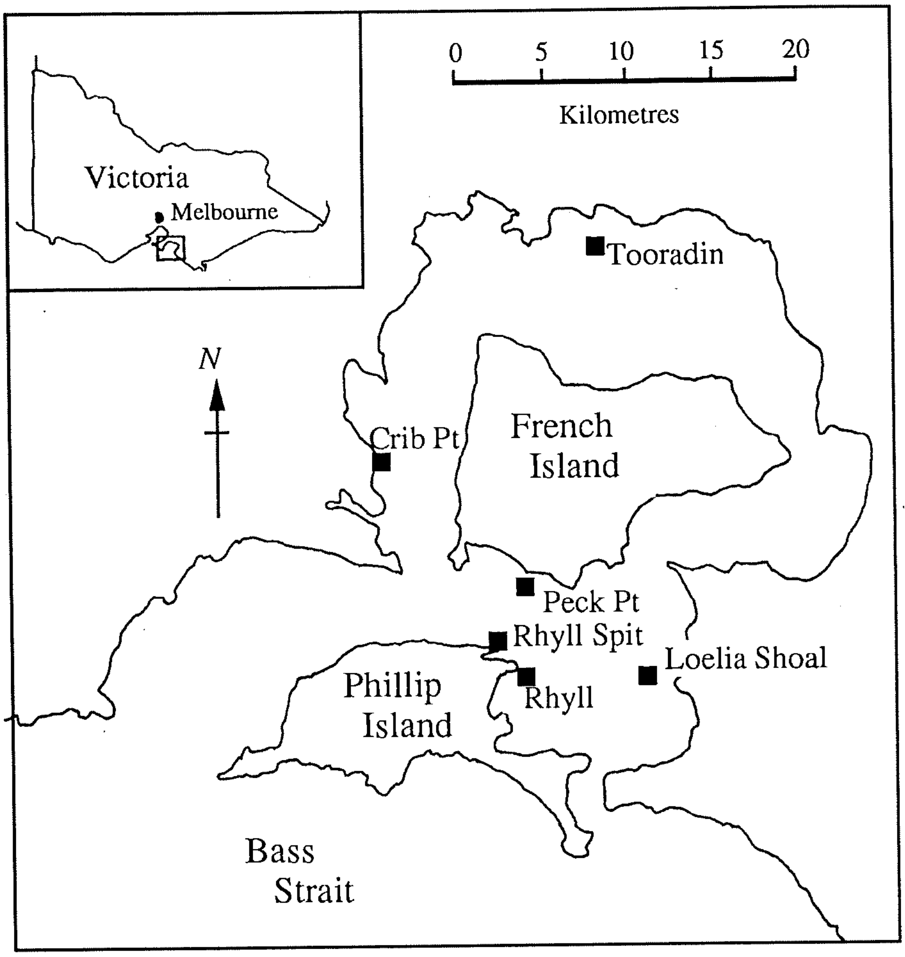

0
5
10
15
20
Kilometres
Victoria
Melbourne
N
Tooradin
Crib Pt
French Island
Peck Pt
Rhyll Spit
Loelia Shoal
Phillip Island
Rhyll
Bass Strait

Fig. 2.2. Seasonal change in mean (± SE) dry weight of above-ground seagrass at different sites.

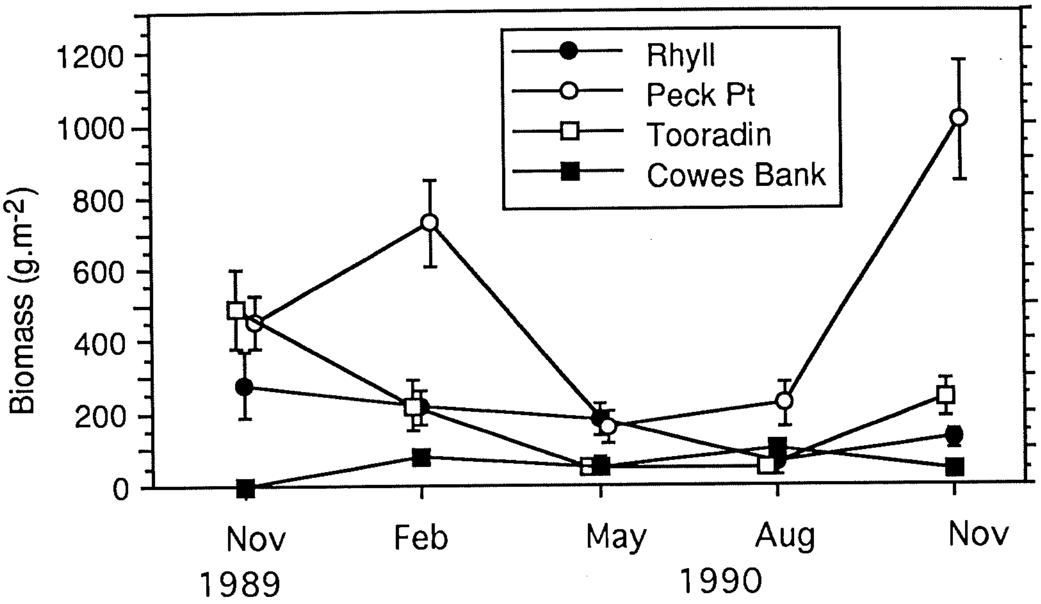

Rhyll
Peck Pt
Tooradin
Cowes Bank
Biomass (g.m-2)
0
200
400
600
800
1000
1200
Nov
1989
Feb
May
Aug
1990
Nov

Fig. 2.3. Percentage of total sediment in each sieve size-class at the sites studied. The organic content of sediment has also been shown after multiplying by a factor of 10 for display (i.e., for the <0.063 mm sieve size class in seagrass habitat at Peck Point, organic material and ash comprised 6.4% and 60%, respectively, of the total dry weight of samples).

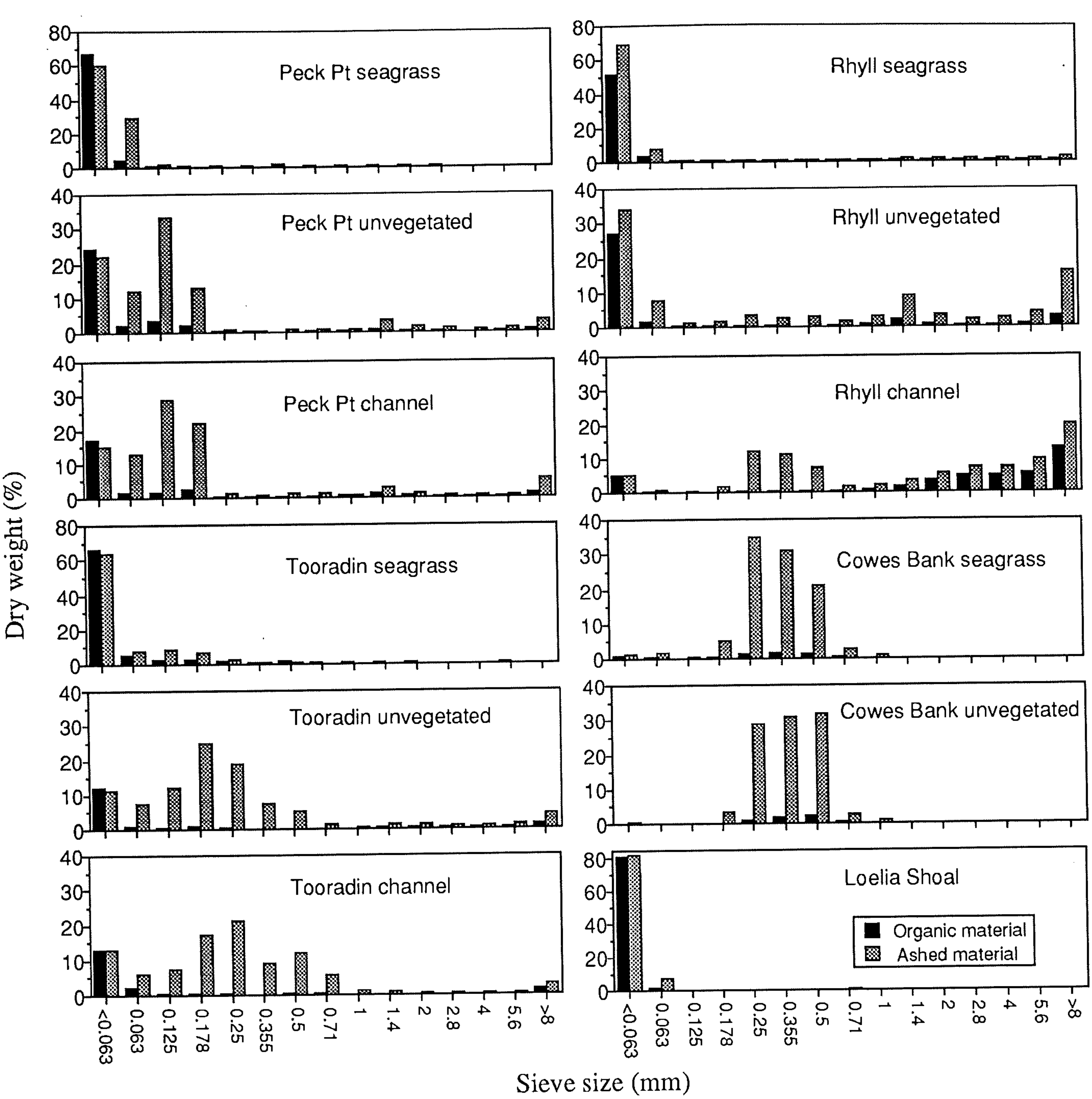

Peck Pt seagrass
Peck Pt unvegetated
Peck Pt channel
Tooradin seagrass
Tooradin unvegetated
Tooradin channel
Rhyll seagrass
Rhyll unvegetated
Rhyll channel
Cowes Bank seagrass
Cowes Bank unvegetated
Loelia Shoal
■ Organic material
▨ Ashed material
Dry weight (%)
0
10
20
30
40
60
80
<0.063
0.063
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
>8
Sieve size (mm)

Fig. 2.4. Total number of macrofaunal species collected at the sites studied.

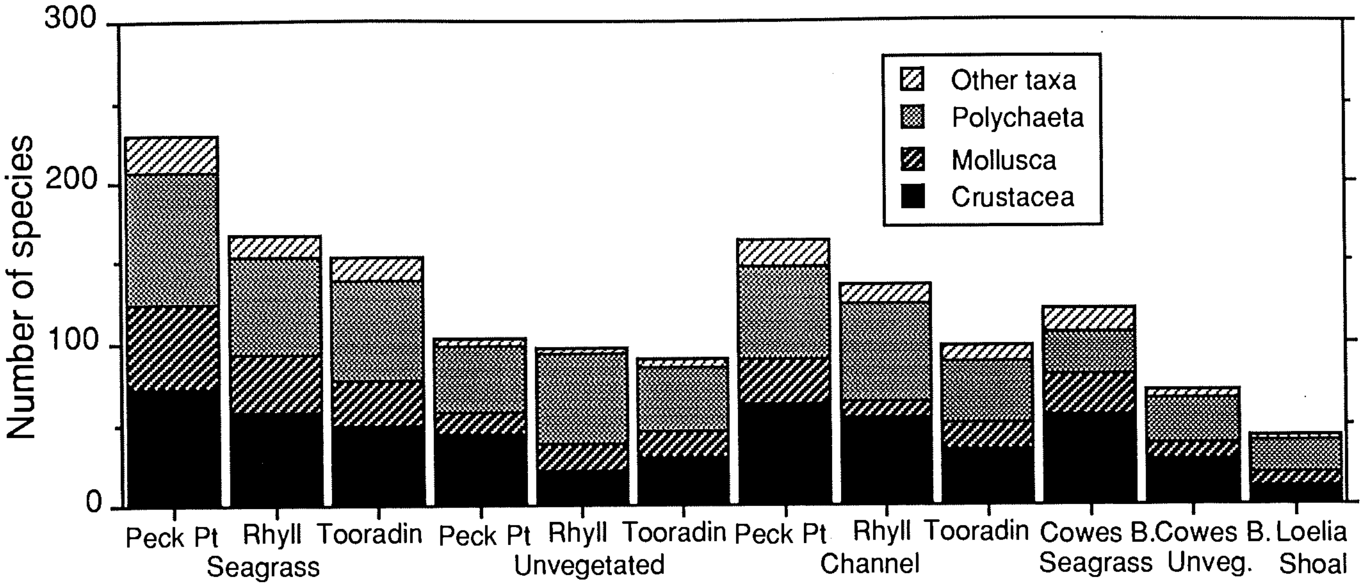

300
200
100
0
Number of species
Other taxa
Polychaeta
Mollusca
Crustacea
Peck Pt
Rhyll
Tooradin
Seagrass
Peck Pt
Rhyll
Tooradin
Unvegetated
Peck Pt
Rhyll
Tooradin
Channel
Cowes B.
Seagrass
Cowes B.
Unveg.
Loelia
Shoal

Fig. 2.5. Estimated biomass (±SE) of macroepifauna and macroinfauna ($g.m^{-2}$) at the sites studied.

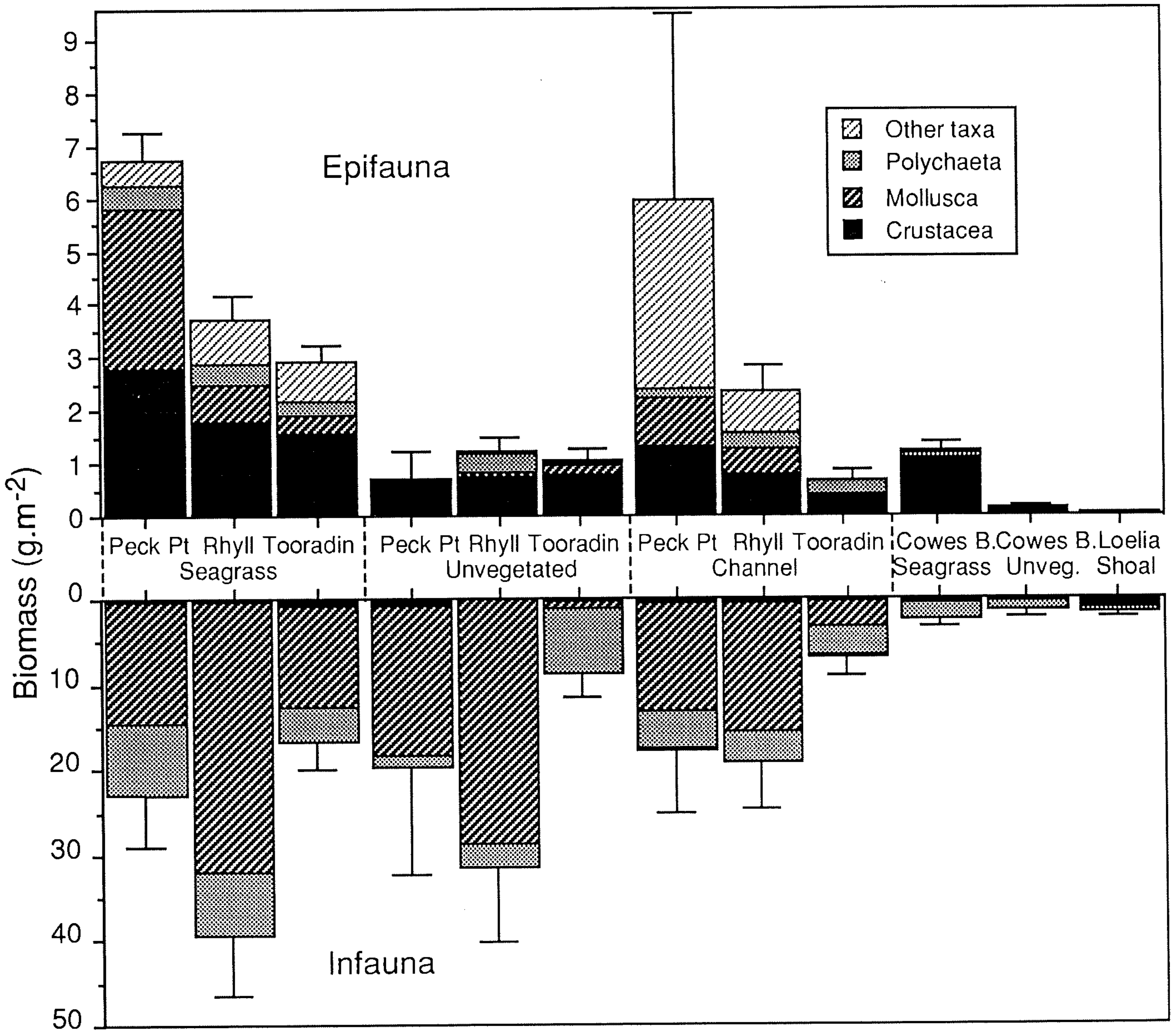

Epifauna
Infauna
Other taxa
Polychaeta
Mollusca
Crustacea
Biomass (g.m-2)
0
1
2
3
4
5
6
7
8
9
0
10
20
30
40
50
Peck Pt
Rhyll
Tooradin
Seagrass
Peck Pt
Rhyll
Tooradin
Unvegetated
Peck Pt
Rhyll
Tooradin
Channel
Cowes B.
Seagrass
Cowes B.
Unveg.
Loelia
Shoal

Fig. 2.6. Estimated annual production of macroepifauna and macroinfauna ($g.m^{-2}.yr^{-1}$) at the sites studied. Error bars indicate the standard deviation in production for the four seasons.

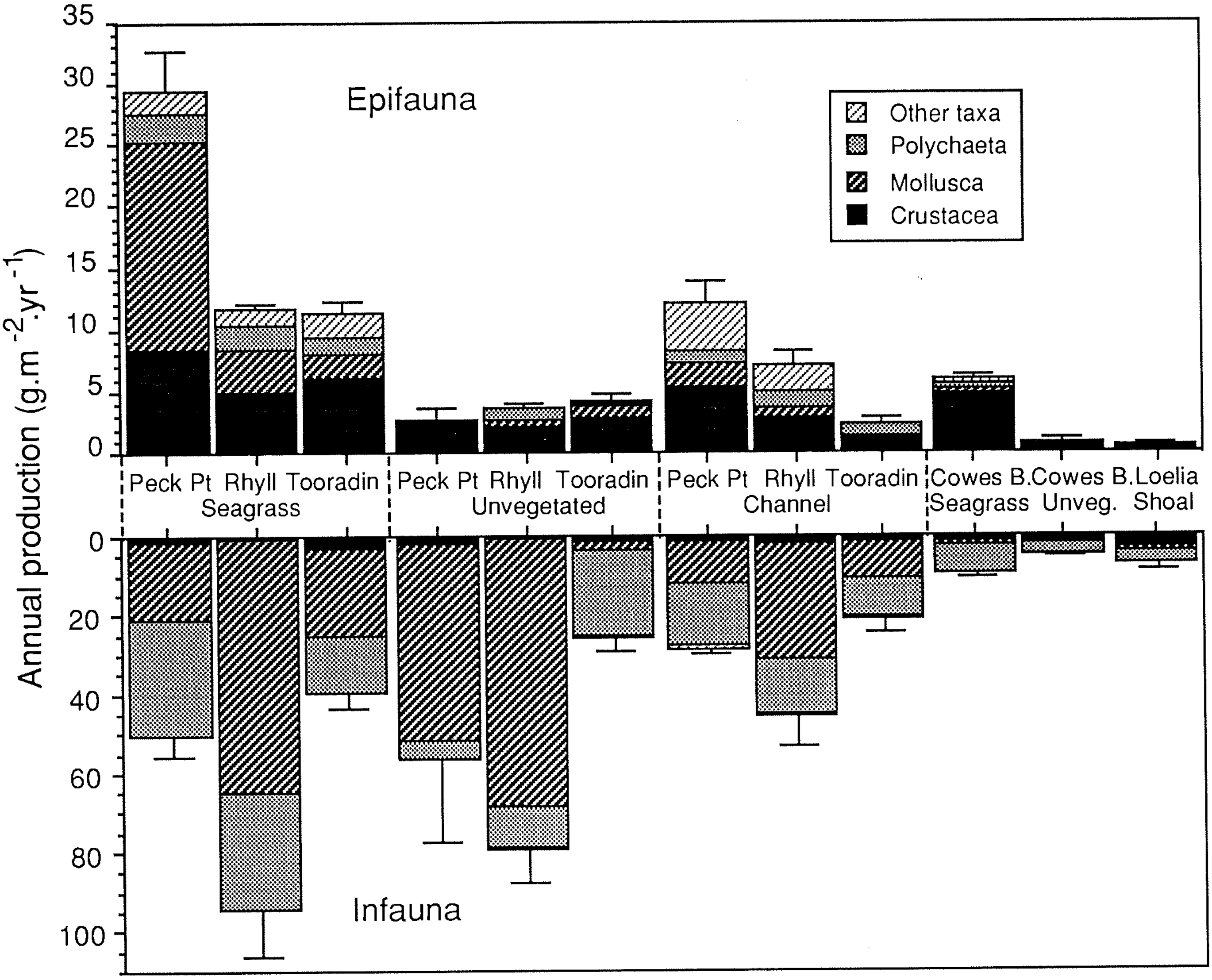

Epifauna
Infauna
Other taxa
Polychaeta
Mollusca
Crustacea
Annual production ($g.m^{-2}.yr^{-1}$)
35
30
25
20
15
10
5
0
20
40
60
80
100
Peck Pt
Rhyll
Tooradin
Seagrass
Peck Pt
Rhyll
Tooradin
Unvegetated
Peck Pt
Rhyll
Tooradin
Channel
Cowes B.
Seagrass
Cowes B.
Unveg.
Loelia
Shoal

Fig. 2.7. Densities (±SD) of invertebrates of 1 mm, 1.4 mm and 2 mm sieve size at different sites, as estimated using corers with two different diameters.

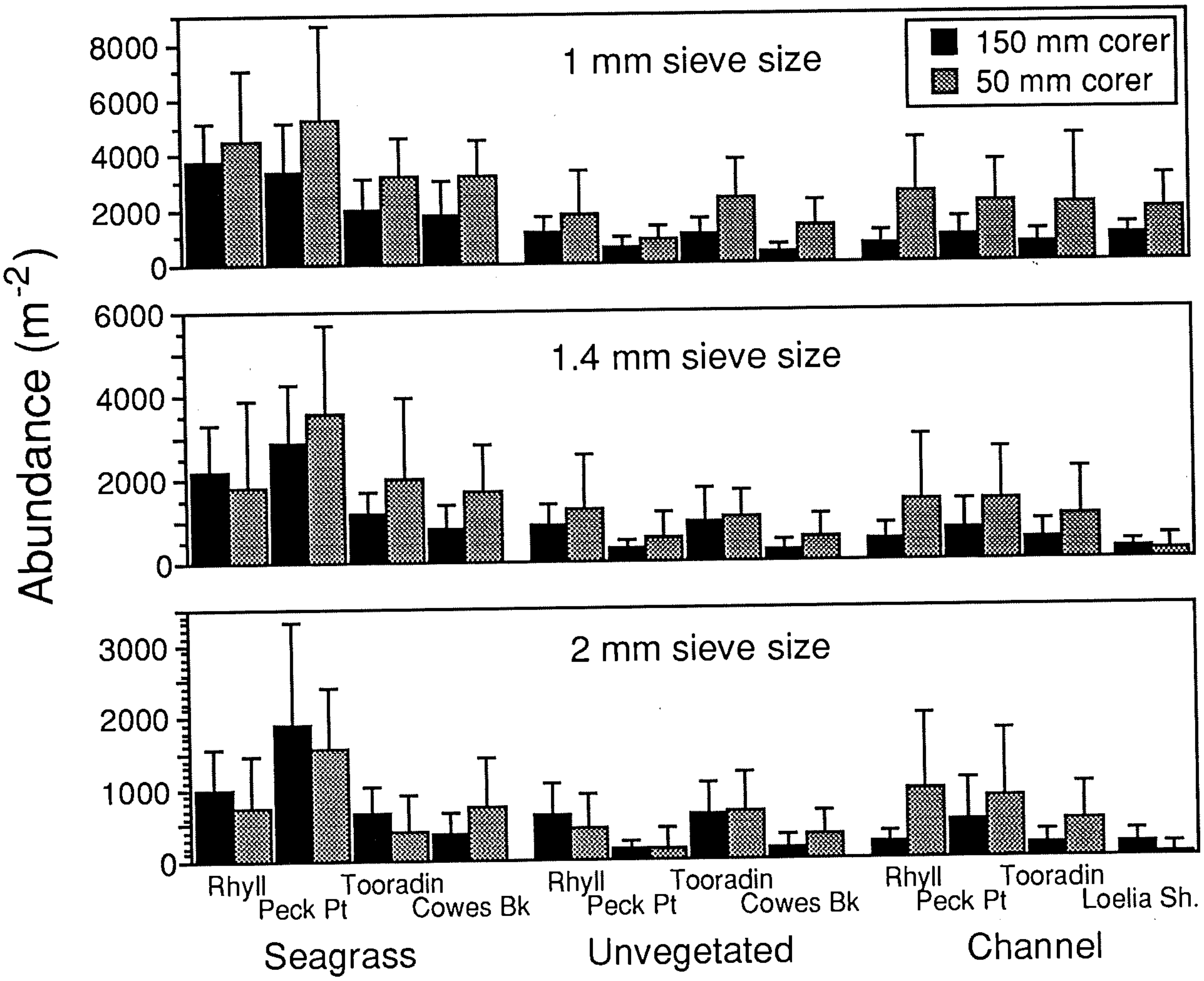

Abundance (m-2)
1 mm sieve size
150 mm corer
50 mm corer
8000
6000
4000
2000
0
1.4 mm sieve size
6000
4000
2000
0
2 mm sieve size
3000
2000
1000
0
Rhyll
Peck Pt
Tooradin
Cowes Bk
Rhyll
Peck Pt
Tooradin
Cowes Bk
Rhyll
Peck Pt
Tooradin
Loelia Sh.
Seagrass
Unvegetated
Channel

Fig. 2.8. Mean P_{20} (±SE) of invertebrates in different sieve size classes at the sites studied. Temperature has not been included in these production estimates but was standardized at 20°C.

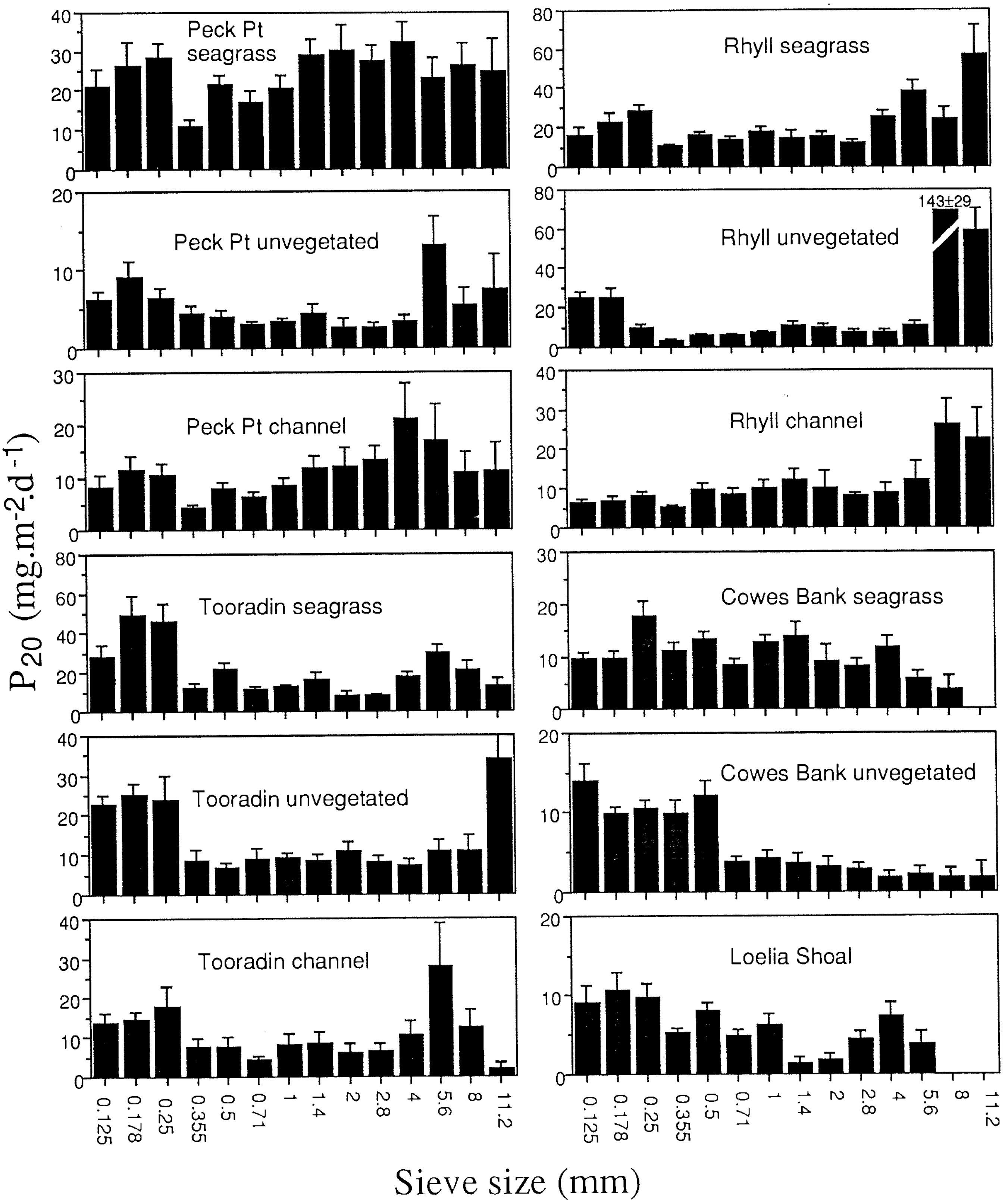

Peck Pt seagrass
Rhyll seagrass
Peck Pt unvegetated
Rhyll unvegetated
143±29
Peck Pt channel
Rhyll channel
Tooradin seagrass
Cowes Bank seagrass
Tooradin unvegetated
Cowes Bank unvegetated
Tooradin channel
Loelia Shoal
P_{20} (mg.m^{-2}.d^{-1})
0
10
20
30
40
60
80
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
Sieve size (mm)

Fig. 2.9. Mean P_{20} (±SE) of crustaceans in different sieve size classes at the sites studied. Temperature has not been included in these production estimates but was standardized at 20°C.

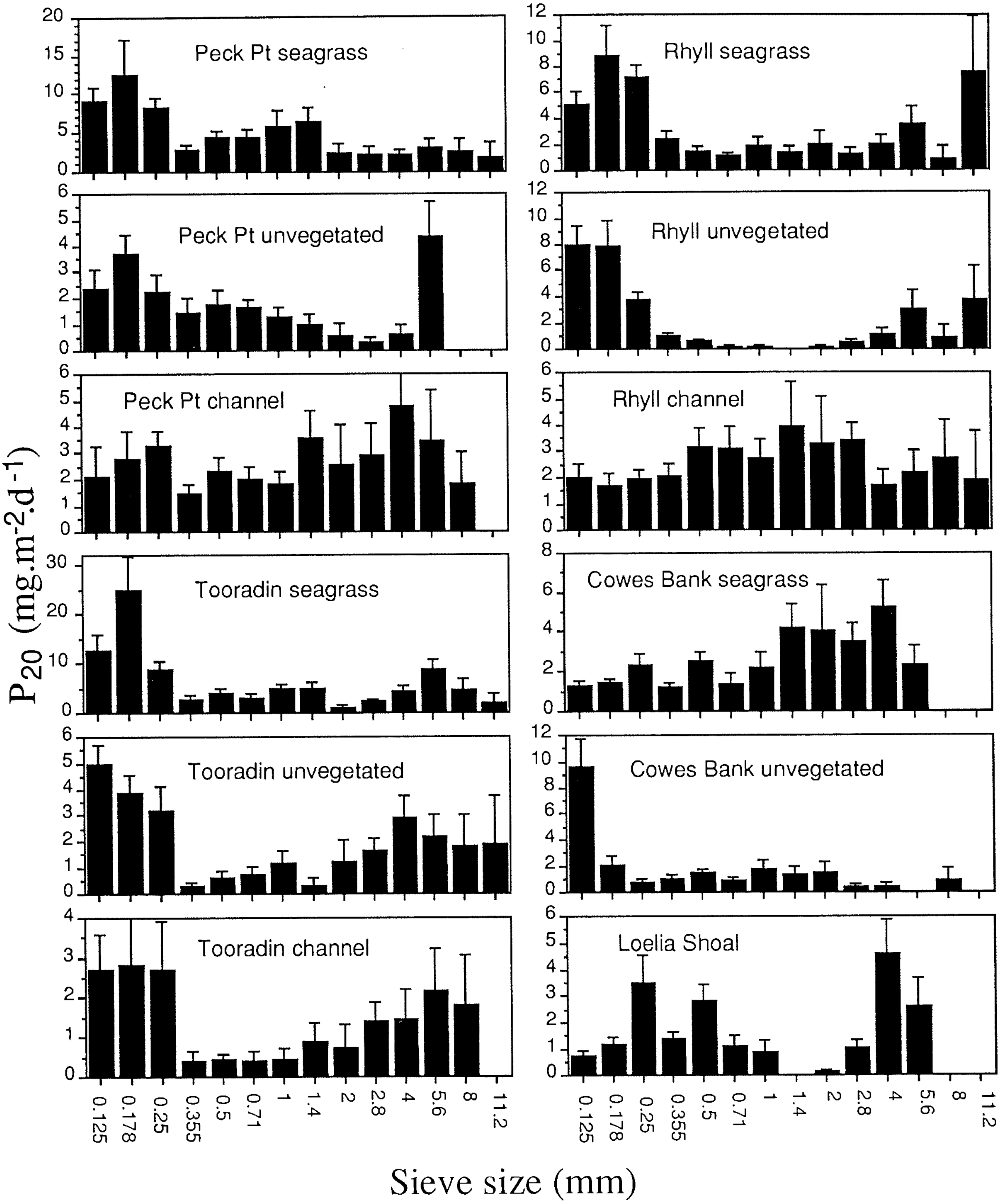

Peck Pt seagrass
Rhyll seagrass
Peck Pt unvegetated
Rhyll unvegetated
Peck Pt channel
Rhyll channel
Tooradin seagrass
Cowes Bank seagrass
Tooradin unvegetated
Cowes Bank unvegetated
Tooradin channel
Loelia Shoal
P_{20} (mg.m^{-2}.d^{-1})
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
Sieve size (mm)

Fig. 2.10. Mean P_{20} of invertebrates in different sieve size classes collected from seagrass, unvegetated and channel habitats at the primary localities during the four sampling months. Error bars indicated the standard deviation of P_{20} estimates from the three primary localities.

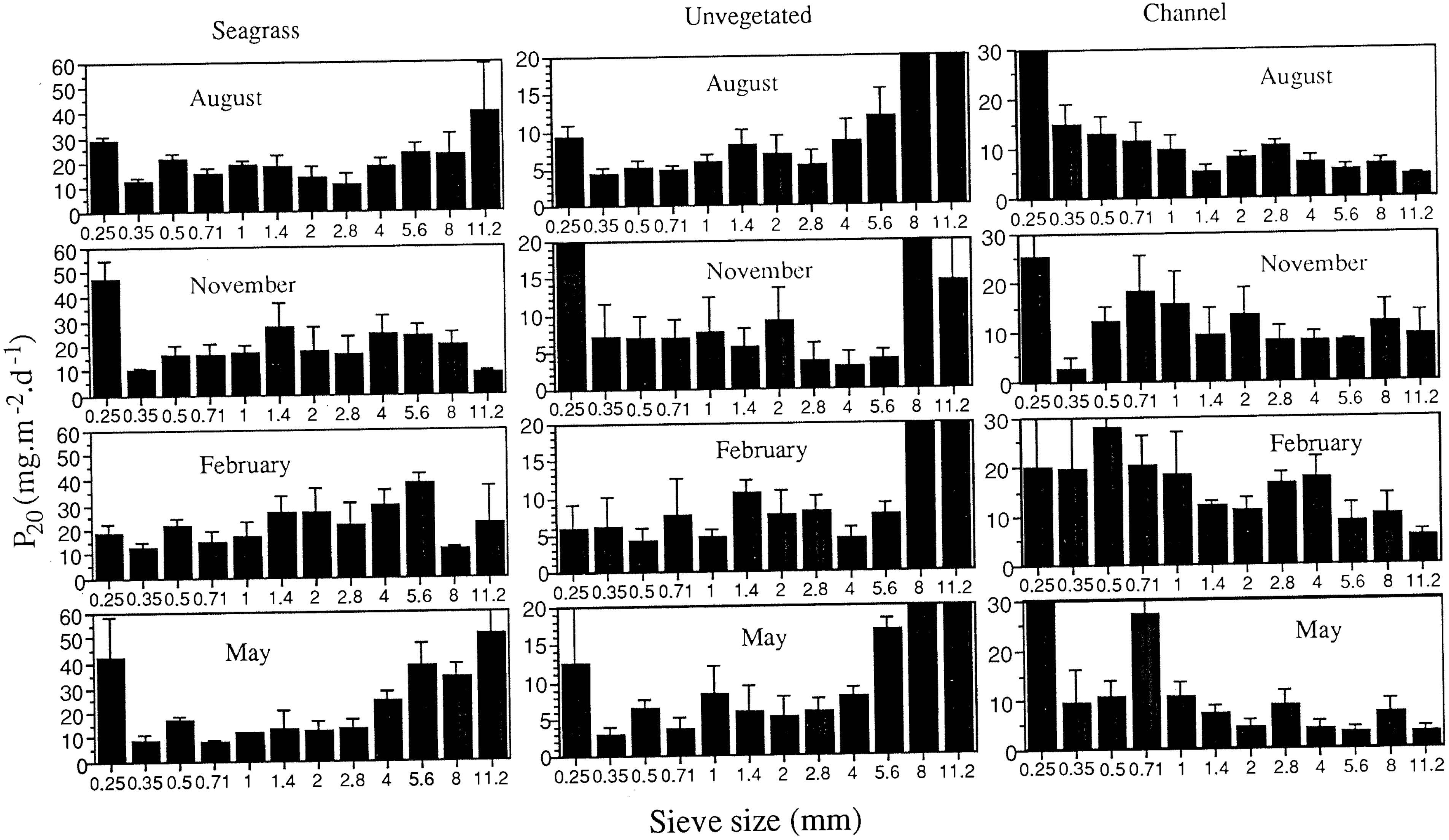
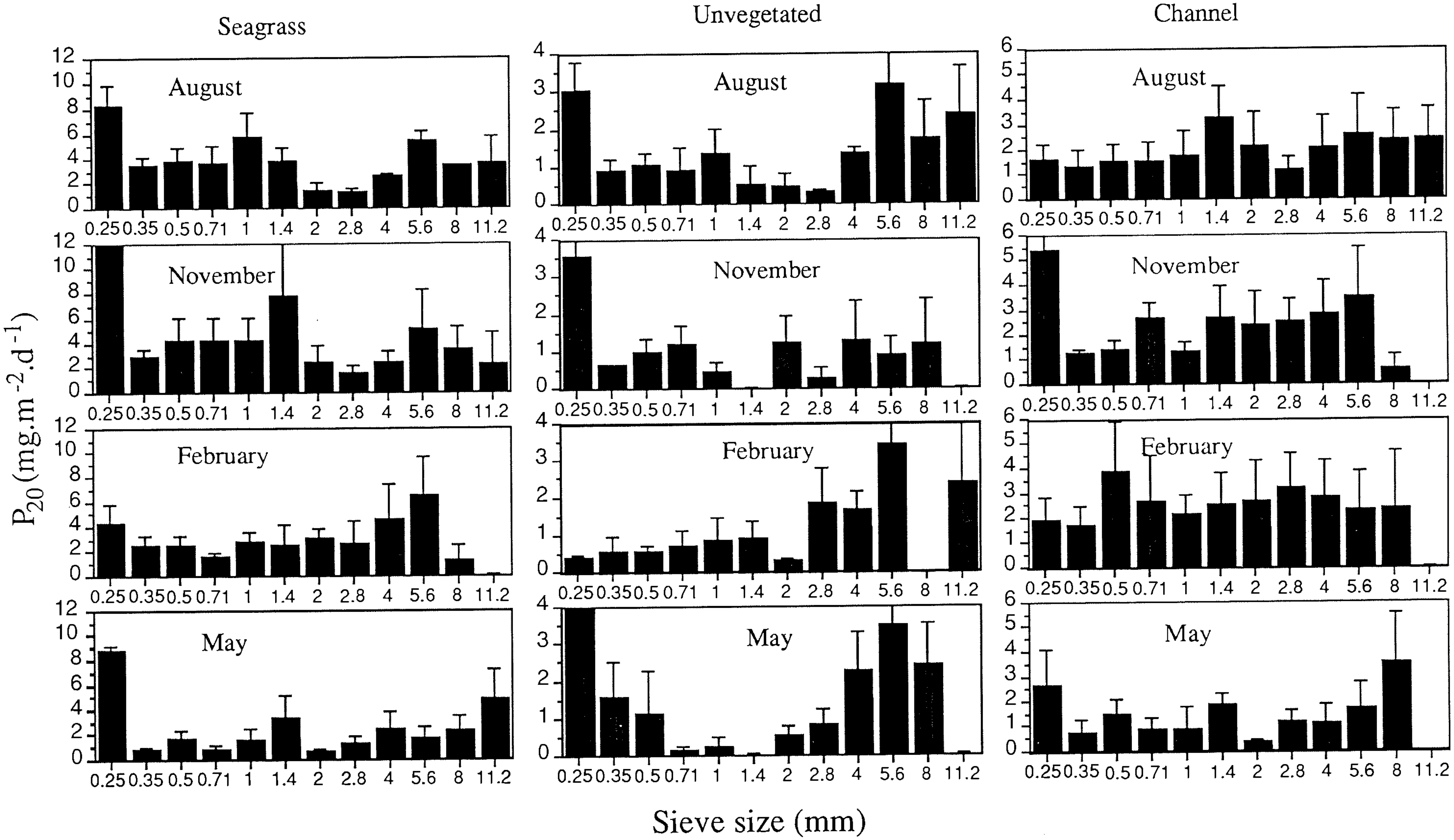

Seagrass
Unvegetated
Channel
August
November
February
May
60
50
40
30
20
10
0
20
15
10
5
0
30
20
10
0
0.25
0.35
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
P_{20} (mg.m^{-2}.d^{-1})
Sieve size (mm)

Fig. 2.11. Mean P_{20} of crustaceans in different sieve size classes collected from seagrass, unvegetated and channel habitats at the primary localities during the four sampling months. Error bars indicated the standard deviation of P_{20} estimates from the three primary localities.


Seagrass
Unvegetated
Channel
August
November
February
May
P_{20} (mg.m^{-2}.d^{-1})
0
2
4
6
8
10
12
0
1
2
3
4
5
6
0.25
0.35
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
Sieve size (mm)

Section 3. Effects of seagrass loss on the species richness, size-distribution and production of fishes in Western Port, Victoria.

3.1 Summary

Approximately twice as many fish species were collected per seine haul from seagrass habitats ($\bar{x}$ = 8.7) as from unvegetated ($\bar{x}$ = 4.7) habitats, with much fewer fishes collected from channel ($\bar{x}$ = 2.3) habitats. The fishes present in seagrass beds within Western Port were widely distributed, so the total number of species present in shallow seagrass habitats has probably changed little since seagrass was much more extensive. A number of coastal species were found at one site (Cowes Bank seagrass) near the entrance to the Bay. These species occurred in low numbers and presumably arrived as pelagic larvae from outside.

Very small fishes (<10 g weight) were much more abundant in seagrass than in unvegetated habitats. However, very few of these small animals belonged to commercially important species. Seagrass beds in Western Port were not found to be more important as nursery habitat for commercial species than unvegetated habitat.

Annual production of small fish assemblages at the primary seagrass sites was estimated to be over twice as productive as at unvegetated sites (5.87 $g.m^{-2}.yr^{-1}$ in seagrass c.f. 2.31 $g.m^{-2}.yr^{-1}$ in unvegetated habitat). The total production of these smaller fishes was very highly correlated with the production of benthic macrofauna, the primary food resource (r = 0.72). Using the same assumptions as used in calculations of losses in macrofaunal production following seagrass dieback, total small-fish production throughout Western Port is estimated to have annually declined by ≈630 tonnes $AFDW.yr^{-1}$ since 1976.

Much of the difference in production of small fishes between habitats did not appear to flow through to the larger, commercial fish species, partly because many of the larger species feed on pelagic rather than benthic food resources. Total catches using large mesh gillnets were similar over seagrass and unvegetated habitats.

3.2 Introduction

Because seagrass and macroalgal beds have a strong effect on fish assemblages in shallow coastal waters, relationships between seagrasses and fishes have been studied at numerous sites worldwide. Although fish densities in seagrass beds are not always higher than bare substrata immediately adjacent to the beds (Ferrell and Bell, 1991), seagrasses generally increase species richness and enhance production of fish assemblages, in the same way that they affect invertebrate assemblages. Fishes nevertheless differ from invertebrates in having a longer lifespan and a relatively long pelagic larval stage, so recruitment presumably plays a more important role in life-history processes than for invertebrate communities. Fishes are also primarily carnivorous, so differ from the majority of benthic invertebrates which feed on algae and detritus. Because many fishes locate prey using visual means, the structural complexity of seagrass habitats should hinder some fish species by concealing prey, as well as aiding others by providing concealment from larger predators.

The primary aims of this section of the project have been to identify differences in the composition and production of fish assemblages associated with seagrass and unvegetated habitats in Western Port, and to determine any general production relationships between invertebrates and fishes. An ancillary aim has been to determine whether seagrass beds have an important nursery function in Western Port, because a widely-accepted paradigm suggests that seagrass beds are nursery grounds for commercially-important fish species (Pollard, 1984). This paradigm has little predictive value because virtually all other marine and estuarine habitats are also nursery grounds for particular commercial fishes; for example, most mud- and sand-flats are utilized by juvenile flatfish as are many reefs by juvenile sparids. The paradigm can be interpreted in a more useful form to mean that seagrass beds support juveniles of more fish species than unvegetated habitats in the vicinity. Surprisingly, this latter hypothesis does not appear to have been empirically tested.

3.3 Methods

Small fishes and epibenthic invertebrates were sampled using a 15 m seine with 3 m drop and 1 mm mesh. Netting was conducted by anchoring a small boat, deploying the net from the boat in a straight line perpendicular to the anchor line and pulling the boat in along the anchor line for 12 m while letting out ropes attached to the two ends of the net. The boat was then retied to the anchor line, and the ropes followed by the net were pulled through the distance of 12 m and into the boat. In depths >2 m the net sank as the leadline was heavily weighted with chain and was much heavier than the floatline. To prevent it lifting from the seabed, the net ropes passed through a 15 kg weight which was clipped around the ropes and dropped overboard before the net was pulled in.

The netting program was conducted in conjunction with the study of benthos described in the previous section. A minimum of four replicate samples were collected from the six Peck Point and Rhyll sites at three monthly intervals between August 1989 and November 1990, at the Cowes Bank seagrass site between February 1990 and November 1990, and at the other five sites between November 1989 and November 1990. Each site was sampled during daylight within four days of the associated benthos sampling date. Seine netting was also carried out at the three Peck Point habitats during the early evening (i.e., two to four hours after sunset) on each sampling occasion between August 1989 and August 1990. Three replicate hauls were done at night.

Larger fishes were sampled using 50 m monofilament gillnets with 2 m drop and equal 64 mm and 108 mm mesh panels. These gillnets were set and retrieved at three hourly intervals over a nine hour period centred on sunset. They were thus set for three hours during the day, three hours over dusk and three hours at night. Because of its labour intensive nature, gillnetting was conducted at fewer sites and on fewer occasions than seine netting. Gillnet samples were collected from seagrass, unvegetated and channel habitats at Rhyll and Peck Point during August 1989, November 1989, February 1990 and May 1990, and from Loelia Shoal and seagrass and unvegetated habitats at Tooradin during November 1989 and May 1990. Three replicate nettings were carried out on each sampling occasion.

Fishes collected by seine net were preserved with formalin, and those collected by gillnet were placed on ice for later identification and gut contents analysis in the laboratory. Animals were weighed in the laboratory after being placed on blotting paper, and length to caudal fork (LCF) and gape height (GH) measured. If >120 animals of a species were collected from a site then 100-120 individuals were subsampled for weighing and measuring.

Calibration of fish density data using box droptraps

In order to allow data collected by seine to be expressed per unit area of seafloor, 1-m^2 box droptraps with 600 mm high sheet metal sides were used at the Peck Point seagrass site on 26 November 1990 and the Rhyll unvegetated site on 27 August 1990, in the same areas as seven replicate seine hauls had been conducted. Similar box traps have been used effectively and their value discussed in other studies of seagrass fishes (Huh, 1984; Sogard et al., 1987, 1989; Holmquist et al., 1989). Fifteen replicate traps were dropped onto the substratum in $\approx$0.3 m water depth from the front of a small boat as it drifted with the current across the study site. Fishes, shrimps and crabs were removed from the traps using small dipnets which were scooped around until no further animals had been collected for 2 minutes.

Estimation of fish production

The production of 10 common fish species collected by seine was calculated from seasonal changes in the modal size of year classes of animals at the different sampling dates (shown in Appendix 1.2). Seasonal changes in size-frequency modes for two other species shown in Appendix 1.2, *Stigmatopora nigra* and *Tetractenos glaber*, were not clearly recognizable.

For the less common species in a sample, production was estimated using a general equation $P = 0.00051 * B^{0.69} T^{1.04}$ which relates daily fish production P (g/d) to ash-free dry weight B (g) and water temperature T (^{o}C). The logged version of this equation, with SE values, is $\log P = -3.30 (\pm 0.39) + 0.69 (\pm 0.03) \log B + 1.04 (\pm 0.31) \log T$ ($r^2 = 0.91$, n=62). This equation relies on the same assumptions, and was formulated using the same method, as the production/biomass regression used for the benthic invertebrate data (Edgar, 1990a). It was calculated using data obtained from the literature on the biomass, estimated daily production and ambient water temperature for 62 fish species distributed worldwide (Table 3.1). For many of the larger fishes included in this table, instantaneous daily production estimates were not available, so the mean daily increase in biomass of animals over a 12 month period was used, as was the mean body size during that period and mean annual water temperature. This regression is slightly less accurate than the macrobenthic invertebrate regression when used for predictive purposes (SD of residuals = 0.33, c.f. 0.26 for macrobenthos).

Wet weights of fishes included in Table 3.1 and those collected in Western Port were converted to ash-free dry weights (AFDW) by multiplying by a factor of 0.22, the mean wet weight/AFDW conversion factor for six common fish species (range 0.18-0.24) collected from Western Port by A.I. Robertson in an earlier study (see Robertson, 1978). Water temperatures measured in Western Port in August 1989, November 1989, February 1990 and May 1990 were 11 °C, 16 °C, 22 °C and 16 °C, respectively.

Data analyses

The species richness of fish collected by seine was analysed using ANOVA. As with analyses of macrofaunal data, habitats and seasons were considered fixed and localities a random factor, with data used in analyses being that collected at the three primary localities on the four sampling occasions between November 1989 and August 1990. Species richness of fish species collected at night was also compared to species richness collected during the day using data from Peck Point collected between August 1989 and August 1990.

3.4 Results

Abundance and species richness of small fishes

A total of 14,714 individuals belonging to 75 fish species were collected from Western Port by seine net. The numbers collected at each site are shown in Table 3.2, with the great majority of species being small, non-commercially important species of gobies (Gobiidae), pipefish (Syngnathidae) and weedfish (Clinidae). Juveniles of commercially-important species were equally distributed between unvegetated and seagrass habitats, with only the rock flathead (*Platycephalus laevigatus*), which lived on sand as juveniles and amongst seagrass beds as adults, showing a clear change in habitat with development.

The mean number of fish species collected per seine haul was much greater in seagrass habitats ($\bar{x}$ = 8.7) than in unvegetated intertidal ($\bar{x}$ = 4.7) and channel ($\bar{x}$ = 2.3) habitats (Table 3.3). As with the number of macrofaunal species collected per core, fish species richness also differed substantially between different localities, with significant higher order interactions also detected by ANOVA (Table 3.3). The number of fish species collected from channel habitats increased more rapidly with additional sampling than samples from seagrass or intertidal bare habitats (Fig. 3.1). While nearly four times as many species were collected per seine haul from seagrass habitats as from channel habitats, the total number of fishes collected from seagrass habitats at the three primary locations was not markedly greater than that collected from channel habitats (44 species from 77 day hauls c.f. 35 from 46 hauls). Thus, fishes in channel habitats were more patchily distributed than fishes in shallow habitats, a similar pattern to that found for macrofauna.

The site with by far the greatest number of fish species was Cowes Bank seagrass (Table 3.2; Fig. 3.1). The fauna here consisted primarily of fishes present at other seagrass sites, with an additional component of vagrant species more commonly associated with coastal reef habitats.

A comparison of data collected during the night with that collected during the day in the three habitats at Peck Point indicated that significantly more fish species were collected during the night ($\bar{x} = 5.4$) than during the day ($\bar{x} = 5.0$), although time of day had only a very minor influence on species richness when compared to differences between habitats (seagrass: $\bar{x} = 11.0$, unvegetated: $\bar{x} = 2.1$, channel: $\bar{x} = 2.5$; Table 3.4).

Calibration of small fish density data

Preliminary studies in which the area swept by the seine net was directly measured indicated that the mean area (±SD) of seabed swept by the net was 77±10 m^2 in water of 1 m depth and was much lower in water of 5 m depth (36±8 m^2) due to the net lifting from the bottom. When the numbers of common fishes collected per seine haul were compared with the absolute densities as determined using box traps (Table 3.5), the seine was found to have an efficiency (i.e., the proportion of fish collected as the seine passed overhead) that varied from 63% for the pipefish *Mitotichthys semistriatus* to 12.3% for the goby *Arenigobius frenatus* which lies partially buried in sediment. The overall efficiency of the net in the Peck Point seagrass habitat was 28% compared to 20% in the Rhyll unvegetated habitat. The overall efficiency when numbers in both habitats were combined was 25.6%, which is equivalent to a conversion factor of 20. Consequently, numbers of fish collected per seine haul have been converted to numbers per m^2 by dividing by 20 for samples from seagrass and unvegetated habitats, and by dividing by 9 (= 20x77/36) for fishes collected in the deeper channel habitat where the net swept over a smaller area.

Production and size-structure of small fish assemblages

The total estimated production of small fishes at different sites varied over a tenfold range, from 0.57 g AFDW.m^{-2}.yr^{-1} at Loelia Shoal to 6.23 g.m^{-2}.yr^{-1} at Tooradin seagrass (Table 3.6). The levels of fish production were consistent at the three primary vegetated sites. Mean fish production at the primary sites was 5.87 g.m^{-2}.yr^{-1} in seagrass, 2.31

$g.m^{-2}.yr^{-1}$ in unvegetated and 2.50 $g.m^{-2}.yr^{-1}$ in channel habitat.

Annual fish production was not significantly correlated (d.f. = 11, $r = 0.41$, $p<0.05$) with annual macrofaunal production (as shown in Table 3.6). However, fish production (F) was closely related to both macroepifaunal production (E) and macrocrustacean production (C) ($F = 1.73 + 0.21 \times E$, $r = 0.72$, $0.01<p<0.05$; $F = 0.08 + 0.68 \times C$, $r = 0.75$, $0.01<p<0.05$), the two major components of macrofaunal production trophically utilised by fishes (see Section 4).

The size-distribution of fish assemblages differed between habitats (Fig. 3.2). At seagrass sites, small fishes less than 10 g wet weight were much more abundant and productive (>20 $mg.m^{-2}.yr^{-1}$) than small fishes in the other habitats. In channel habitats most fish production was contributed by fishes >100 g whereas in unvegetated habitats most production was contributed by fishes at an intermediate size.

Abundance of large fishes

The numbers of the fish species collected by gillnet are shown in Table 3.7, and the mean number of fishes collected from different sites using 64 mm and 108 mm mesh gillnets in Figs 3.3 and 3.4. In contrast to the large difference in number of fishes collected between different habitats using seine nets, no significant difference in number of fishes collected using the 108 mm gillnet was found between habitats (three-way ANOVA using habitat and season as fixed factors and locality as a random factor: d.f. = 2/8, $F = 1.62$, $p>0.05$). The number of large fishes did, however, differ between sites (d.f. = 2/85, $F = 10.60$, $p<0.001$). Approximately twice as many fishes were collected from Loelia Shoal as from the primary localities (Fig. 3.4), probably because of the large number of pelagic fishes collected at that site as they entered the Bay (Table 3.4). The total number of fishes collected by 64 mm gillnet varied significantly between habitats over a threefold range (three-way ANOVA: d.f.= 2/8, $F = 39.63$, $p<0.001$; Fig. 3.3). This variation was due to differences in the number of yellow-eyed mullet collected between sites; the number of fish other than mullet remained constant between habitats at ≈ 3 fish per net at the primary sites (d.f. = 2/8, $F = 3.41$, $p>0.05$).

3.5 Discussion

Seagrasses as nursery habitats

Our study provided no indication that seagrass beds were more important nursery sites than other habitats in Western Port. Two commercial species, six-spined leatherjackets and blue rock whiting, were significantly associated with seagrass beds; however, these two species were associated with seagrasses as adults as well as juveniles, so the seagrasses had more than just a nursery function. The other major commercial species living in seagrass beds, rock flathead, utilised sand areas as a nursery habitat until they reached ≈20 mm size. Other commercial species (viz. greenback and long-snouted flounder and sand flathead) were associated with unvegetated habitats throughout their post-settlement lives, while the majority of the larger, commercial species (e.g., King George whiting, yellow-eyed mullet, school shark, Australian salmon) were collected from both seagrass and unvegetated habitats.

Robertson (1977) considered that King George whiting utilized seagrass habitats as nursery habitats, with this association between juvenile whiting and seagrasses having since been used to explain a decline in whiting catch rates in Western Port following seagrass dieback (Shepherd et al., 1989). Our data indicated that whiting are associated with both vegetated and unvegetated habitats as juveniles (< 70 mm size) but only with unvegetated habitats as adults. The relationship between juvenile whiting and seagrasses appears to be a complex one, with observations while diving (G. Edgar, personal observations) indicating that juvenile whiting live on sandy patches adjacent to seagrass. While this relationship needs to be confirmed, both sand and seagrass habitats appear to be important for juvenile whiting.

The abundance and production of the smallest-sized fishes (<10g weight) was considerably greater in seagrass habitat than in either shallow unvegetated or channel habitats (see Fig. 2.2). Seagrass beds thus have the potential to hold large numbers of juvenile fishes. However, in Western Port, the small fishes were almost exclusively non-commercial species of gobies, pipefish and weedfish which also mature at a small size. In other areas, particularly estuaries, this small fish component may well include juvenile commercial species.

Production of small fishes

Estimates of the annual production of small fishes in Western Port were comparable to estimates for communities elsewhere. Production in Western Port seagrass beds (≈5.9 $g.m^{-2}.yr^{-1}$) was slightly higher than the estimate of Adams (1976) for fish production in an eelgrass bed in North Carolina (≈4.6 $g.m^{-2}.yr^{-1}$) and double the production of the four dominant fish in the Laguna Madre of Texas (≈3.1 $g.m^{-2}.yr^{-1}$; Hellier, 1962). Production at unvegetated Western Port sites (0.6 to 3.7 $g.m^{-2}.yr^{-1}$) were within the range of estimates for sites along the Swedish coast (0.2-5 $g.m^{-2}.yr^{-1}$; Möller et al., 1985)

Effect of seagrass loss on fish communities

Small fish assemblages at the primary seagrass sites were over twice as productive as at unvegetated sites (5.87 $g.m^{-2}.yr^{-1}$ in seagrass c.f. 2.31 $g.m^{-2}.yr^{-1}$ in unvegetated habitat). Using the same assumptions as used in calculations of the effect of seagrass dieback on macrofauna (i.e., that 178 km^2 of former seagrass habitat is now unvegetated, that most of the seagrass loss has occurred on the shallow tidal flats studied at the primary sites, and that communities present on seagrass habitat prior to seagrass dieback were similar to those found in the present study), total small-fish production throughout Western Port is estimated to have annually declined by ≈630 tonnes AFDW.yr^{-1}.

Because gillnets are highly selective in their capture of fish and thus cannot be used for calculations of absolute fish densities, we cannot provide direct estimates of the effect of seagrass loss on larger fishes. The gillnet data nevertheless indicates that only the presence of yellow-eyed mullet elevates total catches of fishes from seagrass beds using the 64 mm mesh gillnet to higher levels than catches from unvegetated habitats. Moreover, no differences in the mean abundance of fishes collected with the 108 mm mesh gillnet were found between seagrass and unvegetated habitats.

One reason for the substantial differences in small fish production between seagrass and unvegetated habitats not translating into major differences in the production of larger fish between these habitats appears to be that many of the larger species feed on pelagic resources which are distributed independently of benthic habitat type. Australian salmon, jack mackerel, barracouta and tailor all primarily consumed clupeoid fishes (see Section 4) which in turn fed on planktonic copepods. The presence of large numbers of these fishes in gillnet catches tended to obscure habitat differences between the demersal species.

The number of yellow-eye mullet collected in seagrass habitat was ≈170% of the number collected in unvegetated habitat, indicating that the loss of seagrass habitat from the Bay may have resulted in a decline in the catch of yellow-eye mullet. However, this prediction is not supported by catch statistics from Western Port, which show that the total catch of mullet increased following the period of seagrass dieback (Shepherd et al., 1989). Catches of the two major species directly associated with seagrass beds, blue rock whiting and six-spined leatherjackets, declined rapidly as expected following the period of rapid seagrass loss.

Catch statistics for the two other species commonly collected in gillnets, gummy shark and elephant shark, are not available for Western Port. The catches of these species would not be expected to have declined significantly due to seagrass loss because neither species was positively associated with seagrass habitat, with only three elephant shark collected from seagrass beds.

The dominant species in the fish assemblages investigated in this study differed greatly from the dominant species collected by Robertson (1980) from Crib Point in 1974/1975. Five of the ten common species listed by Robertson (1980) were rare in our seine samples. We suggest, however, that the difference between studies is more a function of differences in sampling techniques than long term changes in the fauna. Most of the species disproportionately abundant in Robertson's study (i.e., *Atherinasoma presbyteroides, A. microstoma, Tetractenos glaber* and *Aldrichetta forsteri*) tended to remain in shallow water following the tide and thus are concentrated on the waters edge (Edgar & Shaw, unpubl. obs.). Robertson's technique of pulling the net into shore therefore probably resulted in the collection of disproportionately high numbers of these species relative to numbers obtained by pulling the seine into a boat. The high mean density of *Arenigobius bifrenatus* is probably due to *A. frenatus* being misidentified; *A. frenatus* had not been recognized at that time from Victorian waters. The study of Howard and Koehn (1985) nevertheless provides clear evidence that the pipefish fauna has changed substantially during the past 15 years. Howard and Koehn (1985) sampled Rhyll seagrass beds for pipefish in 1978 and collected only two specimens of *Stigmatopora nigra* and no *S. argus*. *Stigmatopora nigra* was by far the most common fish collected from this site during our study, with *S. argus* also common.

Table 3.1. Daily production of fishes (g/d) of different wet weight (g) and at different water temperatures (°C), as estimated from previous studies.

Species	Temp.	Wet weight	Production	Study author
Aldrichetta forsteri	22	5.82	0.114	Chubb et al (1981)
Archosargus probatocephalus	23	221	0.567	Schwartz (1990)
Argyrozona argyrozona	19	98.8	0.179	Nepgen (1977)
Atherinasoma presbyteroides	19	0.407	0.00349	Prince and Potter (1983)
Caranx georgianus	19	1750	4.36	James (1984)
Carcharinus tilstoni	29	3930	6.08	Davenport and Stevens (1988)
Chanos chanos	27	7.34	0.332	Kumagai et al (1985)
Cheilodactylus macropterus	19.5	319	0.363	Tong and Vooren (1972)
Chelidonichthys kumu	19.5	76.0	0.159	Elder (1976)
Chrysophrys auratus	19.5	1320	2.73	Vooren and Coombs (1977)
Clupea harengus	11	1.65	0.0496	De Silva (1973)
Clupea pallasii	7	52.1	0.146	Kanno (1989)
Coracinus capensis	19	215	0.445	Bennett and Griffiths (1986)
Coryphaena hippurus	27	12300	63.8	Oxenford and Hunt (1981)
Cymatoceps nasutus	23	276	0.375	Buxton and Clarke (1989)
Cynoscion arenarius	16	74.4	0.829	Shlossman and Chittenden (1981)
Cynoscion nothus	25	24.1	0.465	DeVries and Chittenden (1982)
Cynoscion regalis	25	0.119	0.00961	Szedimayer, Weinstein and Musick (1990)
Engraulis capensis	20	0.0952	0.00713	Thomas (1986)
Engraulis mordax	14	5.61	0.0255	Parrish et al (1985)
Etrumeus micropus	15	14.2	0.0649	Geldenhuys (1978)
Fundulus heteroclitus	25	0.644	0.00441	Kneib and Stiven (1981)
Galeorhinus australis	16	4040	4.44	Grant et al (1979)
Gobius cobitis	14.5	1.67	0.00784	Gibson (1970)
Gobius paganellus	18	0.493	0.00916	Miller (1961)
Helicolenus lengerichi	9	36.7	0.113	Petrova and Chekunova (1979)
Helicolenus percoides	12	15.0	0.0499	Withell and Wankowski (1988)
Hippoglossoides dubius	9	4.76	0.0183	Nakatani et al (1989)
Katsuwonus pelamis	24	1860	9.37	Uchiyama and Struhsaker (1981)
Lagodon rhomboides	26	0.676	0.0075	Hansen (1969)
Lates calcarifer	27	3070	3.86	Davis and Kirkwood (1984)
Leionura atun	15	40.4	0.483	Grant et al (1978)
Leiostomus xanthurus	10	0.00128	0.000086	Warlen and Chester (1985)
Lesueurigobius friesii	12	0.203	0.00251	Gibson and Ezzi (1978)
Liza subviridis	21	65.6	0.158	Al-Daham and Wahab (1991)
Lutjanus campechanus	28	34.4	0.541	Holt and Arnold (1982)
Lutjanus kasmira	22	110	0.207	Morales-Nin and Ralston (1990)
Menidia menidia	18	3.00	0.0380	Conover and Ross (1982)
Micropogon undulatus	17	0.0714	0.00546	Knudsen and Herke (?1976)
Mugil cephalus	27	72.0	0.547	Grant and Spain (1975)
Mugil curema	25	9.78	0.379	Richards and Castagna (1976)
Mustelus munazo	20	591	0.892	Tanaka and Mizue (1979)
Nematolosa vlaminghi	19	63.4	0.113	Chubb and Potter (1986)
Nemipterus peronii	27	83.4	0.272	Sainsbury and Whitelaw (1984)
Oligocottus maculosus	11.5	1.30	0.00356	Pierce and Pierson (1990)
Pachymetopon blochii	19	11.8	0.0463	Pulfrich and Griffiths (1988)
Pagrus pagrus	20	145	0.436	Manooch and Huntsman (?1975)
Pomatoschistus microps	14	0.500	0.00470	Healey (1972)
Pseudopleuronectes americanus	22	0.40137	0.0108	Mulkana (1966)
Rhombosolea plebeia	15	3.47	0.0901	Colman (1978)
Sardinops neopilchardus	21	3.66	0.0384	Blackburn (1949)
Sardinops ocellata	15	0.856	0.0336	Thomas (1985)
Scomberomorus cavalla	28	0.00511	0.00165	DeVries et al (1990)
Sebastes serranoides	15	131	0.260	Love and Westphal (1981)
Sprattus sprattus	14	1.65	0.0496	De Silva (1973)
Squalus acanthias	12	235	0.248	Ketchen (1975)
Stolephorus purpureus	22	0.277	0.00804	Struhsaker and Uchiyama (1976)
Tanakius kitaharai	10	3.47	0.0170	Yabuki (1989)
Tautolabrus adspersus	15	9370	50.4	Dew (1976)
Trachurus declivus	16	243	0.461	Webb and Grant (1979)
Trachurus trachurus	16	21.0	0.0871	Geldenhuys (1973)
Trisopterus esmarkii	14	10.5	0.110	Gordon (1977)

Table 3.2. Numbers of fishes collected by seine from different sites in Western Port. Sites are abbreviated as follows: Peck Point seagrass (PH), Peck Point unvegetated (PU), Peck Point channel (PC), Rhyll seagrass (RH), Rhyll unvegetated (RU), Rhyll channel (RC), Tooradin seagrass (TH), Tooradin unvegetated (TU), Tooradin channel (TC), Loelia Shoal (LS), Cowes Bank seagrass (CBS), Cowes Bank unvegetated (CBU), Peck Point seagrass night (PHN), Peck Point unvegetated night (PUN), Peck Point channel night (PCN).

Species	Site															
	PH	PU	PC	RH	RU	RC	TH	TU	TC	LS	CBH	CBU	PHN	PUN	PCN	Total
Trygonorhina guanerius Whitley	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Urolophus cruciatis (Lacepede)	0	0	0	0	0	7	0	0	2	0	0	0	0	0	3	12
Urolophus paucimaculatus Dixon	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Urolophus sp.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Spratelloides robustus Ogilby	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Hyperlophus vittatus (Castelnau)	6	25	19	411	57	2	9	17	0	34	109	11	0	0	1	701
Sardinops neopilchardus (Steindachner)	0	0	0	2	0	0	0	0	0	1	32	0	0	1	0	36
Engraulis australis (Shaw)	5	0	1	0	2	0	1	0	0	4	26	1	5	3	5	53
Muraenichthys breviceps Günther	0	0	0	0	0	0	0	0	0	0	0	0	5	2	6	13
Galaxias maculatus (Jenyns)	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
Genypterus tigerinus Klunzinger	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2
Hyporhamphus melanochir (Valenciennes)	0	0	0	0	0	0	1	0	0	0	17	0	0	0	0	18
Kestratherina brevirostris Pavlov,Ivantsoff, Last & Crowley	109	0	0	0	0	0	6	1	0	0	1	0	43	0	0	160
Kestratherina esox (Klunzinger)	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
Hippocampus abdominalis Lesson	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Mitotichthys semistriatis (Kaup)	207	0	1	46	2	0	53	0	0	0	6	0	79	0	1	395
Stigmatopora argus (Richardson)	69	1	2	118	1	2	3	24	3	0	4	1	115	0	1	344
Stigmatopora nigra Kaup	1690	154	55	1109	32	17	109	49	48	0	1125	25	1014	6	21	5454
Stipecampus cristatus (McCulloch & Waite)	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	3
Syngnathus curtirostris Castelnau	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Vanacampus phillipi (Lucas)	330	2	61	19	5	0	57	9	2	0	14	1	303	0	21	824
Urocampus carinirostris Castelnau	150	7	2	25	18	1	191	64	2	0	4	0	254	0	0	718
Gymnapistes marmoratus (Cuvier & Valenciennes)	42	0	1	6	1	0	205	1	0	0	0	0	28	1	2	287
Neosebastes scorpaenoides Guichenot	0	0	2	2	0	4	0	0	0	0	0	0	0	0	0	8
Scopaena ergastulorum Richardson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Chelidonichthys kumu (Lesson & Garnot)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Aploactisoma milesii Richardson	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2
Platycephalus bassensis Cuvier & Valenciennes	0	0	1	0	2	2	0	5	9	16	1	8	0	0	1	45
Platycephalus laevigatus Cuvier & Valenciennes	0	2	2	3	0	4	0	1	1	0	12	5	3	0	1	34
Acanthopegasus lancifer (Kaup)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Apogon conspersus Klunzinger	1	0	0	7	0	0	0	0	0	0	1	0	5	0	0	14
Siphamia cephalotes Castelnau	58	0	2	2	1	0	0	0	0	0	9	0	11	0	0	83
Sillaginodes punctatus Cuvier & Valenciennes	5	7	2	0	2	0	11	8	0	0	3	0	10	5	0	53
Pseudocaranx dentex Bloch & Schneider	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1

Arripis trutta (Bloch & Schneider)	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
Girella tricuspidata (Quoy & Gaimard)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Enoplosus armatus (White)	3	0	0	2	0	0	0	0	0	0	1	0	1	0	0	7
Dactylophora nigricans (Richardson)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aldrichetta forsteri (Cuvier & Valenciennes)	0	0	0	2	1	0	0	1	0	0	4	10	0	2	0	20
Shyraena novaehollandiae (Günther)	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3
Dotalabrus aurantiacus (Castelnau)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Haletta semifasciata (Cuvier & Valenciennes)	32	0	0	6	0	0	0	0	0	0	8	0	11	0	1	58
Neoodax balteatus (Cuvier & Valenciennes)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Cristiceps australis Cuvier & Valenciennes	10	0	1	11	0	0	3	0	0	0	50	1	5	0	1	82
Heteroclinus adelaidei Castelnau	10	0	0	0	0	0	1	0	0	0	9	0	9	0	0	29
Heteroclinus forsteri (Castelnau)	0	0	0	0	0	0	0	0	0	0	4	0	48	0	0	52
Heteroclinus perspicillatus (Cuvier & Valenciennes)	422	7	33	191	13	8	273	0	1	0	20	3	108	0	6	1085
Arenigobius bifrenatus (Kner)	0	0	0	0	2	0	2	89	11	0	0	0	34	0	0	138
Arenigobius frenatus (Günther)	45	10	1	308	631	0	428	237	13	0	3	0	80	1	5	1762
Callogobius depressus (Ramsay & Ogilby)	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	4
Favonigobius tamarensis (Johnston)	1	3	14	5	251	0	17	349	81	0	0	4	18	2	9	754
Favonigobius lateralis (Macleay)	0	2	2	0	2	2	0	7	0	0	1	0	0	0	0	16
Gobiopterus semivestitus (Munro)	13	1	14	63	31	5	101	39	5	0	37	2	20	4	3	338
Nesogobius hindsbyi (McCulloch & Ogilby)	0	0	0	0	0	1	0	0	0	0	4	1	0	0	0	6
Nesogobius pulchellus (Castelnau)	0	2	0	2	0	0	5	0	0	0	3	0	3	0	0	15
Nesogobius sp. 1	3	45	0	0	0	0	0	4	0	0	0	1	0	2	0	55
Nesogobius sp. 2	0	0	0	0	0	1	0	0	0	0	3	2	0	0	0	6
Pseudogobius olorum (Sauvage)	0	0	1	15	53	0	8	134	1	0	0	0	1	0	0	213
Tasmanogobius gloveri Hoese	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Kathetostoma laeve (Bloch & Schneider)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Parvicrepis sp.1	0	0	0	9	1	0	0	0	0	0	68	0	0	0	0	78
Arnoglossus bassensis Norman	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Ammotretis rostratus Günther	0	4	0	0	0	0	0	10	3	0	0	2	0	1	0	20
Rhombosolea tapirina Günther	0	5	1	0	0	1	0	6	0	0	0	0	1	1	0	15
Acanthaluteres spilomelanurus (Quoy & Gaimard)	61	0	0	16	0	0	0	0	0	0	14	0	8	0	0	99
Brachaluteres jacksonianus (Quoy & Gaimard)	4	0	0	4	0	0	0	0	0	0	4	0	0	0	0	12
Eubalichthys gunnii (Günther)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Meuschenia freycineti (Quoy & Gaimard)	42	1	0	3	0	0	28	0	0	0	1	0	13	0	0	88
Penicipelta vittiger (Castelnau)	3	0	0	4	0	0	3	0	0	0	1	0	0	0	0	11
Scobinichthys granulatus (Shaw)	3	0	0	0	0	0	0	0	0	0	1	0	2	0	0	6
Aracana aurita (Gray)	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Contusus brevicaudus Hardy	0	0	1	1	5	0	0	2	1	0	8	0	0	0	0	18
Contusus richei (Freminville)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tetractenos glaber (Freminville)	10	17	1	24	51	0	53	131	13	0	9	36	10	14	0	369
Diodon nicthemerus Cuvier	18	1	2	6	0	3	2	2	3	0	0	0	12	1	0	50
Total	3368	298	224	2425	1166	69	1571	1190	201	55	1629	116	2262	47	93	14714
Number of seine hauls	31	25	25	25	29	21	21	22	21	21	19	22	16	17	16	331

Table 3.3. Results of three-way ANOVA (fixed factors: month and habitat, random factor: locality) using data on the number of fish species collected per seine haul.

Factor	Hypothesis	DF	SS	Percent of total SS	F
Month (M)	M/ML	3	335	14.6	7.6*
Habitat (H)	H/HL	2	950	41.3	10.7*
Locality (L)	L/E	2	53	2.3	7.0**
Month*habitat (MH)	MH/MHL	6	131	5.7	1.7
Month*locality (ML)	ML/E	6	88	3.8	3.9**
Habitat*locality (HL)	HL/E	4	177	7.7	11.6***
Month*habitat*locality (MHL)	MHL/E	12	156	6.8	3.4***
Error (E)		108	411	17.8	

Table 3.4. Results of three-way ANOVA (fixed factors: month, habitat, day/night) using data on the number of fish species collected per seine haul.

Factor	DF	SS	Percent of total SS	F
Month	4	264	10.3	12.1***
Habitat	2	1631	63.8	150.0***
Day	1	33.3	1.3	6.1*
Month x Habitat	8	96.2	3.8	2.2*
Month x Day	4	30.5	1.2	1.4
Habitat x Day	2	13.9	0.5	1.3
Month x Habitat x Day	8	63.9	2.5	1.5
Error	78	424	16.6	

Table 3.5. Mean abundances (±SE) of common fishes collected per seine haul, mean densities (±SE) collected using drop traps, correction factors (i.e., seine net abundance/drop net density) and net efficiencies (i.e., correction factor/mean area swept by net) for common species collected at the Peck Point seagrass and the Rhyll unvegetated habitats in November 1990.

	Seine abundance	Drop net density (m-2)	Correction factor	Net efficiency (%)
Peck Point seagrass				
Siphamia cephalotes	4.9±1.7	0.13±0.09	37	49
Vanacampus phillipi	11.9±1.7	1.07±0.55	11	14
Mitotichthys semistriatus	19.4±3.8	0.40±0.26	49	63
Urocampus carinirostris	6.7±1.0	0.20±0.05	34	44
Stigmatopora nigra	28.7±5.9	0.80±0.23	36	47
Heteroclinus perspiculatus	27.1±5.5	1.07±0.18	25	33
Total	115.4±16.0	5.33±0.93	22	28
Rhyll unvegetated				
Arenigobius frenatus	19.0±4.4	2.00±0.49	10	12
Total	34.3±5.0	2.27±0.59	15	20
Grand mean	74.9	3.8	20	26

Table 3.6. Estimated biomass (g AFDW.m-2), annual production (g AFDW.m-2.yr-1) and P/B ratios of small fish assemblages at different sites in Western Port.

Site	Biomass (g.m-2)	Production (g.m-2.yr-1)	P/B
Peck Point seagrass	1.99	5.71	2.87
Peck Point unvegetated	0.37	0.82	2.22
Peck Point channel	1.39	1.94	1.4
Rhyll seagrass	2.58	5.68	2.2
Rhyll unvegetated	0.94	2.44	2.6
Rhyll channel	2.46	3.32	1.35
Tooradin seagrass	1.67	6.23	3.73
Tooradin unvegetated	2.15	3.68	1.71
Tooradin channel	1.01	2.25	2.23
Cowes Bank seagrass	2.37	4.73	2
Cowes Bank unvegetated	0.7	1.38	1.96
Loelia Shoal	0.44	0.57	1.29

Table 3.7. Total numbers of fishes collected from different sites using gillnets with 64 (Net 1) and 108 mm (Net 2) mesh panels. Sites are abbreviated as follows: Peck Point seagrass (PH), Peck Point unvegetated (PU), Peck Point channel (PC), Rhyll seagrass (RH), Rhyll unvegetated (RU), Rhyll channel (RC), Tooradin seagrass (TH), Tooradin unvegetated (TU), Loelia Shoal (LS).

Site	PH		PU		PC		RH		RU		RC		TH		TU		LS		Total
Net	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
Species																			
Heterodontus portusjacksoni	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Parascyllium ferrugineum	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	5
Juncrus vincenti	0	0	0	0	4	0	0	0	0	0	0	0	3	0	0	0	0	0	7
Mustelus antarcticus	5	32	16	9	7	25	0	1	0	0	0	1	2	5	2	2	0	2	109
Galeorhinus australis	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	9
Trygonorhina guanerius	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	4
Raja lemprieri	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	3
Urolophus cruciatis	0	0	2	0	0	1	0	0	1	0	3	1	0	0	0	0	0	0	8
Urolophus paucimaculatus	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	4
Myliobatis australis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3
Callorhyncus milii	0	1	5	10	6	5	1	1	1	2	5	1	0	0	0	0	156	50	244
Pseudophycis bachus	1	0	9	0	6	0	15	0	6	0	20	0	0	0	0	0	6	0	63
Genypterus tigerinus	1	0	0	0	0	0	0	0	3	0	1	1	0	0	1	0	0	0	7
Hyporhamphus melanochir	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3
Gymnapistes marmoratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Platycephalus bassensis	0	1	13	2	16	0	2	0	13	2	7	0	0	0	0	0	10	3	69
Platycephalus speculator	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Platycephalus laevigatus	35	7	1	0	9	0	22	2	6	0	14	0	8	1	2	0	0	0	107
Chelidonichthys kumu	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Sillaginodes punctatus	3	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	8
Pomatomus saltator	3	0	4	0	1	0	1	0	0	0	1	0	6	0	7	0	10	0	33
Pseudocaranx dentex	1	1	35	0	4	1	3	1	4	0	6	6	21	11	28	13	16	2	153
Trachurus declivis	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	4
Arripis trutta	0	0	355	12	31	0	1	0	1	0	1	0	0	0	1	0	0	0	402
Arripis truttaceous	12	0	102	0	0	0	4	1	2	0	1	0	8	0	5	0	0	0	135
Petaceropsis recurvirostris	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Dactylophora nigricans	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Aldrichetta forsteri	198	0	149	0	16	0	483	1	119	0	13	0	212	0	105	4	0	0	1300
Sphyraena novaehollandiae	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	5
Haletta semifasciata	6	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	9
Thyrsites atun	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	6
Seriolella brama	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ammotretis rostratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	3
Rhombosolea tapirina	1	5	0	1	0	1	1	5	1	3	1	0	1	7	1	3	1	0	32
Meuschenia freycineti	16	4	0	0	0	2	4	0	0	0	3	0	2	0	1	0	0	0	32
Contusus brevicaudus	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	3
Tetractenos glaber	5	0	2	0	0	0	2	0	7	0	1	0	1	0	1	0	0	0	19
Diodon nicthemerus	20	5	3	3	3	2	5	5	1	2	1	7	8	3	0	3	0	0	71
Total	318	59	706	39	113	40	548	22	171	12	90	21	276	29	158	31	204	61	2898

Fig. 3.1. Cumulative number of species of fish collected with increasing number of seine hauls at different Western Port sites. Because little difference was detected in these curves between the three primary sites for each habitat, the mean (±SE) number of species collected is shown for primary seagrass, unvegetated and channel sites.

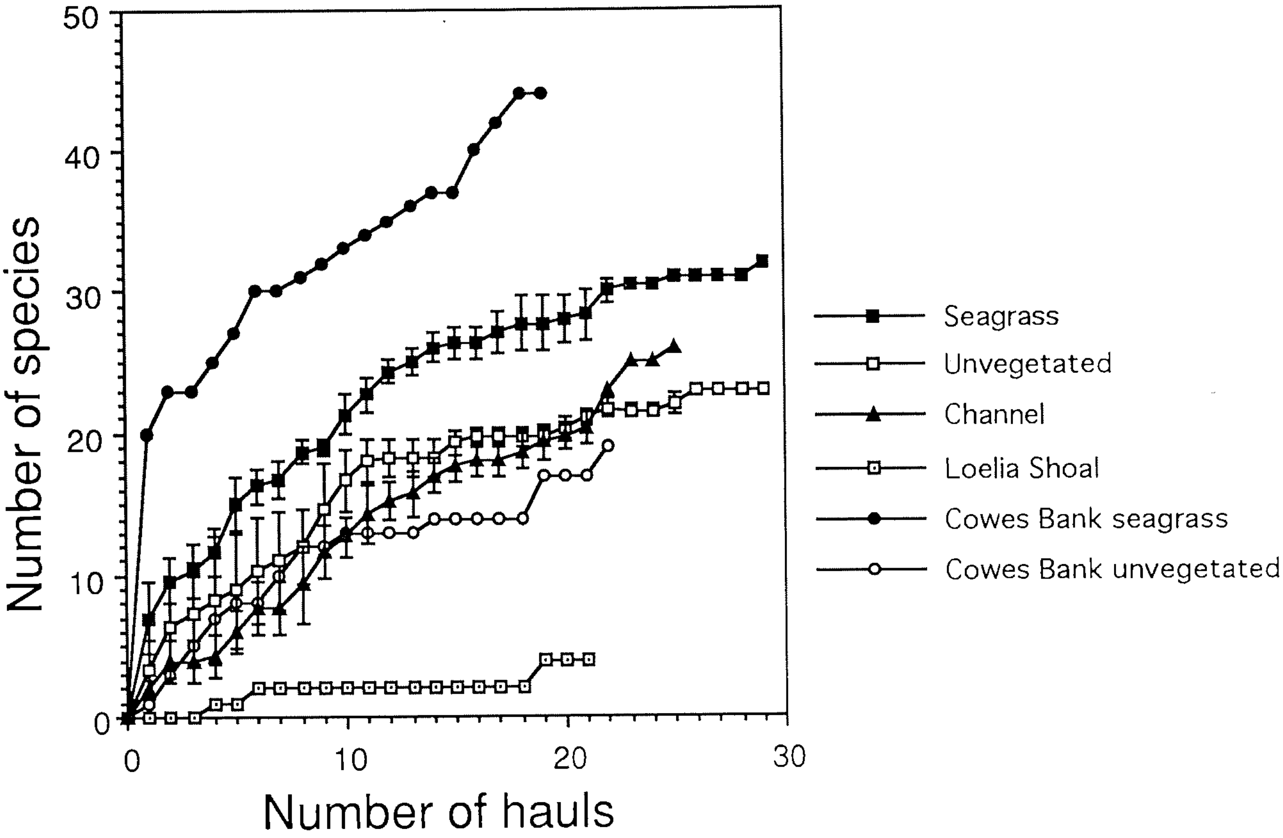

Number of species
0
10
20
30
40
50
Number of hauls
0
10
20
30
Seagrass
Unvegetated
Channel
Loelia Shoal
Cowes Bank seagrass
Cowes Bank unvegetated

Fig. 3.2. Estimated daily production ($mg.m^{-2}.d^{-1}$) of different size classes for small fish assemblages associated with seagrass, unvegetated and channel habitats in Western Port.

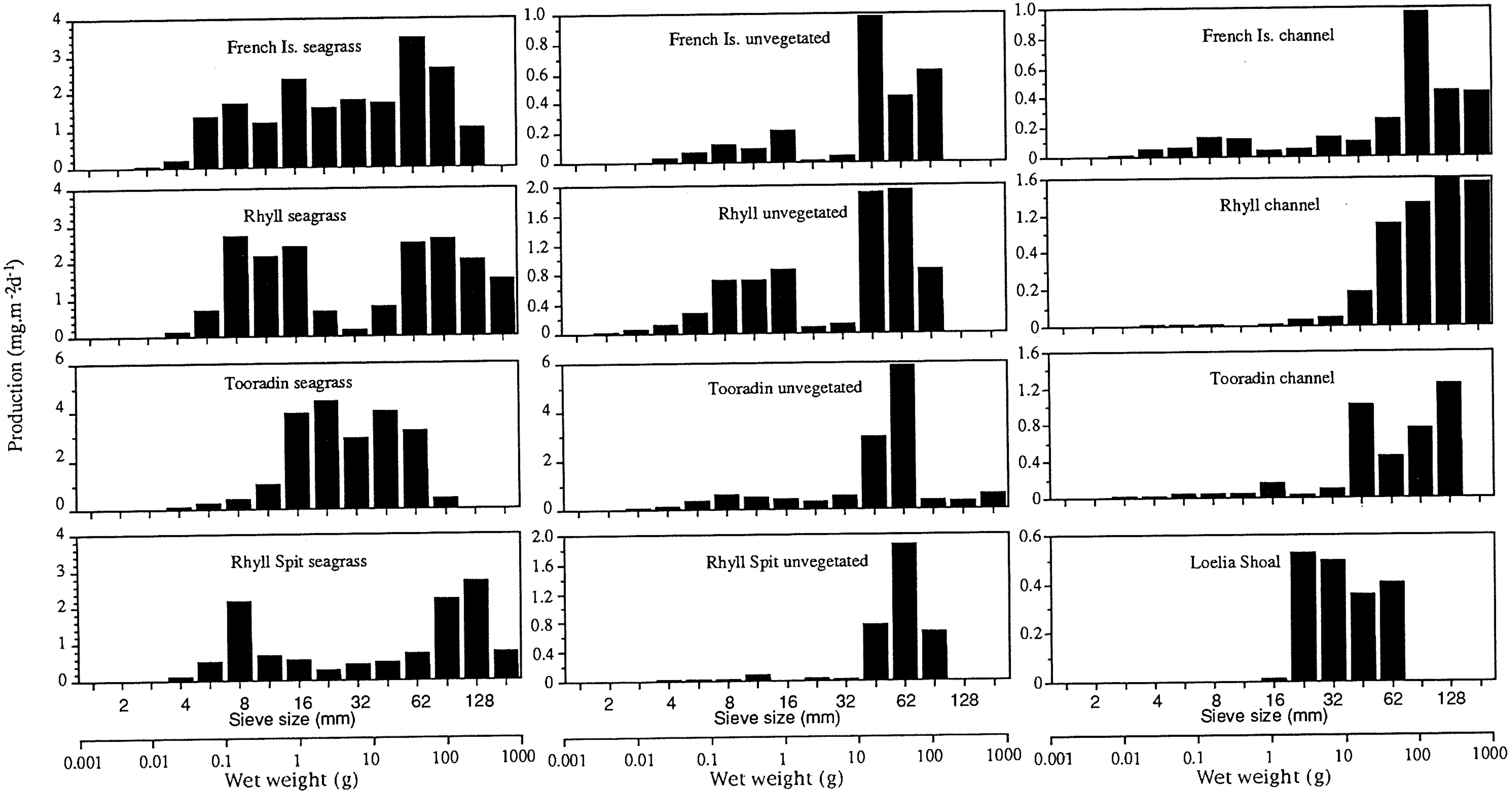

Production (mg.m-2.d-1)
French Is. seagrass
4
3
2
1
0
French Is. unvegetated
1.0
0.8
0.6
0.4
0.2
0
French Is. channel
1.0
0.8
0.6
0.4
0.2
0
Rhyll seagrass
4
3
2
1
0
Rhyll unvegetated
2.0
1.6
1.2
0.8
0.4
0
Rhyll channel
1.6
1.2
0.4
0.2
0
Tooradin seagrass
6
4
2
0
Tooradin unvegetated
6
4
2
0
Tooradin channel
1.6
1.2
0.8
0.4
0
Rhyll Spit seagrass
4
3
2
1
0
Rhyll Spit unvegetated
2.0
1.6
1.2
0.8
0.4
0
Loelia Shoal
0.6
0.4
0.2
0
2
4
8
16
32
62
128
Sieve size (mm)
0.001
0.01
0.1
1
10
100
1000
Wet weight (g)

Fig. 3.3. Mean abundance (±SE) of fish collected in 64 mm mesh gillnets from different sites.

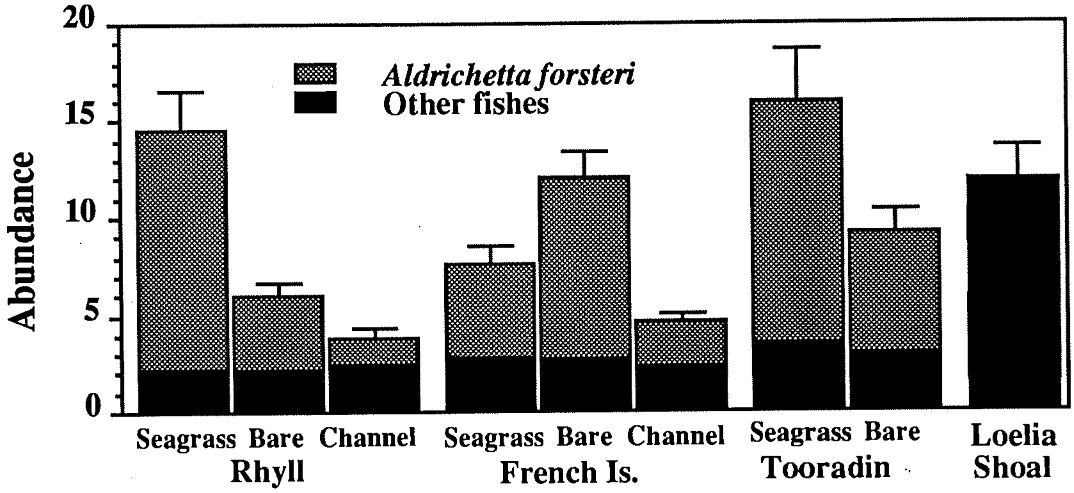
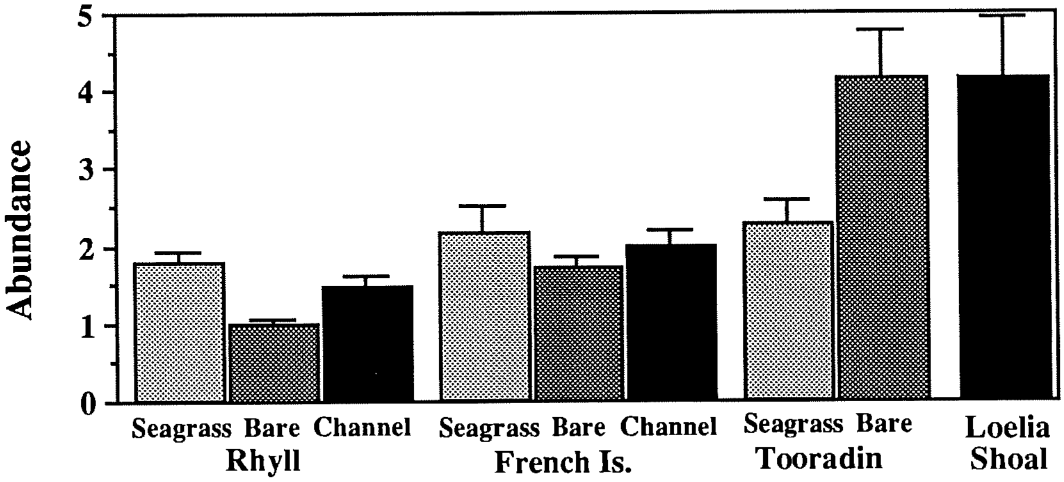

20
15
10
5
0
Abundance
Aldrichetta forsteri
Other fishes
Seagrass
Bare
Channel
Rhyll
Seagrass
Bare
Channel
French Is.
Seagrass
Bare
Tooradin
Loelia
Shoal

Fig. 3.4. Mean abundance (±SE) of fish collected in 108 mm mesh gillnets from different sites.


Abundance
0
1
2
3
4
5
Seagrass
Bare
Channel
Rhyll
Seagrass
Bare
Channel
French Is.
Seagrass
Bare
Tooradin
Loelia
Shoal

Section 4. Diets of fishes associated with seagrass and unvegetated habitats in Western Port, Victoria.

4.1 Summary

A total of 5,113 fishes belonging to 91 species was collected from Western Port for dietary analysis, with 720 animals having empty guts. None of the common fish species examined were found to have a highly specialised diet, with crustaceans the dominant component in the diets of the majority (69%) of species. In general, dietary differences between juveniles and adults of a species were greater than dietary differences between different species at the same body size. Amongst the crustacean feeders, diets generally changed from predominantly copepods to predominantly amphipods, isopods and mysids at ≈0.1 g (wet weight) body mass, and from predominantly amphipods to predominantly crabs and shrimps at ≈100 g body mass. Across the range of species examined, there was a close relationship between the size of ingested prey and the wet weight of the fish. Prey length averaged 7.5% of predator length. The fish with the most atypical diet was the yellow-eyed mullet, the dominant species in gillnet catches, which consumed disproportionately small-sized animals and large quantities of algal material.

Trophic pathways involving fishes differed only slighly between habitats, with the major linkage in all habitats being from benthic microalgae and detritus through epifaunal crustaceans to the smaller fishes. Over half the dietary intake of fishes in all habitats was provided by crustaceans. A large proportion of the production of benthic crustaceans was consumed by fishes in all habitats, indicating that the availability of high quality crustacean prey probably limits the production of fishes. The production of the non-crustacean benthos was an order of magnitude higher than that consumed by fish predators.

4.2 Introduction

Numerous studies worldwide have shown that seagrass plants have little direct trophic importance to small fishes, with very few fish species able to extract energy from seagrass plants (Klumpp et al., 1989). By contrast, invertebrates associated with seagrass plants are heavily exploited by fishes.

The relationship between fishes and their invertebrate prey is probably a complementary one, with the abundance of fishes influencing the population sizes of particular invertebrate species (Edgar & Aoki, 1993), and the abundance of invertebrates influencing food availability, which in turn influences the abundance of fish species (e.g., Brook, 1977). Virtually all work on this complementary relationship has been directed at the impact of fishes on prey. In many cases (e.g., Van Dolah, 1978; Kneib, 1992) studies have centred on a single species only. In a few investigations, the importance of fish to benthic communities has been quantified in terms of abundance or biomass flux (Möller et al,1985 ; Robertson, 1984; Edgar and Aoki, 1993).

In the present study we quantify for the first time the importance of benthic invertebrate production to demersal fish assemblages associated with seagrass and unvegetated habitats at a variety of different sites. In order to do this, we relate the production of benthos to fish consumption and fish production by using the new techniques described in Sections 2 and 3, which enable the size-structure and production of invertebrates and fishes to be estimated with relatively little logistic effort, and by using a novel method of rapidly quantifying gut contents. The study has three aims: (i) to identify the major characteristics of fish diets in Western Port, (ii) to determine any differences between seagrass and unvegetated habitats in trophic linkages involving fish, and (iii) to determine whether excess food (in the form of invertebrate prey) is available to fish.

4.3 Methods

Sites and sampling methods used for the collection of fishes for dietary analyses are described in the previous section. The diets of all fishes collected in Western Port were examined, except when more than 12 individuals of a species were collected from a site on the same sampling date. In these cases, 10 individuals were randomly subsampled for gut content analysis.

In the laboratory, foreguts were removed and the contents placed in petri dishes for observation under a dissecting microscope (within two days of capture for formalin-preserved fish collected by seine and within one day for chilled specimens collected by gillnets). The wet weight of foreguts from gillnet collected fish was also measured before and after contents had been removed in order to determine the total biomass of prey items.

Using the microscope, the number of invertebrates belonging to different sieve size-classes for each prey species were recorded. Animals were allocated to sieve size-classes, in some cases on the basis of shell fragments, using a graticule in the microscope eyepiece and a reference collection consisting of a mixture of different species retained by different-sized sieves. The length of fishes in stomachs were also measured when intact; in cases where fishes had been largely digested, the length of the missing sections were visually estimated. The percentage occurrence of plants, sessile animals (sponges, bryozoans, hydroids and ascidians), unidentifiable digested material and sand in each gut was also estimated by eye.

In the major dietary analyses, food items have been grouped into seventeen major food categories: (1) epifaunal crustaceans, (2) infaunal crustaceans, (3) planktonic crustaceans, (4) epifaunal molluscs, (5) infaunal molluscs, (6) pelagic molluscs (cephalopods), (7) epifaunal polychaetes, (8) infaunal polychaetes, (9) other mobile epifaunal invertebrates,

(10) other infaunal invertebrates, (11) demersal fish, (12) pelagic fish, (13) bryozoans, (14) sponges, (15) ascidians, (16) algae, (17) seagrass. The percentage occurrence by biomass of these categories in stomachs was determined for each fish by estimating the biomass of invertebrates in guts using their estimated sieve-sizes and the biomass/sieve-size relationships described in Edgar (1990a), by calculating the biomass of ingested fishes using the length/weight relationships given in Appendix 1.1, and by using the estimated percentage occurrence of sessile plants and animals. Thus, for example, if in a gut epifaunal crustaceans were estimated to have a total biomass of 16 mg, epifaunal polychaetes a biomass of 8 mg and algae to comprise 40% of the gut contents, then epifaunal crustaceans, epifaunal polychaetes and algae would be calculated to comprise 40%, 20% and 40% of the gut contents, respectively.

The general relationship between the size of fishes collected at Western Port and mean prey size was determined by calculating the regression relating fish biomass to mean biomass of prey in guts for the 48 most abundant fish species (i.e., those with ≥10 individuals collected). Using these regressions, the mean prey biomass was estimated for each fish species at the geometric mean fish size, and these data used to calculate a general regression relating predator to mean prey biomass for the 48 fishes. The general relationships between fish biomass and maximum and minimum biomass of ingested prey were also calculated using data on the median biomass of each abundant fish species and the maximum and minimum biomasses of individual items ingested by the five captured animals closest to this median size. In this analysis it was necessary to pool groups of five fishes and determine the largest and smallest prey ingested by any member of this group, rather than using a single fish, in order to reduce the potential bias caused by some fishes having a single prey only in their guts; such animals provided no indication of the range in prey size they were capable of capturing. Three of the 48 abundant species were not collected in sufficient numbers for this maximum/minimum prey size analysis.

The quantity of benthos ingested by fishes at the twelve Western Port sites was estimated by assuming that each fish consumed 2.5% of its body weight per day. This figure is based on previous studies in Western Port by Robertson (1984) and in a Tasmanian seagrass bed with a similar fish community by Robertson and White (1986), where 14 small fish species were found to consume between 1% and 5% of their body weight per day, with a mean (±SD) of 2.5 (±1.2)%. Total daily consumption of crustaceans (C), for example, by fishes at each site was therefore calculated for each sampling period as:

$$C = \sum_{i=0}^{i=n} \frac{W_i \cdot 0.22 \cdot 0.05 \cdot P_i}{N \cdot H}$$

where W is the wet weight (g) of fish i, n is the total number of fishes collected from the site during that quarterly sampling period, P_i is the percentage of the diet of fish i that consisted of crustaceans, N is the total number of seine hauls conducted during that sampling period, H is the factor used to convert haul data to numbers per m^2 (=20 for seagrass and unvegetated sites and 9 for channel sites), and 0.22 is the wet weight/AFDW conversion factor. Because fish with empty guts contributed to total community consumption but probably fed during the night, individual fish with empty guts were considered to have similar diets to the fish of the same species with closest body size at that sampling period. When no other fish of the same species with a non-empty gut was collected in a given sampling period, then the fish with closest body size over all sampling periods was used. All five specimens collected of the fish species *Odax acroptilus, Urolophus* sp. and *Galaxias maculatus* possessed empty guts so these species were excluded from trophic analyses. Annual consumption was calculated using the mean daily rate of consumption in each season.

4.4 Results

Amongst the 5,113 fish collected for dietary analysis from Western Port, 720 animals had empty guts. The percentage abundance of different dietary items in the guts of fish species collected with non-empty guts are shown in Table 4.1. Crustaceans were the predominant food item in 61 of the 88 (69%) fish species collected, with eight species feeding mainly on other fishes, seven on molluscs, six on polychaetes and one (boarfish, *Pentaceropsis recurvirostris*) feeding on ophiuroids. Only five of the examined species predominantly consumed algae (luderick, *Girella tricuspidata*; yellow-eyed mullet, *Aldrichetta forsteri;* six-spined leatherjacket, *Acanthaluteres spilomelanurus*; and the gobies *Pseudogobius olorum* and *Tasmanogobius gloveri*), with seagrass ingested in large quantities by only one species (adult garfish, *Hyporhamphus melanochir*). The great majority of fishes examined fed on benthic epifaunal prey rather than infaunal or planktonic prey. Of the 61 fishes that fed primarily on crustaceans, 51 fed predominantly on epifauna, nine (four clupeoids, two atherinids, two pipefish and juvenile garfish) on plankton, and only one (a goby) on infauna.

Fishes found in the guts of other fishes are shown in Table 4.2. The fish predators examined can be divided into two groups, those predominantly feeding on pelagic fishes and those feeding on the smaller demersal fishes. Most of the ingested fishes were non-commercial species; however, pilchards were eaten by Australian salmon, garfish by barracouta, and ling by gummy shark.

None of the abundant fishes examined possessed a highly selective diet. Different fish species with comparable body weights were more likely to ingest similar prey species than fish of a single species at vastly different size. Amongst the crustacean feeders, species tended to shift their diets from copepods to amphipods and isopods at ≈0.1 g wet weight, and to crabs and shrimps at ≈100 g weight (Fig. 4.1). The major exception to this pattern was the yellow-eyed mullet, the most abundant species collected by gillnet. Mullet consumed amphipods at a size where other species were feeding on decapods, and copepods at a size where other species were feeding on amphipods.

A close relationship was detected between the log mean wet weight of fishes ($\overline{B_f}$, g) and the log mean AFDW of ingested prey ($\overline{B_P}$, mg) for the abundant species (log $\overline{B_P}$ = -2.40 + 0.98 x $\overline{B_f}$, $R^2 = 0.77$, n = 48, p<0.001; Fig. 4.2). The corresponding relationship between gape height and prey biomass had a slightly lower correlation coefficient ($R^2 = 0.72$). Total length showed a poorer relationship with prey biomass ($R^2 = 0.61$) because relatively small prey were ingested by long narrow fishes such as pipefish. The regression coefficient in the relationship between log fish biomass and log prey biomass was non-significantly different from 1 (=0.98; SE = 0.08), indicating that the ratio of prey size to fish size was largely independent of the size of predator. A fish of 100 g wet weight consumes prey at a mean AFDW of 8.27 mg which, if body mass is proportional to length cubed and AFDW is 22% of wet weight, translates to the mean length of prey being 7.2% of predator length. By comparison, fish with a weight of 0.1 g will ingest prey at a mean size of 7.6% of body length. The species with greatest deviation from the overall regression was the yellow-eyed mullet (see Fig. 4.2). This species consumed much smaller prey than would be expected from the regression; fish weighing 100g consumed invertebrates with a mean weight of 0.081 mg (1.5% of fish length).

Close relationships were also found between the log wet weight of fishes and the log maximum (U) and minimum (L) AFDW of ingested prey (log U = -0.71 + 1.04 x $\overline{B_f}$, R^2 = 0.74, n = 45, p<0.001; log L = -4.52 + 0.78 x $\overline{B_f}$, $R^2 = 0.72$, p<0.001). Although the regression coefficient in the fish weight/mimimum prey weight relationship is considerably less than 1, analysis of covariance indicates that the slopes of the three prey size regressions do not differ significantly from each other (SS = 17.8/420.9, df = 2/132, F = 2.79, p=0.065). Fish weighing 100 g will on average consume prey with sizes ranging from 0.40 mg (2.6% of length) to 59.1 mg (13.9% of length).

Preliminary estimates of the annual consumption of crustaceans, polychaetes and molluscs by small fishes at each site are shown in Table 4.3. Approximately 20% of the total production of benthos >125 mm sieve size (see Section 2) is consumed by fishes when all sites are considered (Table 4.3). The proportion of secondary production consumed by fishes was nearly twice as high in the primary channel habitats (≈22%) as in seagrass and shallow unvegetated habitats (≈13%). The proportion of crustacean production consumed by fishes was extremely high at all sites (an average of 74% for the primary sites), with other major faunal groups contributing in only a minor way to community fish consumption (≈7%). It should be noted that these figures are preliminary; analyses are continuing aimed at determining the proportion of macrofauna and benthic crustaceans in different size-classes consumed.

4.5 Discussion

Gut content analysis

The new method of gut content analysis has two perceived advantages over established methods. Data are obtained in a form that is directly comparable with data obtained using benthic coring techniques. These data can also be converted into other parameters by using the appropriate scaling factors, i.e., into abundance, estimated biomass or estimated production of ingested prey. Moreover, the procedure is extremely rapid, with most guts taking between 5 and 10 minutes to process. Other procedures, such as volumetric and points methods, avoid the subjective step in our procedure whereby prey are allocated to sieve size-classes by eye, but at the cost of considerable extra sorting time or by missing rarer prey items. We considered that, because of the variability in gut contents between individual fish, a more accurate picture of diet could be derived from studying the gut contents of, for example, 100 individuals than from 20 individuals whose gut contents were each determined slightly more accurately. Our procedure suffers the same differential-digestion bias as other techniques in that the importance of prey that are resistant to digestion will be considerably overestimated.

Diet and trophic relations with the benthos

Fishes collected in Western Port showed similar dietary intake patterns to fishes investigated in other studies. In all other studies of southern Australian seagrass fish communities (Burchmore et al., 1984; Rigby, 1984; Robertson, 1984; Watson et al., 1984; Robertson & White, 1986; Scott et al., 1986), and in the great majority of studies worldwide (Pollard, 1984; Huh & Kitting, 1985), crustaceans have also been found to be the major item in fish diets. Bell & Harmelin-Vivien (1983) notably found that crustaceans were the most important food type for 68% of species in a Mediterranean seagrass bed, compared to 69% in Western Port.

Total fish consumption in seagrass habitats (≈ 20 $g.m^{-2}.yr^{-1}$) was estimated in this study to be higher than the rate estimated by Robertson (1984) for seagrass meadows at Crib Point in Western Port (≈ 12 $g.m^{-2}.yr^{-1}$). This difference is probably largely due to the exclusion of many of the smaller fishes (including pipefish) in Robertson's study.

Athough there was an excess of benthic production available for fish to consume in Western Port, most of this production was presumably inaccessible (infauna) or of poor quality for fish. Nevertheless, the apparent surfeit of total benthic production does not preclude populations of fish species being limited by a deficiency of high quality (largely crustacean) food resources. Most crustacean production in Western Port was cropped by fish, hence a doubling in the numbers of fish in the Bay would be unlikely to be supported by the benthos, unless fish can reduce their dependence on crustacean prey.

Cropping rates were particularly high in channel habitats, in the seagrass habitat at Cowes Bank and in the unvegetated habitat at Tooradin. Consumption rates at these sites may have been overestimated due to the presence of non-resident animals such as fish in channels that had moved there after feeding elsewhere at high tide.

Few of the fishes examined consumed algae in any quantity. Two notable exceptions, yellow-eyed mullet and blue-spotted goby, were also species that were extremely abundant. The high densities of these species may be related to the herbivorous diets because an algal supplement possibly allows populations to be less limited by prey availability than other species. Yellow-eyed mullet also selected much smaller prey than other fish species with the same body size, so the great abundance of mullet at the study sites may also be due to mullet targetting the more abundant invertebrates at the bottom of the food chain (i.e., grazing molluscs and peracarid crustaceans) rather than the carnivorous crabs and shrimps selected by other fish species of a similar size.

Table 4.1. Percentage occurrence of different plant and animal groups in the guts of fish species collected in Western Port. * indicates group comprised <0.5% of total biomass in gut. Dietary groups are as follows: epifaunal crustaceans (CE), infaunal crustaceans (CI), planktonic crustaceans (CP), epifaunal molluscs (ME), infaunal molluscs (MI), pelagic molluscs (MP), epifaunal polychaetes (PE), infaunal polychaetes (PI), demersal fish (VE), pelagic fish (VP), other mobile epifaunal invertebrates (OE), other infaunal invertebrates (OI), bryozoans (BR), sponges (SP), ascidians (AS), algae (AL), seagrass (SG). Number of fishes used in analyses (i.e., those with non-empty stomachs) is also shown.

Species	Dietary group																	No. of guts examined
	CE	CI	CP	ME	MI	MP	PE	PI	VE	VP	OE	OI	BR	SP	AS	AL	SG	
Parascyllium ferrugineum				17		20		63										5
Juncrus vincenti	11					69			20									3
Mustelus antarcticus	90	*			*	1	*	5	2			*					*	91
Galeorhinus australis						35		1		64								9
Trygonorhina guanerius	89	1					5	5										3
Raja lemprieri	44	12							45									2
Urolophus cruciatis	54	10					8	27			*	1						15
Urolophus paucimaculatus	48	12		13			16	12										7
Urolophus sp.	72	19					10											2
Myliobatis australis	44	49						*				7						2
Callorhyncus milii	12	4		2	73	4	1	6										86
Spratelloides robustus			100															1
Hyperlophus vittatus	9		76	15														84
Sardinops neopilchardus	7		90	3														14
Engraulis australis	6	1	81	13														23
Muraenichthys breviceps	46						15	20	16								3	11
Pseudophycis bachus	62	12	1	1	*	5	*	1	3	15								69
Genypterus tigerinus	84					15			2									9
Hyporhamphus melanochir	14		39		*		*	4								7	36	26
Kestratherina brevirostris	29		66	4							1							52
Kestratherina esox	1		99															10
Hippocampus abdominalis	53		47															1
Mitotichthys semistriatis	94	*	6	*			*		*									148
Stigmatopora argus	44		54	2														91
Stigmatopora nigra	40	1	59							*								303
Stipecampus cristatus	62						36									3		2
Syngnathus curtirostris	100																	1
Vanacampus phillipi	91		6	*			2	*										169
Urocampus carinirostris	89	*	11	1														214
Gymnapistes marmoratus	87	1	1	1			6	2	3			*				*	*	99
Neosebastes scorpaenoides	54			5			4	36									*	7
Scopaena ergastulorum								100										1
Chelidonichthys kumu	47	33						17	3									2
Aploactisoma milesii	100																	1
Platycephalus bassensis	66	7		3	1	2	*	6	11	3							1	98
Platycephalus laevigatus	69	*	5			2	1	1	21	2						1	*	113
Platycephalus speculator	52								48									2
Acanthopegasus lancifer	58	42																1
Apogon conspersus	95	*						5										12
Siphamia cephalotes	91		9															27

Table 4.1 (Cont.)

Species	Dietary group																	No. of guts examined
	CE	CI	CP	ME	MI	MP	PE	PI	VE	VP	OE	OI	BR	SP	AS	AL	SG	
Sillaginodes punctatus	50	12	13				5	20				*						61
Pomatomus saltator						5			32	63								19
Pseudocaranx dentex	55	8	10	1	4		5	15	1	1	*					1		105
Trachurus declivis									50	50								2
Arripis trutta	2					3		1		92						3		40
Arripis truttaceous	5	1				4		*	12	78							*	74
Girella tricuspidata																100		1
Enoplosus armatus	71		29															7
Petaceropsis recurvirostris											99						1	2
Dactylophora nigricans	36						28	36										3
Aldrichetta forsteri	13	1	6	17	4		1	2			*				2	48	7	472
Sphyraena novaehollandiae										100								4
Dotalabrus aurantiacus	80		20															1
Haletta semifasciata	42	*	2	43	2	*	1	7	1			*				*	1	60
Neoodax balteatus	42			49	10													2
Cristiceps australis	70		2	1					27									31
Heteroclinus adelaidei	85	1	*	1			12	1									1	25
Heteroclinus forsteri	96						4											4
Heteroclinus perspicillatus	71	*		2			13	10	1			*				1	2	209
Arenigobius bifrenatus	48	6	6	3	1		1	7								28		51
Arenigobius frenatus	43	2	2	4	*		2	6			1	1				40		343
Callogobius depressus	32	21						47										4
Favonigobius tamarensis	69	7	5	2			2	13			*					3		185
Favonigobius lateralis	49	11	12	5			6	8								8		24
Gobiopterus semivestitus	54		44	2														74
Nesogobius hindsbyi	50	43						8										6
Nesogobius pulchellus	70	3		15				12										16
Nesogobius sp. 1	59	23	1	9			4	4								1		30
Nesogobius sp. 2	30	66	4															4
Pseudogobius olorum	30	1		1												68		106
Tasmanogobius gloveri	43	3		5							5					45		3
Thyrsites atun										100								4
Seriolella brama	100																	1
Parvicrepis sp.1	84		2	1			*	7			5							28
Arnoglossus bassensis	63	37																3
Ammotretis rostratus	47	32	*		4			18								*		21
Rhombosolea tapirina	27	11		3	9	*	*	49				1						43
Acanthaluteres spilomelanurus	30	*	*	10			1	2					8	2	*	45	1	73
Brachaluteres jacksonianus	69		1	20			11											12
Eubalichthys gunniii	45			50												5		1
Meuschenia freycineti	19	1		21	*	*	5	2			1	*	9	15	8	12	7	86
Penicipelta vittiger	76		1	16									8					8
Scobinichthys granulatus	32			4			1						12	4	28	19	*	6
Aracana aurita	64	6						30										2
Contusus brevicaudus	36		9	*	55													11
Contusus richei	4						10	86										1
Tetractenos glaber	70	4		6	4		*	10			2	*			1	3	1	207
Diodon nicthemerus	73	1		3	16	1	*	4			1					*	*	102

Table 4.2. Number of fishes collected from the guts of fishes.

Predator	Prey															
	Hyperlophus vittatus	*Sardinops neopilchardis*	*Engraulis australis*	*Muraenichthys breviceps*	*Genypterus tigerinus*	*Kestratherina brevirostris*	*Mitotichthys semistriatis*	*Stigmatophora nigra*	*Vanacampus phillipi*	*Urocampus carinirostris*	*Gymnapistes marmoratus*	*Aldrichetta forsteri*	*Heteroclinus perspicillatus*	*Arenigobius frenatus*	*Favonigobius tamarensis*	*Tetractenos glaber*
Juncrus vincenti	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Mustelus antarcticus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Muraenichthys breviceps	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pseudophycis bachus	1	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnapistes marmoratus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Platycephalus bassensis	1	0	0	1	0	0	0	0	0	0	1	0	0	18	0	0
Platycephalus laevigatus	0	0	0	0	0	0	1	0	10	1	1	0	13	9	1	0
Pomatomus saltator	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachurus declivis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Arripis trutta	84	1	9	0	0	0	0	0	0	0	0	1	0	0	0	0
Arripis truttaceous	63	7	32	0	0	5	0	7	0	0	0	0	0	13	0	0
Aldrichetta forsteri	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sphyraena novaehollandiae	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
Haletta semifasciata	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Thyrsites atun	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 4.3. Estimated annual consumption ($g.m^{-2}.y^{-1}$) of different faunal groups by small fishes at the sites studied in Western Port. The percentage of the total annual production of benthos (>125 mm sieve size; as calculated in Chapter 2) consumed by small fishes is also shown for the total benthos, crustaceans and non-crustacean taxa. Dietary groups are as follows: epifaunal crustaceans (CE), infaunal crustaceans (CI), benthic molluscs (M), polychaetes (P), demersal fish (F), sessile invertebrates (S), algae (Alg), seagrass (SG), plankton (Pl), other mobile epifaunal invertebrates (O).

Species	Dietary group											Proportion consumed (%)		
	CE	CI	M	P	F	S	Alg	SG	Pl	O	Total	Total	Crust.	Other
Peck Point seagrass	9.6	0.3	1.6	2.6	0.3	1.7	0.3	0.6	1	0.1	18.2	11	36	6
Peck Point unvegetated	2	0.1	0.2	0.6	0.4	0	*	0	0.1	0.1	3.4	5	22	2
Peck Point channel	8.1	0.1	*	2.7	0.9	0	*	*	0.1	0.8	12.7	20	65	9
Rhyll seagrass	17.1	*	1.3	2.6	*	*	1.8	*	0.7	*	23.5	17	102	5
Rhyll unvegetated	5.2	*	1.2	0.6	0.1	0.1	1.1	0	*	0.2	8.6	6	46	2
Rhyll channel	11.3	1	5.4	4	0.2	0	0	0	0.5	0	22.4	30	95	16
Tooradin seagrass	10.1	*	0.9	1.1	0.3	*	2.2	0.4	0.2	*	15.2	13	31	6
Tooradin unvegetated	11.3	0.1	6.4	1.4	*	0	0.4	0	*	0	19.6	27	117	13
Tooradin channel	6.7	0.6	0.5	1.2	0	0	0.2	0	*	*	9.2	16	110	4
Cowes Bank seagrass	16.9	0.1	0.4	1.6	0.7	*	0.1	0.3	1.5	*	21.6	44	147	12
Cowes Bank unvegetated	3.5	2.1	0.5	0.4	0	0	*	0	*	*	6.4	21	70	4
Loelia Shoal	2.6	0.7	*	0.1	0	0	0	0	0.6	0	4	15	46	4

Fig. 4.1. Percentage of total crustacean biomass in the guts of fishes of different size consisting of copepods, peracarids (amphipods, isopods and mysids) and decapods.

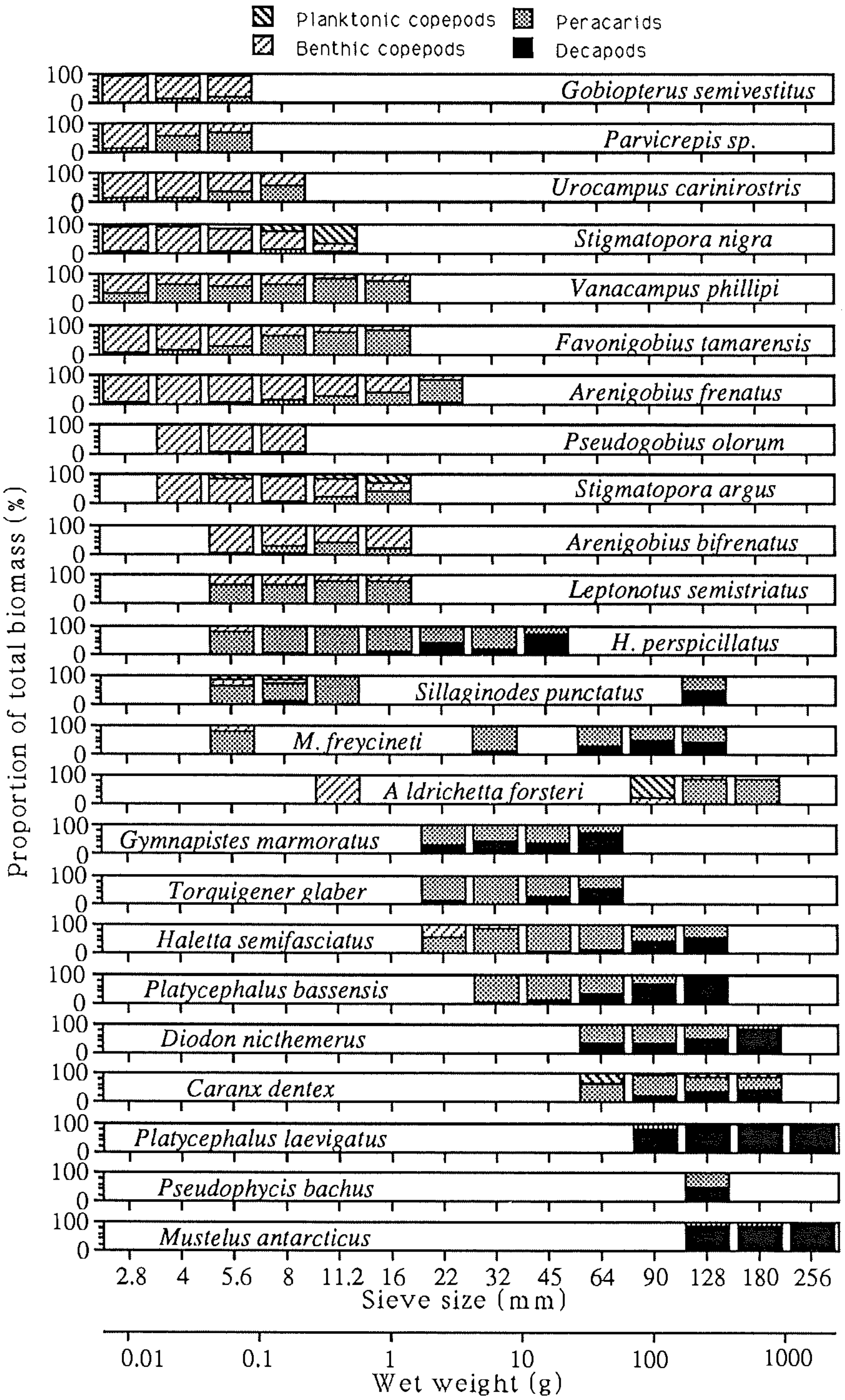
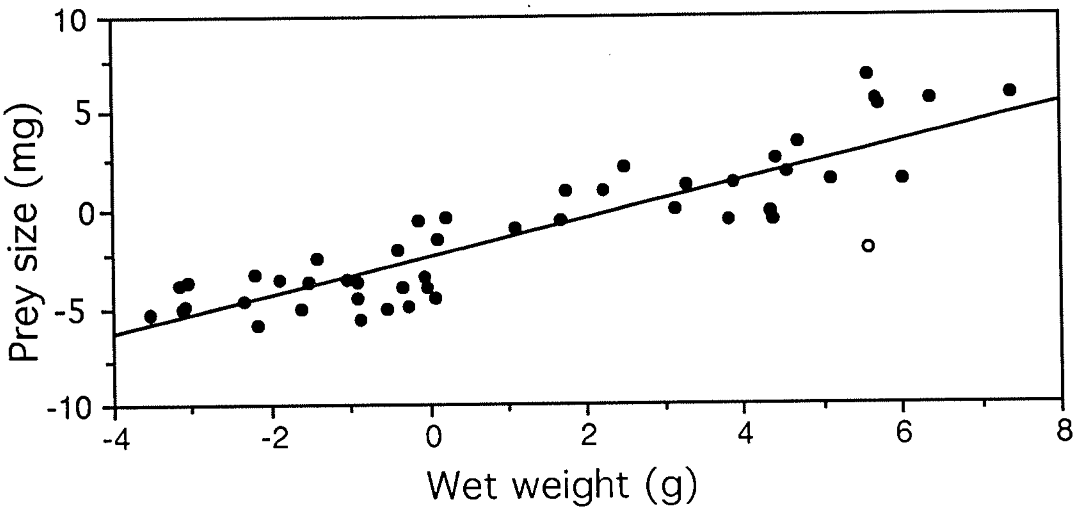

▧ Planktonic copepods
▨ Benthic copepods
▩ Peracarids
■ Decapods
Gobiopterus semivestitus
Parvicrepis sp.
Urocampus carinirostris
Stigmatopora nigra
Vanacampus phillipi
Favonigobius tamarensis
Arenigobius frenatus
Pseudogobius olorum
Stigmatopora argus
Arenigobius bifrenatus
Leptonotus semistriatus
H. perspicillatus
Sillaginodes punctatus
M. freycineti
Aldrichetta forsteri
Gymnapistes marmoratus
Torquigener glaber
Haletta semifasciatus
Platycephalus bassensis
Diodon nicthemerus
Caranx dentex
Platycephalus laevigatus
Pseudophycis bachus
Mustelus antarcticus
100
0
Proportion of total biomass (%)
2.8
4
5.6
8
11.2
16
22
32
45
64
90
128
180
256
Sieve size (mm)
0.01
0.1
1
10
100
1000
Wet weight (g)

Fig. 4.2. Relationship between wet weight of fish (g) and the mean ash-free dry weight of prey (mg) in guts for 48 fish species collected in Western Port. Data point for yellow-eyed mullet is shown by open circle.


10
5
0
-5
-10
Prey size (mg)
-4
-2
0
2
4
6
8
Wet weight (g)

Section 5. General relationships between sediments, seagrasses, invertebrates and fishes in southern Australia.

5.1 Summary

Fishes, invertebrates and sediments were sampled at 14 locations extending from Rottnest Island (W.A.) to Jervis Bay (N.S.W), and including two locations in Tasmania. The major patterns identified in the Western Port study were confirmed over the greater geographical range. Seagrasses were not found to have an important nursery role at the coastal sites, in contrast to the likely situation in euryhaline estuaries. However, seagrasses play an important role in coastal processes by enhancing invertebrate and fish production. Fish production was highly correlated with seagrass biomass and crustacean production, and negatively correlated with fetch. Crustacean production was in turn highly correlated with seagrass biomass and the silt/clay content of sediments. Regressions relating these variables that can be used for predictive purposes are provided.

5.2 Introduction

In order to determine whether the relationships identified for Western Port are widely applicable to other sites, we describe in this section the abundance and production of fishes and invertebrates at 14 shallow-water localities extending from Rottnest Island, W.A, to Jervis Bay, N.S.W. The diets of fishes were also studied but await detailed analysis. The major physical features measured in this study were sediment characteristics because sediments exert a strong direct influence on the distribution of animals (Whitlach, 1981). The size of sediment particles larger than muds are also correlated with water energy (Allen, 1970), hence particle size is also indicative of wave exposure, another major factor known to affect inshore animals (see, e.g., Gibbons, 1988). The biotic variables examined were fish and invertebrate density and seagrass biomass. As in other sections of the study, particular emphasis has been placed on identifying the size-distributions of fish and invertebrate assemblages.

5.3 Methods

The sites examined (Fig. 5.1) and dates of sampling were Thomsons Bay (Rottnest Island, W.A.; 9 Jan 1991), Porpoise Bay/Parker Point (Rottnest Island, W.A.; 23 Jan 1991), Woodmans Point (Cockburn Sound, W.A.; 17 Jan 1991), Rockingham (Cockburn Sound, W.A.; 12 Jan 1991), Princess Royal Harbour (near Albany, W.A.; 27 Jan 1991), Frenchmans Bay (near Albany, W.A.; 26 Jan 1991), Port Gawler (near Adelaide, S.A.; 10 Feb 1992), Barker Inlet (near Adelaide, S.A.; 11 Feb 1992), Crib Point (Western Port, Vic; 29 Aug 1991), French Island (Western Port, Vic; 28 Aug 1990), Lake King (Gippsland Lakes, Vic; 5 Feb 1992), Bagot Point (near Swansea, Tas; 4 Apr 1992), Cloudy Lagoon (Bruny Island, Tas; 29 Mar 1992) and Cararma Inlet (Jervis Bay, NSW; 31 Mar 1990). The Western Australian sites are discussed in greater detail by Edgar & Shaw (1993), and data from Crib Point, Western Port, was discussed briefly in Section 2. Data on the physical characteristics of sites are given in Table 5.1. At most localities, samples were collected from paired vegetated (*Posidonia* spp., *Heterozostera tasmanica* or *Zostera muelleri*) and unvegetated habitats in shallow (<4 m) depths (Fig. 5.1; Table 5.1). At two localities, Barker Inlet (S.A.) and Jervis Bay (N.S.W.), *Posidonia australis* and zosteroid habitats were both sampled in addition to the bare habitat, while at French Island only the unvegetated habitat was sampled, and at Princess Royal Harbour an *Amphibolis antarctica* seagrass bed also was sampled. The meiofauna was collected at each site using 5 replicate 50 mm diameter cores, and macrofauna using 5 replicate 150 mm diameter cores, in the same way as the seasonal samples were collected and processed in the Western Port study. At Jervis Bay, the first locality investigated, macrofauna was collected using 15 replicate 50 mm diameter cores sorted to 0.5 mm sieve size, rather than by using the 150 mm cores sorted to 1 mm sieve size.

The quantities of organic material and ash in sediments at each site were measured by amalgamating sediments collected from replicate meiofaunal cores, and then weighing the sediments collected by different sieves after drying at 60 °C and again after ashing at 550 °C. The biomass of live seagrass leaves, rhizomes and debris collected from macrofaunal core samples was also measured after drying at 60°C for at least 2 d.

Fishes were sampled with a small beach seine (15 m long, 3 m drop, 1 mm mesh) dragged through a 12 m distance into the boat in the same way as described in Section 3. The area swept by the net was measured in the earlier study to be 77±10 (SD) m^2 in shallow water. Trials using this net in Western Port indicated that the capture efficiency of the seine for small fish species varied from 12% to 63%, with an overall mean efficiency of 26%. The numbers collected in each haul therefore were converted to numbers per m^2 by dividing by 20 (=77x0.26). In the laboratory, fishes were weighed, and length to caudal fork (LCF) recorded. If >120 animals of a species were collected from a site then 100-120 individuals were subsampled for weighing and measuring. Invertebrate and fish production were calculated using the methods described earlier.

5.4 Results

Benthic Invertebrates

Data from the six Western Australian locations have been most thoroughly analysed to date, with the results presented in a paper by Edgar & Shaw (1993; included as Appendix 2). The estimated biomass and production of the benthos, and the production of the major macrofaunal components, for all sites are shown in Table 5.2. Estimated daily production of macrobenthos varied over two orders of magnitude, with highest production occurring in the estuarine seagrass beds of Lake King, and the lowest production occurring in the unvegetated habitat at Woodmans Point. Macrofaunal production was higher at vegetated sites than adjacent unvegetated sites, except for the two South Australian locations where a gastropod (Port Gawler) and spionid polychaete (Barker Inlet) were extremely abundant in unvegetated areas. Crustaceans provided approximately half of the total secondary production at most of the Western Australian, Tasmanian and New South Wales seagrass sites, whereas polychaetes and molluscs tended to dominate the macrofauna in other areas. The estimated production of meiobenthos (0.125-1 mm sieve size animals) was high at all sites, including sites with low macrobenthic production.

Both total faunal production and crustacean production were strongly correlated with the proportion of sediment that was silt or clay ($r \approx 0.65$, $p>0.001$, Table 5.3) and less strongly correlated with other sediment characteristics. These correlation coefficients did not change greatly when data from the Western Port sites discussed in earlier sections were included in calculations (Table 5.3). Crustacean production was also strongly correlated with the biomass of seagrass leaves. The percentage of silt/clay and seagrass biomass were not highly correlated with each other, consequently most of the variation in crustacean production can be explained using a regression equation incorporating these parameters (Table 5.4).

Estimated production of total fauna and crustaceans in different size classes for the different sites are shown in Figs 4.2, 4.3, 4.4 and 4.5. For sites where crustaceans contributed a large proportion of total benthic production (e.g., the Western Australian seagrass sites), the production of crustaceans and total fauna tended to peak and trough at the same size-classes, whereas at other sites (e.g., the South Australian sites) crustacean production maxima rarely coincided at the same size classes as maxima for the total fauna. No clear relationship could be deduced between the size-structure of assemblages at different sites and sediment or seagrass characteristics (see Table 5.1). However, at the most sheltered locations little difference in faunal size-structure was evident between adjacent seagrass and unvegetated sites (e.g., Lake King and Cloudy Lagoon, Figs 5.2 and 5.3), while at exposed locations size-structure patterns were quite different between seagrass and unvegetated sites (e.g., Thomsons Bay and Frenchmans Bay, Fig. 5.5).

Fishes

Approximately three times as many fish (21,609) were collected from the 16 southern Australian seagrass sites compared with the 14 unvegetated sites investigated (7,388; see Table 5.5). The number of species collected from seagrass sites was also considerably higher than for unvegetated areas (83 c.f. 53). However, virtually all the abundant species in seagrass sites had little commercial value, with more than 10 specimens of only two commercial species (*Meuschenia freycineti* and *Haletta semifasciata*) being collected during the study from seagrass beds. By comparison, two other commercially important species (*Rhombosolea tapirina* and *Ammotretis rostratus*) were represented by more than 10 specimens in collections from unvegetated habitats.

The presence of atherinids (particularly *A. presbyteroides* and *A. microstoma*) and clupeoids greatly elevated the estimates of total fish production at a number of sheltered sites (e.g., Princess Royal Harbour and Parker Point). These fishes occurred in large schools near the water surface and fed primarily on planktonic food resources, hence would not be expected to interact greatly with benthic invertebrates. Fish production has consequently been calculated in two ways: as total fish production and as demersal fish production without the pelagic species (Table 5.6).

A high correlation was found between estimated daily fish production and estimated crustacean production ($r = 0.52$ for total production and $r = 0.56$ for demersal production; Table 5.7). Demersal fish production was also highly correlated with seagrass leaf biomass ($r = 0.49$; $0.001<p<0.01$), whereas seagrasses were relatively unimportant to the pelagic atherinids and clupeoids. Pelagic fishes were disproportionately abundant at the most sheltered sites, consequently a strong negative correlation was found between total fish production and fetch ($r = -0.44$, $p = 0.01$). Demersal fish production was also negatively correlated with wave exposure; however, this relationship was partly obscured by a positive relationship between wave exposure and leaf biomass (see regression equation in Table 5.4).

5.5 Discussion

Seagrass beds as nursery habitat

Our data provided no support for the theory that seagrass beds provide critical habitat for juveniles of large numbers of commercially important species (Pollard, 1984). Only two commercially important species, blue rock whiting and six-spined leatherjackets, were collected in statistically greater abundance from seagrass beds than unvegetated areas, with two species of flounder showing the contrary trends. These species were also abundant in Western Port and were discussed in Section 3.

While several studies elsewhere in the world (e.g., Heck and Thoman, 1984) have also failed to show that seagrass beds provide important nursery habitat for commercial species of fish, we suggest that the discrepancy between our results and Pollard's (1984) view has arisen because, with two exceptions, our sampling sites were located in fully marine locations. Fully marine seagrass beds in southern Australia appear to support few commercially-important species. By contrast, the lower salinity reaches of southern Australian estuaries are utilized by juveniles of species such as bream, snapper and luderick (Pollard, 1981; Rigby, 1984). Whether seagrasses are critical for the survival of commercial fishes or whether commercial fishes can survive without seagrasses in euryhaline estuaries remains to be adequately determined. Seagrass are possibly so widespread in shallow estuaries that the misconception has arisen that seagrass is the primary environmental factor to which fish respond. In this context it is worth noting that our Western Port study showed that many more small fishes, albeit non-commercial species, were found in seagrass beds than in unvegetated habitats. The two low salinity locations investigated in our study, Lake King in the Gippsland Lakes and Bagot Point near the mouth of the Swan River, both possess juvenile bream populations (Last, 1983; Rigby, 1984). However, because only two bream were collected (from Lake King seagrass), we could not test the importance of seagrass as nursery habitat in these areas.

Production relationships

The close relationships found between fish production, crustacean production, seagrass biomass and sediment characteristics in Western Port were confirmed over a much larger geographical range. Given the small number of replicates sampled at different sites (and hence large possible error in estimate of mean), and the arbitrary selection of environmental variables (such as the use of fetch as an indication of wave exposure), the regression equations provided in Table 5.4 are surprisingly accurate as they explain ≈50% of the variation in log production. As an indication of the accuracy of these regression equations, they have been used to predict crustacean (>1 mm sieve size), macrofaunal and fish production for the twelve major sites investigated in Western Port (Table 5.8). [Note that data used in this analysis are independent of data used to derive the equations]. Many of the predictions are quite accurate; however, some predictions, most notably macrofaunal production at Loelia Shoal and fish production at the Tooradin unvegetated site, are poor. Rather than causing concern, the largest discrepancies between predicted and measured values are interesting because they allow anomalous sites to identified, and perhaps subjected to more detailed sampling to determine the reasons for the anomalies. The Loelia Shoal site, for example, differed from other sites in containing extremely soft muds. Hence, despite the high percentage of organic matter (in dried sediments) greatly elevating predictions of macrofaunal production at Loelia Shoal, the relatively low density of organic matter in sediments (when water content is included) may reduce production levels. On the other hand, the atypically high estimated fish production at the Tooradin unvegetated site was probably caused by the massive number of non-resident toadfish that were collected not being supported by local benthic production (as also indicated by gut content analysis that showed many of the Tooradin unvegetated toadfish fed on epifaunal animals not present in the immediate area). These hypotheses, and others for additional anomalous sites, can be examined by further sampling or experimental work.

In conclusion, it should be stressed that, while the regression equations listed in Table 5.4 provide a quantum advance in predictive ability, they are a first step which can readily be passed by sampling sites in greater detail (i.e., with more replication and incorporating seasonal trends), increasing the number of sites examined, and increasing the environmental parameters included in calculations (particularly by incorporating data on turbidity, depth, salinity and nutrient concentrations).

Table 5.1. Fetch, sediment (modal particle size, proportion of silt and clay, proportion of organic material) and seagrass characteristics (leaf, rhizome and debris biomass; ±SE) for sites investigated. Fetch is expressed as the maximum unimpeded distance for a 30° arc from the site.

Site	Fetch (km)	Modal size (µm)	Proportion <63 µm (%)	Organic (%)	Leaf biomass ($g.m^{-2}$)	Rhizome biomass ($g.m^{-2}$)	Debris biomass ($g.m^{-2}$)
Thomsons Bay *Posidonia*	33	180	1.27	2.8	997±204	207±110	2421±527
Thomsons Bay unvegetated	22	220	0.04	2	0	0	0
Porpoise Bay *Posidonia*	20	150	2.61	5.3	629±76.3	1442±310	4519±1468
Parker Point unvegetated	2	200	0.43	2.6	0	0	0
Woodmans Point *Posidonia*	7.5	220	0.58	1.8	787±113	714±278	1940±471
Woodmans Point unvegetated	7.5	210	0.06	3	0	0	0
Rockingham *Posidonia*	12	220	8.97	4.2	879±344	651±259	1659±489
Rockingham unvegetated	16	255	3.44	3.4	0	0	0
Princess Royal Harbour *Posidonia*	7	210	7.85	12	621±142	3667±624	0
Princess Royal Harbour *Amphibolis*	7	210	1.13	1.3	3351±1572	501±352	0
Princess Royal Harbour unvegetated	7	240	0.22	0.6	0	0	0
Frenchmans Bay *Posidonia*	9.5	185	2.99	2.5	525±136	4279±1076	0
Frenchmans Bay unvegetated	12	240	0.08	0.1	0	0	0
Cararma Inlet *Posidonia*	10	245	0.44	1.6	100±10.7	607±105	10.9±2.21
Cararma Inlet *Zostera*	10	270	0.52	0.8	149±26.8	648±242	10.2±2.66
Cararma Inlet unvegetated	10	250	0.16	0.6	0	0	0
Bagot Point *Zostera*	1.2	100	10.6	7.3	47.2±15.3	26.6±8.26	3.23±3.23
Bagot Point unvegetated	1.2	165	0.3	1.1	0	0	0
Cloudy Lagoon *Heterozostera*	2.5	125	2.79	2.6	129±49.5	52.1±10.9	0
Cloudy Lagoon unvegetated	2.5	145	0.59	0.8	0	0	0
French Island unvegetated	13	100	8.78	1.7	0	0	0
Lake King *Zostera*	2.5	40	72	6.1	79.6±15.6	68.8±13.4	101±35.8
Lake King unvegetated	2.5	40	60.1	4.5	0	0	0
Crib Point *Heterozostera*	11	55	30.9	4.9	141±22.4	814±106	0
Crib Point unvegetated	11	180	6.86	1	0	0	0
Port Gawler *Posidonia*	120	145	1.41	2.7	206±38.9	665±147	332±84.3
Port Gawler *Heterozostera*	120	150	5.95	5.3	185±55	97.6±25.2	330±91.3
Port Gawler unvegetated	120	357	1.17	3.7	0	0	0
Barker Inlet *Heterozostera*	3.5	145	14	3.2	199±32.8	254±22.4	0
Barker Inlet unvegetated	3.5	205	1.53	0.8	0	0	0

Table 5.2. Biomass (±SE) of total macrofauna (i.e., invertebrates >1 mm sieve size), estimated production of total macrofauna and major macrofaunal groups, and estimated production of total fauna and crustaceans >125 μm sieve size.

	Biomass (fauna >1 mm) ($g.m^{-2}$)	Production (fauna >1 mm) ($mg.m^{-2}.d^{-1}$)					Production (fauna >125 μm) ($mg.m^{-2}.d^{-1}$)	
	Total	Crustacea	Mollusca	Polychaeta	Other	Total	Crustacea	Total
Thomsons Bay *Posidonia*	10.2±3.6	36±13	35±17	39±17	12±5	123±35	100±39	246±72
Thomsons Bay unvegetated	0.5±0.4	0.3±0.2	3.5±3.5	1.8±0.2	0	5.6±3.6	7±15	87±16
Porpoise Bay *Posidonia*	10.3±1.9	35±8	22±11	65±16	9.3±3.3	132±18	130±21	299±19
Parker Point unvegetated	1.0±0.2	13±4	2.1±1.3	3.3±0.7	0	18±5	54±17	80±16
Woodmans Point *Posidonia*	4.6±1.3	57±17	16±7	1.8±0.2	0	75±22	86±46	189±44
Woodmans Point unvegetated	0.13±0.02	1.1±0.2	0	1.8±0.2	0	2.8±0.3	18±4	94±4
Rockingham *Posidonia*	15±6	127±45	59±45	52±7	7.2±2.5	245±94	313±140	513±145
Rockingham unvegetated	14±5	22±11	0.8±0.2	125±30	16±15	164±42	149±38	443±60
Princess Royal Harbour *Posidonia*	22±4	143±34	77±27	59±8	6.6±1.9	285±43	221±105	459±110
Princess Royal Harbour *Amphibolis*	14±5	66±20	30±13	100±22	20±17	216±60	107±53	601±60
Princess Royal Harbour unvegetated	16±7	4.7±2.5	113±42	27±11	0.9±0.8	146±51	27±49	309±63
Frenchmans Bay *Posidonia*	11±5	24±7	44±24	38±19	1.0±0.3	107±42	97±78	253±90
Frenchmans Bay unvegetated	0.9±0.2	8.5±3.6	0	6.3±1.1	0.2±0.2	15±3	16±14	90±15
Cararma Inlet *Posidonia*	2.0±0.7	2.2±1.1	15±6	5.6±2.3	5.3±2.5	28±8	56±32	163±30
Cararma Inlet *Zostera*	16±10	29±12	98±55	14±6	6.6±2.9	147±71	76±21	276±78
Cararma Inlet unvegetated	1.0±0.2	1.2±0.9	4.3±2.8	15±3	1.0±0.3	22±5	12±27	140±26
Bagot Point *Zostera*	17±4	40±18	98±26	83±19	1.0±0.6	222±47	187±92	504±96
Bagot Point unvegetated	5.7±1.0	5.3±3.2	5.4±1.7	51±4	0	62±8	37±8	145±8
Cloudy Lagoon *Heterozostera*	10.0±2.9	35±14	36±13	61±16	3.8±1.2	135±37	271±159	656±167
Cloudy Lagoon unvegetated	5.7±2.6	17±15	4.9±3.2	31±6	1.3±0.7	54±15	81±26	260±26
French Island unvegetated	8.0±1.3	21±12	54±7	40±8	0	115±14	38±31	220±25
Lake King *Zostera*	62±19	55±5	679±224	119±24	0.1±0.1	853±214	124±89	1142±208
Lake King unvegetated	18±3	7.3±1.4	231±43	42±7	0.2±0.2	280±47	47±99	434±104
Crib Point *Heterozostera*	12.2±0.4	41±8	33±5	70±10	9.3±7.0	152±7	77±20	309±17
Crib Point unvegetated	2.3±0.5	14±6	13±6	6.2±1.7	0	33±6	30±18	124±17
Port Gawler *Posidonia*	60±18	70±16	51±27	301±116	58±22	480±130	108±44	590±127
Port Gawler *Heterozostera*	55±17	57±10	453±132	37±9	6.3±3.2	553±134	103±85	1235±96
Port Gawler unvegetated	113±47	8.2±5.0	669±298	33±7	16±15	726±287	110±77	935±324
Barker Inlet *Heterozostera*	45±7	50±11	212±35	84±8	17±15	363±52	54±29	442±65
Barker Inlet unvegetated	71±16	2.7±1.5	280±77	401±74	0.8±0.4	685±145	34±162	1082±257

Table 5.3. Pearson correlation coefficients relating log benthos production (>1 mm and >125μm sieve size) and log crustacean production with various physical parameters (also log-transformed). Analysis 1 includes data from 30 sites (excluding Western Port sites discussed in Chapter 4) and Analysis 2 includes all shallow vegetated and unvegetated sites investigated during the study.

	Analysis 1 (30 sites)				Analysis 2 (38 sites)			
	>1mm size		>125μm size		>1mm size		>125μm size	
	Total	Crust.	Total	Crust	Total	Crust.	Total	Crust
Fetch	0.14	0.06	0.16	0.02	0.10	0.05	0.08	-0.05
Particle mode	-0.32	-0.26	-0.29	-0.17	-0.39	-0.23	-0.34	-0.16
Particles <63μm	0.71	0.65	0.63	0.60	0.68	0.55	0.53	0.43
Organic (%)	0.40	0.49	0.42	0.56	0.44	0.46	0.44	0.51
Seagrass biomass	0.32	0.66	0.29	0.58	0.27	0.61	0.31	0.59
Rhizomes biomass	0.27	0.57	0.17	0.51	0.23	0.53	0.21	0.53
Debris biomass	0.20	0.42	0.14	0.38	0.17	0.41	0.16	0.40

Table 5.4. Regression equations relating production of crustaceans (>1 mm and >125 µm sieve size) and demersal fish to most important variables at 30 sites in southern Australia. C_1: production of crustaceans >1 mm size (in $mg.m^{-2}.d^{-1}$); C_{125}: production of crustaceans >125 µm size ($mg.m^{-2}.d^{-1}$); T_1: production of macrofauna ($mg.m^{-2}.d^{-1}$); T_{125}: production of fauna >125 µm size ($mg.m^{-2}.d^{-1}$); D: production of demersal fish ($mg.m^{-2}.d^{-1}$); L: seagrass leaf biomass ($g.m^{-2}$); S: proportion of sediment <125 µm sieve size (%); F: fetch (km).

$\log C_1 = 1.77\ (\pm 0.22) + 0.27\ (\pm 0.06) \ln (L+1) + 0.35\ (\pm 0.09) \ln S$; $R^2 = 0.70$; $SE = 0.85$

$\log C_{125} = 3.60\ (\pm 0.16) + 0.16\ (\pm 0.04) \ln (L+1) + 0.20\ (\pm 0.06) \ln S$; $R^2 = 0.59$; $SE = 0.61$

$\log T_1 = 3.85\ (\pm 0.38) + 0.26\ (\pm 0.15) \ln F + 0.53\ (\pm 0.09) \ln S$; $R^2 = 0.56$; $SE = 0.97$

$\log T_{125} = 5.25\ (\pm 0.24) + 0.16\ (\pm 0.09) \ln F + 0.26\ (\pm 0.06) \ln S$; $R^2 = 0.45$; $SE = 0.61$

$\log D = 1.87\ (\pm 0.57) - 0.71\ (\pm 0.22) \ln F + 0.40\ (\pm 0.09) \ln (L+1)$; $R^2 = 0.50$; $SE = 1.41$

Table 5.5. Abundances of fish species collected by seine at different sites. TBP Thomsons Bay *Posidonia*; TBU Thomsons Bay unvegetated; PBP Porpoise Bay *Posidonia*; PPU Parker Point unvegetated; WPP Woodmans Point *Posidonia*; WPU Woodmans Point unvegetated; RCP Rockingham *Posidonia*; RCU Rockingham unvegetated; PRP Princess Royal Harbour *Posidonia*; PRA Princess Royal Harbour *Amphibolis*;PRU Princess Royal Harbour unvegetated; FBP Frenchmans Bay *Posidonia*; FBU Frenchmans Bay unvegetated, CIP Cararma Inlet *Posidonia*; CIZ Cararma Inlet *Zostera*;CIU Cararma Inlet unvegetated; BPZ Bagot Point *Zostera*; BPU Bagot Point unvegetated; CLH Cloudy Lagoon *Heterozostera*; CLU Cloudy Lagoon unvegetated; FIU French Island unvegetated; LKZ Lake King *Zostera*; LKU Lake King unvegetated; CPH Crib Point *Heterozostera*; CPU Crib Point unvegetated; PGP Port Gawler *Posidonia*; PGH Port Gawler *Heterozostera*;PGU Port Gawler unvegetated; BIH Barker Inlet *Heterozostera*; BIU Barker Inlet unvegetated.

Fish species	Site																													
	TBP	TBU	PBP	PPU	WPP	WPU	RP	RU	PRP	PRA	PRU	FBP	FBU	CIP	CIZ	CIU	BPZ	BPU	CLH	CLU	FIU	LKZ	LKU	CPH	CPU	PGP	PGH	PGU	BIH	BIU
Spratelloides robustus Ogilby	0	0	76	71	19	0	0	0	7	1	115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sardinops neopilchardus (Steindachner)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
Hyporhamphus melanochir (Valenciennes)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0
Hyporhamphus regularis (Günther)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Atherinasoma microstoma (Günther)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8407	228	0	0	0	356	0	0	0
Atherinasoma presbyteroides (Richardson)	0	0	0	1494	144	0	0	0	1629	2150	0	0	0	12	2	8	705	243	0	2441	0	0	0	0	0	0	0	11	0	0
Craterocephalus honoriae (Ogilby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kestratherina brevirostris Pavlov,Ivantsoff, Last & Crowley	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	455	0	0	0	0	0
Kestratherina esox (Klunzinger)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Filicampus tigris (Castelnau)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippocampus breviceps Peters	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Histiogamphelus cristatus (Macleay)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kaupus costatus (Waite & Hale)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	47	0
Leptoichthys fistularius Kaup	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mitotichthys c.f. meraculus (Whitley)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mitotichthys semistriatis (Kaup)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	0	0	4	0	0	0	0	0	0
Stigmatopora argus (Richardson)	3	0	1	0	10	0	13	0	1	0	1	0	0	0	0	0	6	0	12	0	0	2	0	0	0	27	0	3	0	0
Stigmatopora nigra Kaup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	55	1	0	0	0	2	0	6	0	0	0	0	6	0
Syngnathus curtirostris Castelnau	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Vanacampus margaritifer (Peters)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vanacampus phillipi (Lucas)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	1	1	1	4	0	0	0	12	0	1	0	0	42	0
Vanacampus poecililaemus (Peters)	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urocampus carinirostris Castelnau	0	0	0	0	0	0	0	0	0	0	0	0	0	3	21	1	0	0	0	0	0	19	3	17	0	0	0	0	0	0
Centropogon australis (Shaw)	0	0	0	0	0	0	0	0	0	0	0	0	0	34	40	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Gymnapistes marmoratus (Cuvier & Valenciennes)	0	0	0	0	0	0	27	0	6	0	0	0	0	3	6	0	40	0	0	0	0	2	0	3	1	8	0	0	58	0
Maxillicosta scabriceps Whitley	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aploactisoma milesii Richardson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Laeviprora inops (Jenyns)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onigocia spinosa (Temmink & Schlegel)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycephalus bassensis Cuvier & Valenciennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	2	0	0	0	0	0	0	0	0	0	0
Laeviprora laevigatus (Cuvier)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelates quadrilineatus (Bloch)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelates sexlineatus (Quoy & Gaimard)	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	281	0

Table 5.5 (Cont.)

Fish species	Site																													
	TBP	TBU	PBP	PPU	WPP	WPU	RP	RU	PRP	PRA	PRU	FBP	FBU	CIP	CIZ	CIU	BPZ	BPU	CLH	CLU	FIU	LKZ	LKU	CPH	CPU	PGP	PGH	PGU	BIH	BIU
Velambassis jacksoniensis (Macleay)	0	0	0	0	0	0	0	0	0	0	0	0	0	197	7	126	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vincentia conspersa (Klunzinger)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apogon ruepellii (Günther)	0	0	1	0	585	0	3638	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphamia cephalotes Castelnau	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
Sillaginodes punctatus Cuvier & Valenciennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	7	0	0	1
Sillago bassensis Cuvier	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocaranx dentex Bloch & Schneider	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthopagrus australis (Owen)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Girella tricuspidata (Quoy & Gaimard)	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parachaetodon ocellatus (Cuvier)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enoplosus armatus (White)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Threpterius maculosus Richardson	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aldrichetta forsteri (Cuvier & Valenciennes)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0
Myxus elongatus Günther	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dotalabrus aurantiacus (Castelnau)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haletta semifasciata (Cuvier & Valenciennes)	0	0	0	0	4	0	37	0	20	0	3	0	0	9	0	0	4	0	1	0	0	0	0	0	0	1	0	0	196	0
Halichoeres brownfeldii (Whitley)	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoodax balteatus (Cuvier & Valenciennes)	0	0	0	0	1	0	35	0	211	0	0	0	0	2	0	0	145	0	239	0	0	0	0	0	0	73	0	0	1	0
Notolabrus parilus (Richardson)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odax acroptilus (Richardson)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphonognathus argyrophanes Richardson	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphonognathus radiatus (Quoy & Gaimard)	17	0	13	0	16	0	1	7	0	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
Parapercis haackei (Steindachner)	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schizochirus sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudaphritis bursinus Cuvier	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	2	0	0	0	0	0	0	3	0
Petroscirtes lupus (De Vis)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cristiceps australis Cuvier & Valenciennes	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	3	0	5	0	0	0	0	0	0	3	0	0	0	0
Heteroclinus adelaidei Castelnau	0	0	0	0	2	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Heteroclinus macrophthalmus Hoese	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Heteroclinus perspicillatus (Cuvier & Valenciennes)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	5	0	0	0	6	0	0	0	0	31	0
Ophiclinops pardalis (McCulloch & Waite)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophiclinus gracilis Waite	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Callionymus goodladi (Whitley)	0	0	0	1	0	3	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Philypnodon grandiceps (Krefft)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Arenigobius bifrenatus (Kner)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	58	0	0	0	2	0
Arenigobius frenatus (Günther)	0	0	0	0	0	0	0	0	0	0	0	0	0	23	12	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Bathygobius kreffti (Steindachner)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Favonigobius tamarensis (Johnston)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	15	16	0	0	0	0	3	1	0	1	24	0	0	0	0	0
Favonigobius lateralis (Macleay)	0	0	0	0	0	0	0	13	0	23	0	0	0	3	4	9	0	0	0	0	6	0	0	0	0	1	46	14	80	106
Gobiopterus semivestitus (Munro)	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	2	7	0	1	1	0	0	0	3	7

Table 5.5 (Cont.)

	Site																													
Fish species	TBP	TBU	PBP	PPU	WPP	WPU	RP	RU	PRP	PRA	PRU	FBP	FBU	CIP	CIZ	CIU	BPZ	BPU	CLH	CLU	FIU	LKZ	LKU	CPH	CPU	PGP	PGH	PGU	BIH	BIU
Nesogobius pulchellus (Castelnau)	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nesogobius sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	7	596	0	0	0	0	0	0	0	0	0	0
Nesogobius sp.2	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nesogobius sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	37	0	0	0	0	0	0	0	0	0	0
Pseudogobius olorum (Sauvage)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66	736	292	0	58	0	7	0	20	0
Redigobius macrostoma (Günther)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	4	0	0	0	0	0	0	0
Tasmanogobius lasti Hoese	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	520	0	0	0	0	7	0	0	0	0	0
Gobiidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
Gobiidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptoscopid sp.	0	3	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alabes dorsalis (Richardson)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cochleoceps spatula (Günther)	0	0	2	0	19	0	12	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0
Parvicrepis sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Parvicrepis sp.2	0	0	1	0	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
? *Parvicrepis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Pseudorhombus jenynsii (Bleeker)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ammotretis rostratus Günther	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	2	0	0	0	0	0	0	0	0	0	0
Rhombosolea tapirina Günther	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	19	0	10	0	0	0	0	49	0	0	0	0	2
Synaptura nigra Macleay	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Acanthaluteres spilomelanurus (Quoy & Gaimard)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	82	0	122	0	0	0	0	0	0	4	0	0	0	0
Bigener brownii (Richardson)	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachaluteres jacksonianus (Quoy & Gaimard)	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Meuschenia freycineti (Quoy & Gaimard)	0	0	0	0	0	0	1	0	3	0	0	0	0	5	0	0	13	0	3	0	0	0	0	0	0	1	0	0	0	0
Penicipelta vittiger (Castelnau)	0	0	8	0	2	0	59	0	23	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Scobinichthys granulatus (Shaw)	1	0	3	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Aracana aurita (Gray)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Contusus brevicaudus Hardy	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Tetractenos glaber (Freminville)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	7	0	0	0	0	0
Tetractenos hamiltoni (Gray & Richardson)	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicotylichthys punctulatus Kaup	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.6. Estimated production (±SE) of all fishes and demersal fishes (excludes pelagic atherinids and clupeoids) at sites investigated.

Site	Total production ($mg.m^{-2}.d^{-1}$)	Demersal production ($mg.m^{-2}.d^{-1}$)
Thomsons Bay *Posidonia*	2.4±0.4	2.4±0.4
Thomsons Bay unvegetated	0.70±0.54	0.69±0.54
Porpoise Bay *Posidonia*	2.0±0.5	1.6±0.4
Parker Point unvegetated	44.2±16.4	0.68±0.48
Woodmans Point *Posidonia*	10.0±2.5	7.3±0.8
Woodmans Point unvegetated	0.30±0.19	0.30±0.19
Rockingham *Posidonia*	70.6±13.9	70.6±13.9
Rockingham unvegetated	1.8±0.5	1.8±0.5
Princess Royal Harbour *Posidonia*	89.6±32.4	25.8±4.1
Princess Royal Harbour *Amphibolis*	92.1±5.0	82.7±4.1
Princess Royal Harbour unvegetated	23.9±10.3	0.65±0.09
Frenchmans Bay *Posidonia*	10.9±3.0	9.8±2.5
Frenchmans Bay unvegetated	0.021±0.015	0.021±0.015
Cararma Inlet *Posidonia*	31.4±8.2	30.8±8.4
Cararma Inlet *Zostera*	8.9±1.3	8.8±1.2
Cararma Inlet unvegetated	3.5±0.3	2.7±0.7
Bagot Point *Zostera*	92.0±31.9	57.7±14.5
Bagot Point unvegetated	38.3±9.6	19.8±8.4
Cloudy Lagoon *Heterozostera*	47.6±10.7	47.6±10.7
Cloudy Lagoon unvegetated	91.9±24.5	16.6±4.6
French Island unvegetated	3.6±1.9	3.6±1.9
Lake King *Zostera*	113.7±89.0	8.6±2.1
Lake King unvegetated	3.4±1.1	1.5±0.4
Crib Point *Heterozostera*	1.9±0.8	1.6±0.7
Crib Point unvegetated	24.3±12.5	7.8±1.6
Port Gawler *Posidonia*	8.3±1.0	8.3±1.0
Port Gawler *Heterozostera*	17.2±6.5	2.2±0.7
Port Gawler unvegetated	0.73±0.41	0.40±0.24
Barker Inlet *Heterozostera*	77.8±7.8	77.8±7.8
Barker Inlet unvegetated	4.4±2.1	4.4±2.1

Table 5.7. Pearson correlation coefficients relating log fish production (1: including pelagic atherinids and clupeoids; 2: excluding pelagic atherinids and clupeoids) with various physical and biological parameters (also log-transformed). Analysis 1 includes data from 30 sites (excluding Western Port sites discussed in Chapter 4) and Analysis 2 includes all shallow vegetated and unvegetated sites investigated during the study.

	Analysis 1 (30 sites)		Analysis 2 (38 sites)	
	Fish Prod.1	Fish Prod.2	Fish Prod.1	Fish Prod.2
Fetch	-0.44	-0.34	-0.42	-0.30
Particle mode	-0.20	-0.14	-0.05	-0.05
Particles <63μm	0.42	0.42	0.24	0.29
Organic (%)	0.26	0.21	0.18	0.16
Seagrass biomass	0.32	0.49	0.33	0.43
Rhizomes biomass	0.25	0.41	0.27	0.36
Debris biomass	-0.01	0.06	0.03	0.06
Macrofaunal biomass	0.37	0.37	0.29	0.30
Macrofaunal production (>1mm)	0.40	0.39	0.33	0.33
Crustacean production (>1mm)	0.47	0.48	0.44	0.44
Macrofaunal production (>125 μm)	0.36	0.38	0.34	0.34
Crustacean production (>125μm)	0.52	0.56	0.50	0.51

Table 5.8. Predicted macrocrustacean, macrofaunal and demersal fish production for Western Port sites as estimated using the regression equations listed in Table 5.4, with measured values shown in parentheses.

Site	Crustacean production (mg.m^{-2}.d^{-1})	Macrofaunal production (mg.m^{-2}.d^{-1})	Fish production (mg.m^{-2}.d^{-1})
Peck Point seagrass	138.1 (25.0)	309 (218)	21.4 (15.6)
Peck Point unvegetated	18.0 (10.5)	182 (161)	1.9 (2.3)
Peck Point channel	15.8 (18.2)	149 (112)	1.8 (5.3)
Rhyll seagrass	108.0 (14.7)	316 (290)	16.2 (15.6)
Rhyll unvegetated	20.8 (6.6)	220 (226)	2.2 (6.7)
Rhyll channel	10.8 (11.9)	81 (144)	1.6 (9.1)
Tooradin seagrass	113.9 (23.5)	316 (139)	16.7 (17.1)
Tooradin unvegetated	14.2 (11.1)	127 (82)	1.7 (10.1)
Tooradin channel	14.8 (7.4)	135 (64)	1.8 (6.2)
Cowes Bank seagrass	21.0 (15.5)	37 (42)	5.9 (13.0)
Cowes Bank unvegetated	3.8 (4.0)	17 (15)	0.9 (3.8)
Loelia Shoal	28.4 (7.8)	357 (21)	2.5 (1.6)

Fig. 5.1. Localities sampled during the southern Australian study.

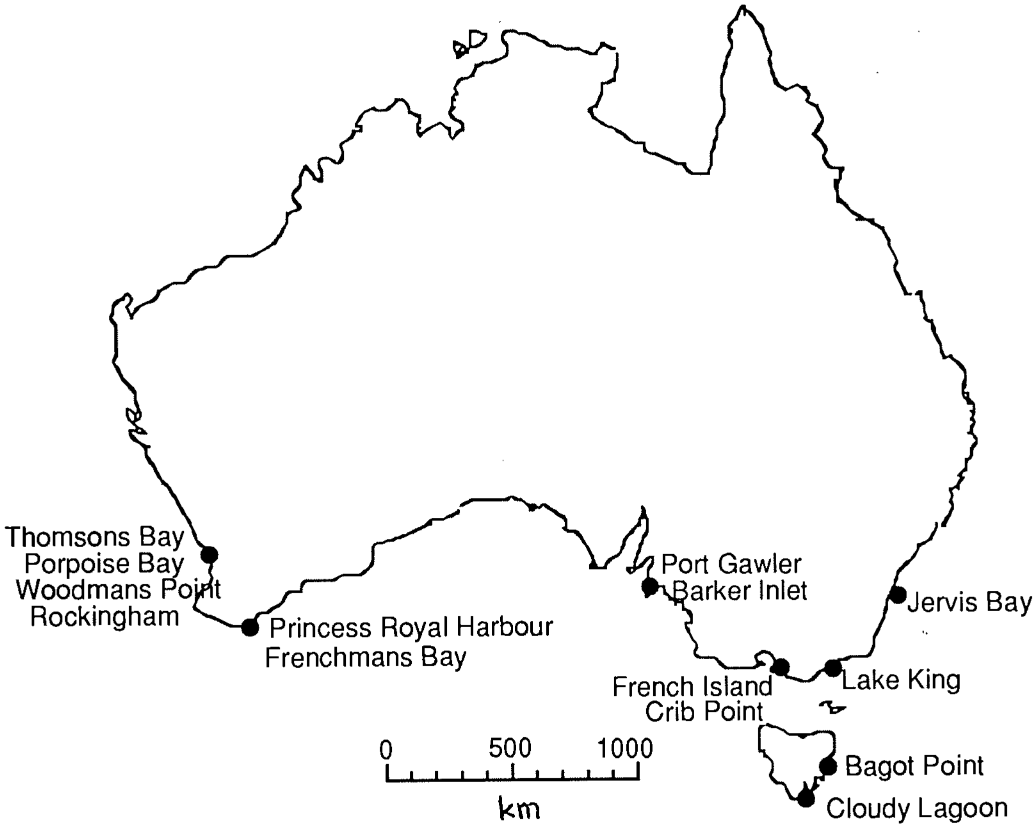

Thomsons Bay
Porpoise Bay
Woodmans Point
Rockingham
Princess Royal Harbour
Frenchmans Bay
Port Gawler
Barker Inlet
Jervis Bay
French Island
Crib Point
Lake King
Bagot Point
Cloudy Lagoon
0
500
1000
km

Fig. 5.2. Estimated total invertebrate and crustacean production of different sieve-sized components of the benthos at the New South Wales and Tasmanian localities studied.

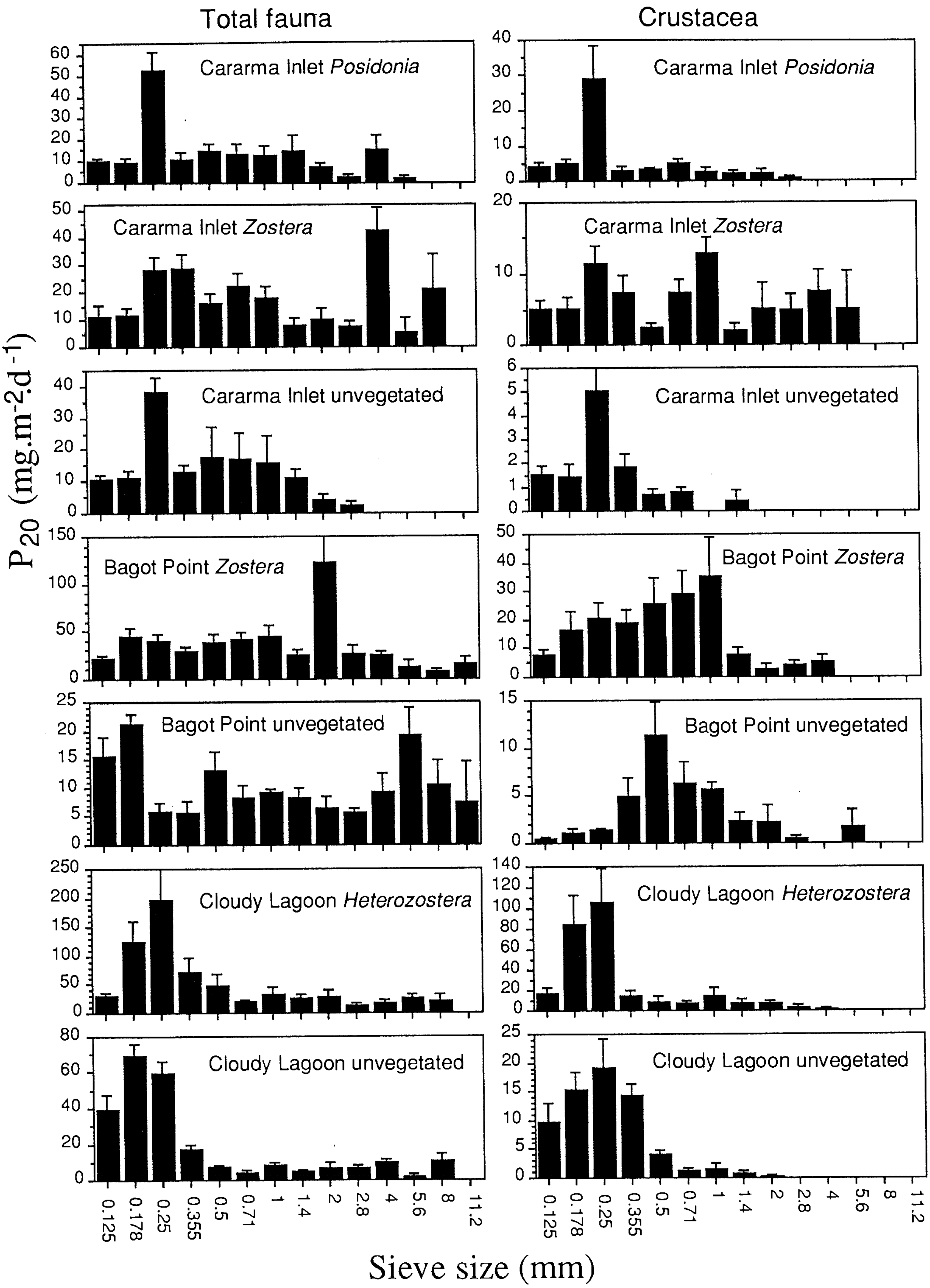

Total fauna
Crustacea
Cararma Inlet *Posidonia*
Cararma Inlet *Zostera*
Cararma Inlet unvegetated
Bagot Point *Zostera*
Bagot Point unvegetated
Cloudy Lagoon *Heterozostera*
Cloudy Lagoon unvegetated
P_{20} (mg.m-2.d-1)
0
10
20
30
40
50
60
100
120
140
150
200
250
1
2
3
4
5
6
15
25
80
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
Sieve size (mm)

Fig. 5.3. Estimated total invertebrate and crustacean production of different sieve-sized components of the benthos at the Victorian localities studied.

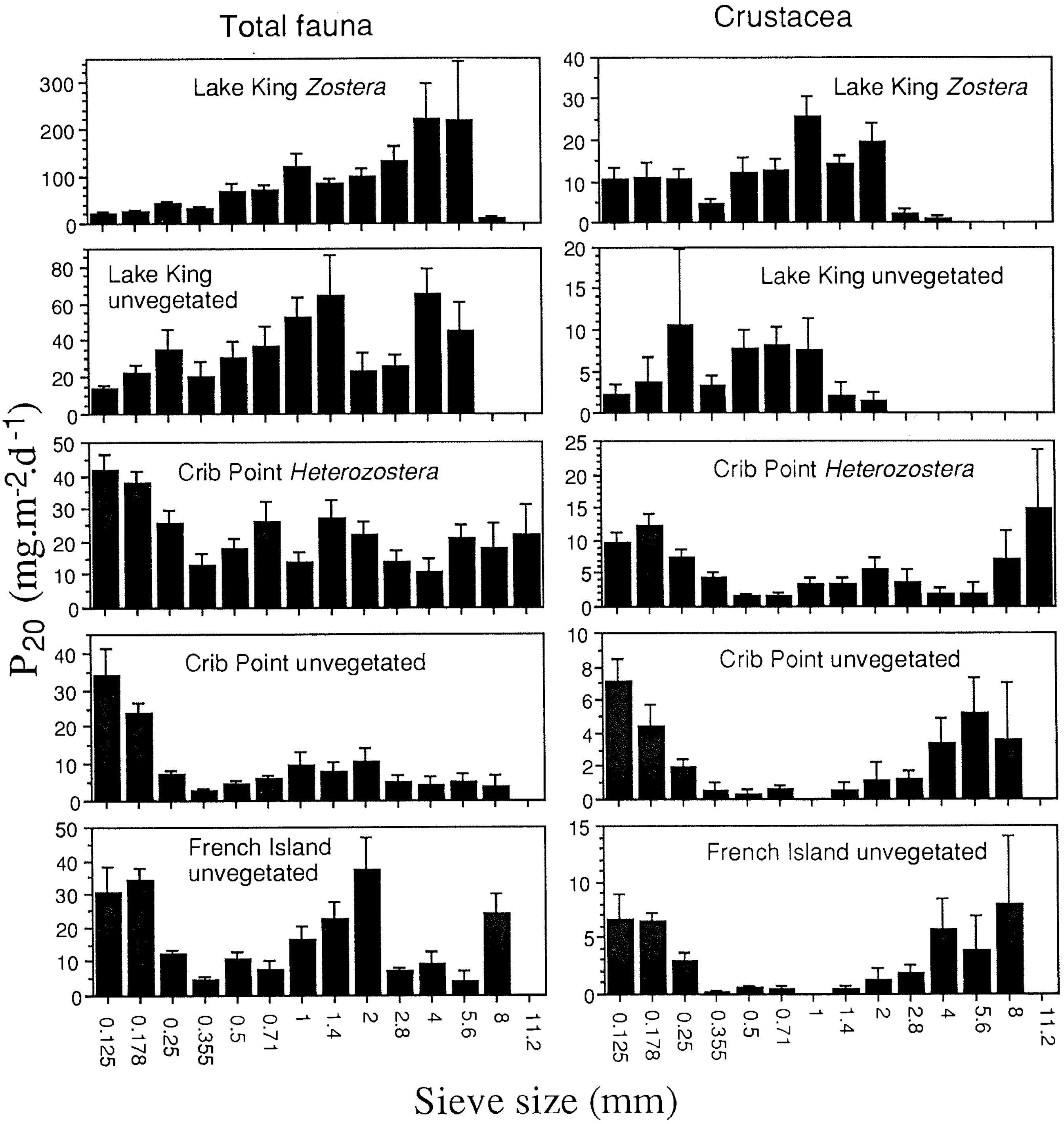

Total fauna
Crustacea
Lake King *Zostera*
Lake King unvegetated
Crib Point *Heterozostera*
Crib Point unvegetated
French Island unvegetated
P_{20} (mg.m^{-2}.d^{-1})
Sieve size (mm)
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2
0
100
200
300
20
40
60
80
10
30
50
5
15
25
2
4
6
8

Fig. 5.4. Estimated total invertebrate and crustacean production of different sieve-sized components of the benthos at the South Australian localities studied.

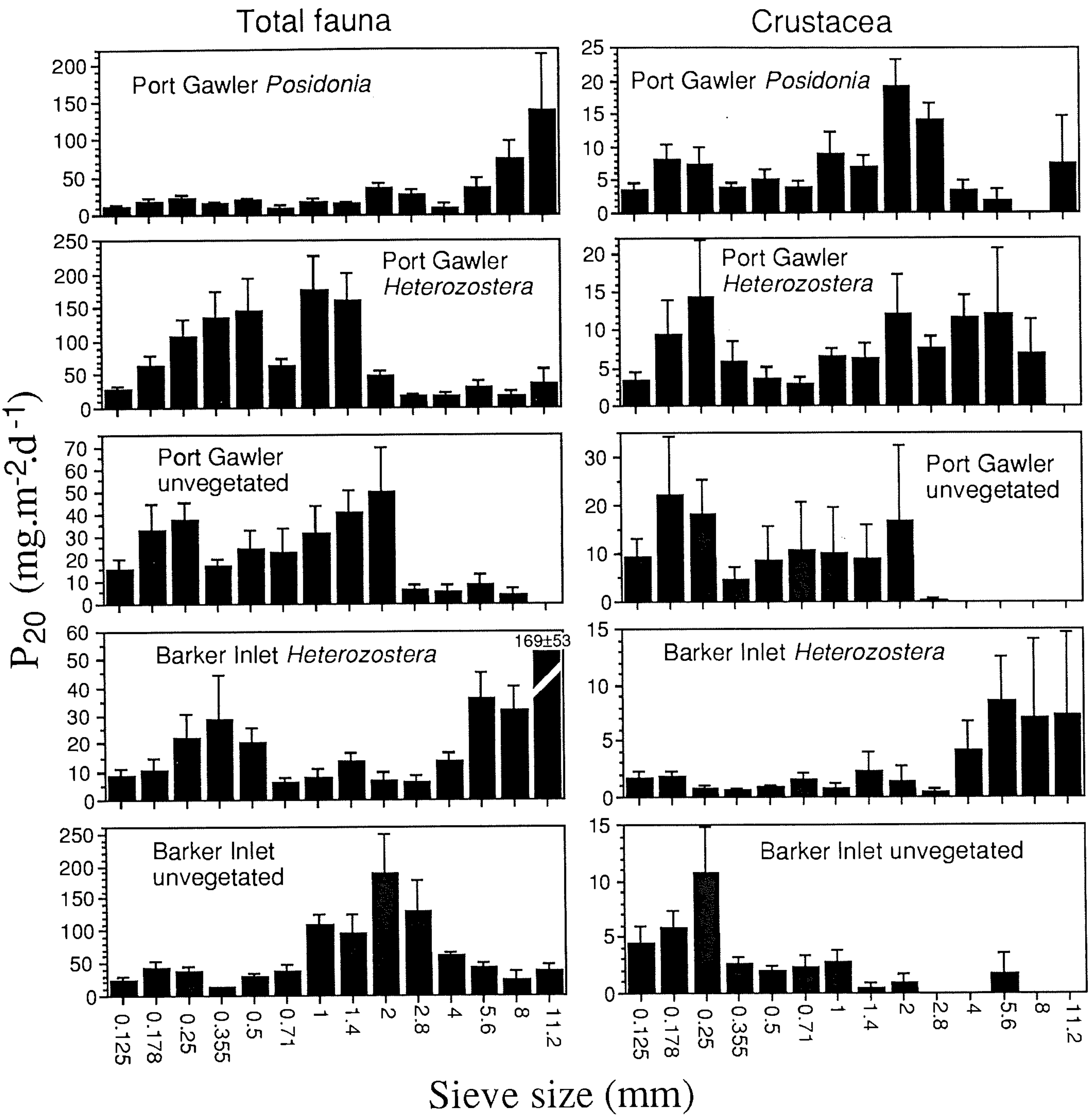
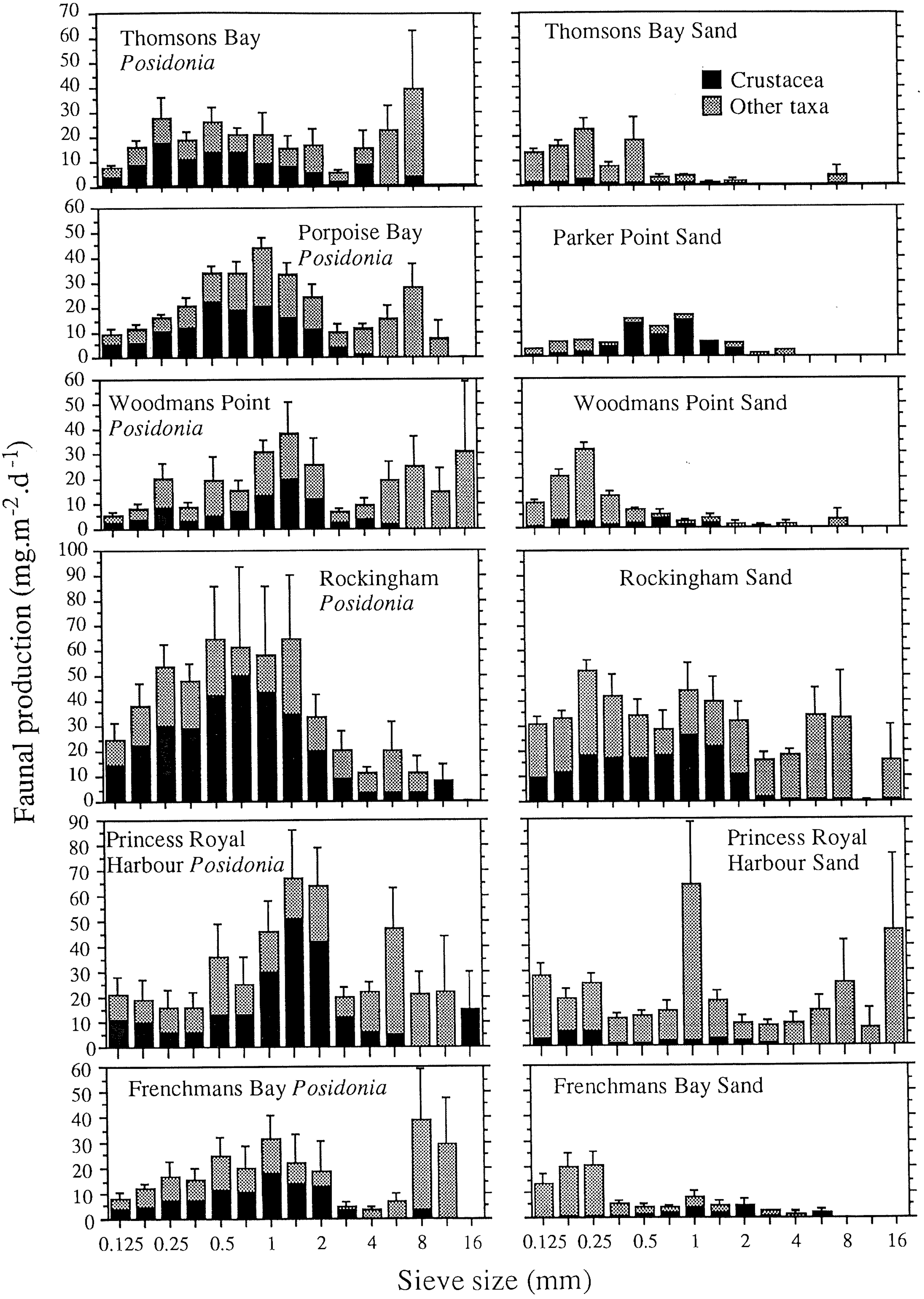

Total fauna
Crustacea
Port Gawler *Posidonia*
Port Gawler *Heterozostera*
Port Gawler unvegetated
Barker Inlet *Heterozostera*
Barker Inlet unvegetated
169±53
P_{20} (mg.m^{-2}.d^{-1})
Sieve size (mm)
0.125
0.178
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8
11.2

Fig. 5.5. Estimated total invertebrate and crustacean production of different sieve-sized components of the benthos at the Western Australian localities studied.


Thomsons Bay *Posidonia*
Thomsons Bay Sand
Crustacea
Other taxa
Porpoise Bay *Posidonia*
Parker Point Sand
Woodmans Point *Posidonia*
Woodmans Point Sand
Rockingham *Posidonia*
Rockingham Sand
Princess Royal Harbour *Posidonia*
Princess Royal Harbour Sand
Frenchmans Bay *Posidonia*
Frenchmans Bay Sand
Faunal production (mg.m^{-2}.d^{-1})
Sieve size (mm)
0.125
0.25
0.5
1
2
4
8
16
0
10
20
30
40
50
60
70
80
90
100

Section 6. Colonisation of artificial seagrass patches by invertebrates and fishes.

6.1 Summary

Manipulative experiments using artificial seagrasses were set up at two locations, Western Port, Victoria, and Cloudy Lagoon, Tasmania, in order to identify whether invertebrates and fishes were principally attracted to the structural features of seagrass habitats or to the high levels of associated food production. Invertebrates were attracted in much greater numbers to seagrass debris than to artificial seagrass leaves, and were not attracted at all to buried seagrass debris. Epifaunal invertebrate production thus appears to be strongly coupled with food availability. Recruitment of fishes to all treatments was poor, preventing us from conducting statistical tests with sufficient power to separate the effect of environment from the effect of food on fish numbers. The relationship between fish production and food is less clearly defined than the relationship between the production of macrofauna and food, possibly because of a lag between epifaunal food buildup and fish recruitment.

6.2 Introduction

Fish productivity was shown in the previous section to be highly correlated with the productivity of the major prey group, crustaceans, and both of these parameters were found to be highly correlated with the biomass of seagrass. The question of whether fish respond directly to the shelter of seagrasses, or to the high productivity of invertebrates which themselves respond to seagrasses, is a contentious one that can be unequivocally answered only by manipulative experiments (Bell & Pollard, 1989). One way to address this question is to compare the abundance of fishes in habitats with shelter but minimal food with the abundance of fish in habitats with food but minimal shelter.

In this section of the project, we report the results of experiments designed to distinguish between the shelter and food value of habitats for fishes and invertebrates. Due to practical difficulties which make it impossible to reduce the food value of natural seagrass beds, our experiments involved artificial seagrass patches. Variation in the level of associated food was achieved by the addition of seagrass debris and organic-rich sediment to particular treatments. Epifaunal invertebrates were expected to be rapidly attracted to treatments with debris (Edgar, 1990b), with infaunal invertebrates responding to organic enrichment (Dauer & Conner, 1980; Spies et al., 1988). Fishes that respond to food should thus be attracted in disproportionately high numbers to food addition treatments even in the absence of seagrass structure, while animals attracted to sites with high levels of structural complexity should show contrary trends. Experiments were conducted in two areas, Cowes Bank (Western Port, Vic) and Cloudy Lagoon (S.E. Tasmania), in order to see if similar trends occur over a wide geographic scale.

6.3 Methods

Artificial seagrass units (ASUs) used in experiments were constructed by tying 200 clumps of green polypropylene ribbon (5 mm width) to squares of trawl netting with 1.42 m sides. Each clump contained 16 artificial seagrass 'leaves', with each leaf being 700 mm long. The 2 m^2 ASUs thus each contained 3,200 leaves with a total surface area of 22.4 m^2. The edge of the ASU was attached to a heavy surrounding chain so that it remained weighted to the seabed. When placed on site, ≈8 wire pegs were pushed into the substratum through the mesh in order to provide additional anchorage.

The initial experimental site was located at Cowes Bank in Western Port, in an area of well-sorted sand, ≈100m from the site used for routine seasonal sampling (Section 2). At this site, 32 ASUs were deployed at ≈0.1 m above low water mark during the low tide periods on two nights (1-2 Oct 1991). These evenings corresponded with spring tides, so ASUs were not exposed to air during the neap period of the monthly lunar cycle. Three factors were investigated (artificial seagrass addition; seagrass debris addition; sediment enrichment) using an orthogonal experimental design with each of the eight treatment combinations replicated four times. An additional set of four control samples were collected from areas of seabed marked for sampling but left undisturbed. ASUs lacking artificial seagrass contained the base netting and chain but lacked artificial leaves. ASUs with added seagrass debris contained 10 kg (wet weight) dead seagrass leaves which had been harvested the previous day and left soaking overnight in freshwater to kill associated fauna. This debris was placed underneath the ASUs before they were pegged to the substratum. ASUs with organic enrichment were set out the same way as ASUs with added seagrass debris; however, the debris was buried ≈50 mm deep rather than being laid on the sediment surface. To maintain a consistent level of disturbance at all sites, ASU sites without sediment enrichment were dug up and refilled with sand in the same way as sites with sediment enrichment.

Invertebrate colonization of ASUs was monitored at Cowes Bank by collecting core samples and clumps of artificial seagrass leaves 2, 8, 24 and 35 days after the commencement of the experiment. Core samples were obtained by pushing 50 mm diameter cores (see Section 2) to a depth of 100 mm through the sediment and associated seagrass debris and extracting the sediment with associated animals. On the final sampling date (i.e., day 35), the debris and sediment components of the core were collected separately. 'Leaf' samples were obtained by removing two clumps of artificial seagrass grouped together within the ASU, and placing these with associated animals into a plastic bag. Invertebrates were extracted from samples using the procedures described in Section 2.

On the same days as the final invertebrate cores were collected (i.e., on 5 and 6 Nov 1991), fishes associated with ASUs were sampled by surrounding individual ASUs with a 1 mm mesh seine net, removing the ASU and shaking out associated fishes and epibenthic invertebrates. The seine net was then passed through the site and pursed to collect additional animals.

The second experiment was conducted at Cloudy Lagoon (Bruny Island, Tasmania), a small ($\approx$6 km^2) marine estuary connected by a 100m wide 5 m deep channel to the Tasman Sea. This experiment also involved the manipulation of three factors, with two factors (artificial seagrass addition; seagrass debris addition) being the same as at Cowes Bank. Rather than increasing the organic content of sediments, the third (sand addition) factor at this site involved reducing the organic load by mixing into the naturally-occurring sediment well-sorted sand with little organic content that was collected from a nearby ocean beach. Sand patches on which ASUs were deployed were treated by first placing 2 m (length) x 2 m (width) x 0.6 m (height) square metal collars onto the sediment in water depths of $\approx$0.2 m during the period of low water and then digging out sand to a depth of 100 mm. The sediment at sites with sand addition was returned with $\approx$50% clean sand from the ocean beach; the sediment at other sites was returned with no outside sediment. ASUs at Cloudy Lagoon were deployed on 29 March 1992 and collected on 20 April 1992. Three replicates for each treatment combination were used, giving a total of 24 ASUs deployed, with a further three undisturbed control areas also designated.

6.4 Results

While invertebrates were attracted very rapidly to both seagrass debris and artificial seagrass leaves, they were collected from seagrass debris in much higher numbers than from artificial seagrass leaves or from natural sediments (Table 6.1). The addition of seagrass debris increased total faunal abundance and biomass of ASUs by an order of magnitude. Organic enrichment of sediments, on the other hand, did not significantly affect the total biomass of fauna associated with ASUs (2-way ANOVA, $F = 4.15$, d.f. = 1/16, $p>0.05$), although it did reduce the density of invertebrates (2-way ANOVA, $F = 10.61$, d.f. = 1/16, $0.001<p<0.01$), particularly the small-sized animals such as nematodes.

Abundances of nematodes were also reduced in the Cloudy Lagoon sand addition treatment (3-way ANOVA, $F = 9.48$, d.f. = 1/16, $0.001<p<0.01$). Sediments in this treatment had a reduced proportion of fine organic particles compared with treatments containing *in situ* sand (3-way ANOVA, $F = 6.63$, d.f. = 1/16, $0.01<p<0.05$), while debris addition treatments had increased proportions of fine organic particles (3-way ANOVA, $F = 15.4$, d.f. = 1/16, $0.001<p<0.01$). No significant differences in faunal biomass were found for cores collected in different treatments at Cloudy Lagoon, except for the the debris addition treatment (3-way ANOVA, $F = 76.5$, d.f. = 1/16, $p<0.001$; see Table 6.1).

The density of animals >0.125 mm sieve-size associated with the polypropylene 'leaves' at Cowes Bank was much lower than at Cloudy Lagoon after 1 mo (18,000 m^{-2} and 125,000 m^{-2}, Table 6.1). This difference between sites was principally due to a very low abundance of harpacticoid copepods being attracted to artificial seagrass leaves at Cowes Bank compared with Cloudy Lagoon (12,600 m^{-2} and 109,000 m^{-2}, respectively). The total biomass of animals associated with artificial seagrass leaves was not significantly different (2-way ANOVA; $p>0.05$) at the two sites (Table 6.1). Neither total abundance nor biomass of animals associated with artificial seagrass leaves were significantly affected by seagrass debris addition, organic enrichment of sediments or sand addition ($p>0.05$ for all ANOVAs).

In contrast to the high numbers of invertebrates attracted to ASUs, few fish were collected during experiments (Tables 6.2 and 6.3). Numbers associated with ASUs in the Cowes Bank experiment were not sufficient to allow the fish data to be statistically analysed. Numbers collected from ASUs at Cloudy Bay were much higher than at Cowes Bank but consisted principally of gobies that were associated with sand surrounding the ASU. The density of these gobiid fishes was negatively affected by the addition of seagrass debris (Table 6.4).

Although seagrass-associated fishes collected from ASUs were not found to be significantly ($p<0.05$) affected by any factor using ANOVA (Table 6.4), the low number of animals collected from ASUs and very low power of the analysis possibly precluded a statistically significant result. Over twice as many seagrass-associated fishes were collected from artificial seagrass addition treatments as from treatments with no artificial seagrass, with the result of the statistical analysis close to significant ($0.05<p<0.1$). The most common epibenthic invertebrate collected, the shrimp *Macrobrachium intermedium*, occurred in significantly higher numbers in association with ASUs containing artificial seagrass and also those with added seagrass debris, but was not affected by sand addition or factor interactions (Table 6.4).

6.5 Discussion

Our results indicate that the biomass and production of invertebrates is greatly enhanced by the presence of seagrass debris at the sediment surface, and to a lesser extent with artificial seagrass leaves, but not with buried seagrass debris. These results agree with the results of a study of natural seagrass beds in Western Australia (Edgar, 1990b), where each gram of seagrass debris was found to increase macrofaunal production by 0.78 $mg.d^{-1}$, each gram of live seagrass was found to increase macrofaunal production by 0.16 $mg.d^{-1}$, while buried debris had no effect on production. Buried debris at Cowes Bank in fact reduced the abundances of some infaunal species such as nematodes. This effect was probably caused by sediments in contact with high concentrations of debris becoming anoxic and thus unsuitable as habitat for many species. Infaunal abundance and biomass have been found elsewhere to precipitously decrease when anoxic conditions prevail (Pearson & Rosenberg, 1978), in contrast to the more generally recognised positive relationship between organic content of sediment and infaunal numbers (Dauer & Conner, 1980; Spies et al., 1988). It is notable that the moderate decrease in the proportion of fine organic particles in sediments at Cloudy Lagoon in the sand addition treatment resulted in moderate decreases in nematode abundance, indicating a positive relationship between organic loading and infaunal numbers.

If production of fish is solely a function of food availability, then very high numbers of fish should be associated with the debris addition treatments where the total production of invertebrates is an order of magnitude higher than in other treatments (see Table 6.1). This prediction was contrary to the results of the experiments as fishes were not attracted to any treatment in high numbers, and one major group of species, the gobiid fishes, was negatively affected by the presence of debris (Table 6.4). Gobies presumably actively selected sand habitats, with the consequence that numbers were low in debris addition treatments because of the alienation of much of the habitat space.

Settlement of seagrass-associated fish on ASUs was relatively poor compared to settlement rates on artificial habitats used in studies elsewhere (Mills, 1991; Sogard, 1989; G. Jenkins, pers. comm.). Possible reasons for this low settlement are that the sites were atypical, that ASUs were deployed during a season of poor settlement, or that ASUs were not placed in the field for sufficient time to acrue a full and stable fauna. The latter explanation is unlikely as both Sogard (1989) and G.Jenkins (pers. comm.) found little difference in the numbers of fish associated with ASUs placed in the water for 2-3 weeks and those placed on site for longer periods.

Maximum seasonal recruitment of fish to seagrasses, and presumably also ASUs, occurs between November and January in southern Australia (Appendix 1.2; Jenkins et al., 1993). Our experiments were conducted just outside this period, possibly contributing to the low number of fish collected. Very few fish collected from our ASUs were post-larvae that had recently recruited from the plankton, unlike the fish collected in the other major Australian study in which ASUs were used (Bell et al., 1985). Almost all fish associated with ASUs at Cowes Bank and Cloudy Lagoon had crossed sand patches to reach the ASUs as large juveniles or adults.

Whatever the reason for the poor recruitment, larger-scale experiments using ASUs with patch size >5 m^2 are needed if the importance of epifaunal production and seagrass structure to fish production is to be unequivocally demonstrated. Our results nevertheless indicate that fish are not nearly as strongly coupled with food as are benthic invertebrates. One explanation for these trophic differences between fish and invertebrates is that most fishes have a pelagic larval stage lasting in excess of a month that prevents them from immediately capitalizing on newly available benthic food resources. Future studies should be carried out in different seasons in order to determine whether the different responses of invertebrates and fishes to food resources is related to fundamental differences in recruitment.

Table 6.1. Total abundance, biomass (g) and P_{20} (mg.d^{-1}) of invertebrates associated with different components of 2 m^2 ASUs placed at Cowes Bank, Victoria, and Cloudy Lagoon, Tasmania. n.a. indicates data not available. Abundances of animals from sediment cores are those from untreated sediments.

	Fauna >0.125 mm			Fauna >1 mm		
Component	Number	Biomass	P_{20}	Number	Biomass	P_{20}
Cowes bank						
Artificial seagrass leaves	36,100	3.39	62	3,800	1.29	26.3
Seagrass debris	n.a.	n.a.	n.a.	29,000	56.8	744
Sediment cores	862,000	4.95	159	5,480	4.3	79.3
Cloudy Lagoon						
Artificial seagrass leaves	250,000	2.63	68.6	3,600	0.8	17.1
Seagrass debris	8,210,000	85.6	2,370	61,000	51.5	765
Sediment cores	1,880,000	21.0	403	8,320	17.5	204

Table 6.2. Mean numbers of fishes and epibenthic invertebrates collected from ASUs placed at Cowes Bank. ASU treatments are artificial seagrass addition (H), seagrass debris addition (D), organic enrichment (E), ASU control (O), open control (C).

	Treatment								
	HDE	HD	HE	H	DE	D	E	O	C
Stigmatopora nigra	0	0	0	0	0	0.3	0.3	0	0.8
Platycephalus laevigata	0.5	0.3	1.3	1	0	0.3	0	0.3	0
Heteroclinus perspicillatus	0	0	0	0	0	0	0.3	0	0
Arenigobius frenatus	0	0	0	0.3	0	0	0	0	0
Gobiopterus semivestitus	2.3	0.3	1	0.8	0	0.3	0	0	0
Ammotretis rostratus	1	0.3	0.8	0.5	0.3	0.5	0.3	0.3	1
Rombosolea tapirina	0.3	0	0	0	0	0	0	0	0.5
Acanthaluteres spilomelanurus	0	0.3	0.3	0.8	0	0	0	0	0
Contusus brevicaudus	0	0	0	0	0	0	0	0	0.3
Tetractenos glaber	0.3	0.3	0.5	0	0.3	0.3	0.3	1.8	3.3
Total fishes	4.3	1.3	3.8	3.3	0.5	1.5	1	2.3	5.8
Macrobrachium intermedium	2.8	2	3.8	4.5	0.5	0.3	0.5	0	0
Chlorotocella leptorhyncus	0	0.3	0	0	0	0	0	0	0
Hippolyte caradina	0	0	0.3	0	0	0	0	0	0
Pontophilus intermedius victoriensis	0	1.5	1.5	1.8	0	1.5	1.5	0.8	0
Pontophilus intermedius	15	10	11	3.5	13	9.5	21	15	37
Pontophilus flindersi	0	0	0	0	0	0	0	0	0.3
Alpheus euphrosyne	0	0	0	0.3	0.3	0	0.3	0	0
Halicarcinus ovatus	35	30	29	24	17	69	12	10	1
Halicarcinus rostrata	0.5	0.3	0.5	0.5	0.5	1.5	0.5	0.3	0
Trigonoplax longirostris	0	0	0.3	0.3	0	0	0	0	0
Leptomithrax gaimardii	0.8	0.3	0	0	0	0.3	0	0	0
Nectocarcinus integrifrons	1	2	1.8	3	1.5	1	1.3	0.5	0
Paragrapsus gaimardii	1	0.3	0.5	0.5	0	0	0	0	0
Macrophthalmus latifrons	0	0	0	0	0.3	0	0	0	0
Litocheira bispinosa	0	0	0.3	0	0	0	0	0	0
Ebalia intermedia	0	0	0	0	0	0	0.5	0	0
Philyra laevis	0	0	0.3	0.3	0	0.5	0	0	0
Idiosepius notoides	2	1	0.3	0.5	0	0.5	1	1.8	1.3
Euprymna tasmanica	0.3	0	0	0.3	0.3	0	0.3	0	0
Total invertebrates	59	47	50	39	33	84	39	28	40

Table 6.3. Mean numbers of fishes and epibenthic invertebrates collected from ASUs placed at Cloudy Bay, Tasmania. ASU treatments are artificial seagrass addition (H), seagrass debris addition (D), sand addition (S) ASU control (O), open control (C).

	Treatment								
	HDS	HD	HS	H	DS	D	S	O	C
Atherinasoma presbyteroides	0	0	0	0	0	0	2.3	0	49
Vanacampus phillipi	0.7	1.7	0.3	0.7	0.7	1	1.3	0.7	0
Gymnapistes marmoratus	0.3	0	0	0	0	0	0	0	0
Alabes parvulus	2.7	1	0	0.3	0.3	1	0.3	0.7	0
Heteroclinus perspicillatus	1	0.7	0.7	0.7	0	0.7	0	0	0
Heteroclinus heptaeolus	0	0	0	0	0.3	0	0	0	0
Cristiceps australis	0.7	0.3	1.7	1	0.3	0	0	0	0.3
Nesogobius hindbyi	3.7	3	4	2	2.3	1.7	1.3	1.7	3
Nesogobius sp.1	9.3	7.7	13	11	6	5.3	13	13	19
Nesogobius sp.2	7.3	6	3.3	4	3.3	3.3	6	6	1.7
Tasmanogobius gloveri	0.7	0.7	0	0	0	0	0	1	0.3
Tasmanogobius lasti	2	3.7	3.3	4	1	2	6.3	7.3	14
Neoodax balteatus	0.7	0.3	0.3	0.3	0	0	0	0	0
Acanthaluteres spilomelanurus	0	0.3	0	0	0	0	0	0	0
Total	29	25	27	25	14	15	28	30	38
Seagrass associated fishes	6	4.3	3	3	1.7	2.7	1.7	1.3	0.3
Gobiid fishes	23	21	24	22	13	12	26	29	38
Macrobrachium intermedium	38.7	43.7	8.7	8.7	12	10.3	0.7	1.3	2.3
Macrobrachium sp.	2.7	3	1.3	2.3	0.3	0.7	2	0.7	0.3
Palaemon serenus	2.3	2	0	0.3	0	0.3	0	0	0
Pontophilus intermedius victoriensis	0	0	0.3	0	0	0	0	0	0
Chlorotocella leptorhyncus	0.3	0	0	0	0	0	0	0	0
Halicarcinus ovatus	0	0.3	0	0	0	0	0	0	0
Notomithrax ursis	1.3	0	0	0	0.3	0	0	0	0
Nectocarcinus integrifrons	0.3	0.7	0	1	0	0.3	0	0	0
Paragrapsus gaimardii	0.3	0	0	0	0	0.3	0	0	0
Paragrapsus quadridentatus	0.7	0	0	0	0	0	0	0	0
Philyra laevis	0.3	0	0	0	0.3	0.3	0.3	1.7	0.3
Ovalipes australiensis	0	0	0	0.7	0	0.3	0	0	0
Idiosepius notoides	0.3	2.3	1.7	2	0.7	1.3	0.3	0.3	0.3
Total invertebrates	47	52	12	15	14	14	3.3	4.0	3.3

Table 6.4. Results of three-way ANOVAs using log density data for fishes and shrimp (*Macrobrachium intermedium*) collected in association with ASUs at Cloudy Lagoon. The three treatments were artificial seagrass (seagrass), seagrass debris addition (debris) and sand addition (sand). *, 0.01<p<0.05; ***, p<0.001. Seagrass fish include the non-gobiid fishes.

Treatment		Total fish		Seagrass fish		Gobiid fish		*M. intermedium*	
	d.f.	SS	F	SS	F	SS	F	SS	F
Seagrass	1	0.429	1.89	2.052	4.18	0.202	0.88	14.9	24.2***
Debris	1	0.77	3.39	0.563	1.15	1.085	4.71*	14.9	24.2***
Sand	1	0.002	0.01	0.009	0.02	0.00	0.00	0.10	0.16
Seagrass*debris	1	1.235	5.44*	0.272	0.55	1.342	5.82*	0.02	0.03
Seagrass*sand	1	0.133	0.59	0.018	0.04	0.119	0.51	0.27	0.45
Debris*sand	1	0.022	0.1	0.016	0.03	0.031	0.13	0.14	0.23
Seagrass*debris*sand	1	0.001	0.01	0.127	0.26	0.008	0.03	0.01	0.02
Error	16	3.64		7.86		3.69		9.84	

References

Adams, S.M. (1976) The ecology of eelgrass *Zostera muelleri* (L.) fish communities. II. Functional analysis. J. Exp. Mar. Biol. Ecol. 22, pp. 293-311.

Al-Daham, N.K. & N.K. Wahab (1991) Age, growth and reproduction of the greenback mullet, *Liza subviridis* (Valenciennes), in an estuary in southern Iraq. J. Fish Biol. 38, pp. 81-88.

Allen, J.R.L. (1970) Physical processes of sedimentation: an introduction. Earth Science Series, No. 1. Allen and Unwin, London.

Bell, J.D. & M.L. Harmelin-Vivien (1983) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. I. Feeding habits. Tethys 11, pp. 1-14.

Bell, J.D. & D.A. Pollard (1989) Ecology of fish assemblages and fisheries associated with seagrasses. pp. 565-609, in *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*, ed. A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, Netherlands.

Bell, J.D., A.S. Steffe & M. Westoby (1985) Artificial seagrass: how useful is it for field experiments on fish and macroinvertebrates. J. Exp. Mar. Biol. Ecol. 90, pp. 171-177.

Bennet, B.A. & C.L. Griffiths (1986) Aspects of the biology of galjoen *Coracinus capensis* (Cuvier) off the South-Western Cape, South Africa. S. Afr. J. mar. Sci. 4, pp. 153-162.

Blackburn, B. (1949) Age, rate of growth. and general life-history of the Australian pilchard (*Sardinops neopilchardus*) in New South Wales. CSIRO Bull. 242, pp. 1-86.

Brook, I.M. (1977) Trophic relationships in a seagrass community (*Thalasia testudinum*) in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. Trans. Am. Fish. Soc. 106, pp. 292-299.

Burchmore, J.J., D.A. Pollard & J.D. Bell (1984) Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. Aquat. Bot. 18, pp. 71-87.

Buxton, C.D. & J.R. Clarke (1989) The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. S. Afr. J. mar. Sci. 8, pp. 57-65.

Chubb, C.F. & I.C. Potter (1986) Age, growth and condition of the Perth herring, *Nematolosa vlaminghi* (Munro) (Dorosomatinae), in the Swan Estuary, south-western Australia. Aust. J. Mar. Freshw. Res. 37, pp. 105-12.

Chubb, C.F., I.C. Potter, C.J. Grant, R.C.J. Lenanton & J. Wallace (1981) Age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon River system, Western Australia. Aust. J. Mar. Freshw. Res. 32, pp. 605-628.

Coleman, N. (1976) The molluscs of Crib Point. J. Malac. Soc. Aust. 3, pp. 239-255.

Coleman, N., W. Cuff, M. Drummond & J.D. Kudenov (1978) A quantitative survey of the macrobenthos of Western Port, Victoria. Aust. J. Mar. Freshw. Res. 29, pp. 445-466.

Colman, J.A. (1978) Tagging experiments on the sand flounder, *Rhombosolea plebia* (Richardson), in Canterbury, New Zealand, 1964 to 1966. Fish. Res. Bull., Fish. Res. Div. N.Z. 18, pp. 1-42.

Conover, D.O. & M.R. Ross (1982) Patterns in seasonal abundance, growth and biomass of the Atlantic silverside, *Menidia menidia*, in a New England estuary. Estuaries 5, pp. 275-286.

Daly, H.R. (1977) General ecology of the epifaunal gastropods of eelgrass at Crib Point, Victoria. B.Sc. (Hons) Thesis, University of Melbourne, Victoria, 32 pp.

Dauer, D.M. & W.G. Conner (1980) Effects of moderate sewage input on benthic polychaete populations. Estuar. Coast. Shelf Sci. 10, pp. 335-346.

Davenport, S. & J.D. Stevens (1988) Age and growth of two commercially important sharks (*Carcharinus tilstoni* and *C. sorrah*) from northern Australia. Aust. J. Mar. Freshw. Res. 39, pp. 413-433.

Davis, T.L.O. & G.P. Kirkwood (1984) Age and growth studies on barramundi, *Lates calcarifer* (Bloch), in northern Australia. Aust. J. Mar. Freshw. Res. 35, pp. 673-689.

De Silva, S.S. (1973) Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. J. Exp. Mar. Biol. Ecol. 12, pp. 119-144.

DeVries, D.A. & M.E. Chittenden, Jr. (1982) Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. Fish. Bull. 80, pp. 487-500.

De Vries, D.A. , C.B. Grimes, K.L. Lang & D.B. White (1990) Age and growth of king and Spanish mackerel larvae and juveniles from the Gulf of Mexico and U.S. South Atlantic Bight. Environ. Biol. Fish. 29, pp. 135-143.

Dew, C.B. (1976) A contribution to the life history of the cunner, *Tautogolabrus adspersus*, in Fishers Island Sound, Connecticut. Chesapeake Sci. 17, pp. 101-113.

Edgar, G.J. (1990) The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J. Exp. Mar. Biol. Ecol. 137, pp. 215-240.

Edgar, G.J. (1990) The use of the size-structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. J. Exp. Mar. Biol. Ecol.137, pp. 195-214.

Edgar, G.J. (1993) Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. Oecologia, in press.

Edgar, G.J. (1994) Observations on the size-structure of macrofaunal assemblages. J. Exp. Mar. Biol. Ecol., in press.

Edgar, G.J. & M. Aoki (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese Sargassum. Oecologia, in press.

Edgar, G.J. & H. Kirkman (1990) Recovery and restoration of seagrass habitat of significance to commercial fisheries. Working Paper No. 19, Vic. Inst. Mar. Sci., pp. 1-37.

Edgar, G.J. & C. Shaw (1993) Relationships between sediments, seagrasses, benthic invertebrate and fishes in shallow marine habitats off south-western Australia. pp. 429-442, in *Proceedings of the Fifth International Marine Biological Workshop: the flora and fauna of Rottnest Island, Western Australia*, ed. F.E. Wells & D.I. Walker, W.A. Museum, Perth.

Elder, R.D. (1976) Studies on age and growth, reproduction and population dynamics of red gurnard, *Chelidonichthys kumu* (Lesson and Garnot), in the Hauraki Gulf, New Zealand. Fish. Res. Bull., Fish. Res. Div. N.Z. 12, pp. 1-77.

Fenchel, T. (1967) The ecology of marine microbenthos 1: The quantitative importance of ciliates compared with metazoans in various types of sediments. Ophelia 4, pp. 121-137.

Ferrell, D.J. & J.D. Bell (1991) Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar. Ecol. Prog. Ser. 72, pp. 15-24.

Fonseca, M.S., W.J. Kenworthy, D.R. Colby, K.A. Rittmaster & G.W. Thayer (1990) Comparisons of fauna among natural and transplanted eelgrass *Zostera marina* meadows: criteria for mitigation. Mar. Ecol. Prog. Ser. 65, pp. 251-264.

Geldenhuys, N.D. (1973) Growth of the South African maasbanker *Trachurus trachurus* Linnaeus and age composition of the catches, 1950-1971. Sea Fish. Br. Invest. Rep., S.A. Dept Industries 101, pp. 1-24.

Geldenhuys, N. D. (1978) Age determination of the South African round herring *Etrumeus micropus* and length and age composition of the commercial catches, 1965-1973. Sea Fish. Br. Invest. Rep., S.A. Dept Industries 115, pp. 1-16.

Gerlach, S.A., A.E. Hahn & M. Schrage (1985) Size-spectra of benthic biomass and metabolism.

Mar. Ecol. Prog. Ser. 26, pp. 161-173.

Gibbons, M.J. (1988) The impact of wave exposure on the meiofauna of *Gelidium pristoides* (Turner) Kuetzing (Gelidiales: Rhodophyta). Estuar. Coast. Shelf Sci. 27, pp. 581-593.

Gibson, R.N. (1970) Observations on the biology of the giant goby *Gobius cobitis* Pallas. J. Fish Biol. 2, pp. 281-288.

Gibson, R.N. & I.A. Ezzi (1978) The biology of a Scottish population of Fries' goby, *Lesueurigobius friesii*. J. Fish Biol. 12, pp. 371-389.

Gordon, J.D.M. (1977) The fish populations in inshore waters of the west of Scotland. The biology of the Norway pout (*Trisopterus esmarkii*). J. Fish Biol. 10, pp. 417-430.

Grant, C.J., T.R. Cowper & D.D. Reid (1978) Age and growth of snoek, *Leionura atun* (Euphrasen), in south-eastern Australian waters. Aust. J. Mar. Freshw. Res. 29, pp. 435-44.

Grant, C.J., R.L. Sandland & A.M. Olsen (1979) Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. Aust. J. Mar. Freshw. Res. 30, pp. 625-637.

Grant, C.J. & A.V. Spain (1975) Reproduction, growth and size allometry of *Mugil cephalus* Linnaeus (Pisces: Mugilidae) from North Queensland inshore waters. Aust. J. Zool. 23, pp. 181-201.

Hansen, D.J. (1969) Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-65. Fish. Bull. 68, pp. 135-146.

Harrison, P.G. (1987) Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. Estuar. Coast. Shelf Sci. 24, pp. 799-812.

Healey, M.C. (1972) On the population ecology of the common goby in the Ythan estuary. J. Nat. Hist. 6, pp. 133-145.

Heck, K.L. & T.A. Thoman (1984) The nursery role of segrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7, pp. 70-92.

Hellier, T.R. (1962) Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publs Inst. Mar. Sci. Univ. Texas 8, pp. 1-22.

Holmquist, J.G., G.V.N. Powell & S.M. Sogard (1989) Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. Mar. Biol. 100, pp. 473-483.

Holt, S.A. & C.R. Arnold (1982) Growth of juvenile red snapper *Lutjanus campechanus*, in the northwestern Gulf of Mexico. Fish. Bull. 80, pp. 644-648.

Homziak, J., M.S. Fonseca & W.J. Kenworthy (1982) Macrobenthic community structure in a transplanted eelgrass (*Zostera*) meadow. Mar. Ecol. Prog. Ser. 9, pp. 211-221.

Howard, R.K. (1984) The trophic ecology of caridean shrimps in an eelgrass community. Aquat. Bot. 18, pp. 155-174.

Howard, R.K. & J.D. Koehn (1985) Population dynamics and feeding ecology of pipefish (Syngnathidae) associated with eelgrass of Western Port, Victoria. Aust. J. Mar. Freshw. Res. 36, pp. 361-370.

Howard, R.K., G.J. Edgar & P.A. Hutchings (1989) Faunal assemblages of seagrass beds. Pp. 536-564, in *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*, ed. A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, Netherlands.

Huh, S.H. (1984) Seasonal variations in populations of small fishes concentrated in shoalgrass and turtlegrass meadows. J. Oceanol. Soc. Korea 19, pp. 44-55.

Huh, S.H. & C.L. Kitting (1985) Trophic relationships among concentrated populations of small fishes in seagrass meadows. J. Exp. Mar. Biol. Ecol. 92, pp. 29-43.

James, G.D. (1984) Trevally, *Caranx georgianus* Cuvier: Age determination, population biology, and the fishery. Fish. Res. Bull., Fish. Res. Div. N.Z. 25, pp. 1-51.

Jenkins, G.P., G.F. Watson & L.S. Hammond (1993) Final report to the FRDC committee on the project VMS 2Z 89-2 "Patterns of utilization of seagrass (*Heterozostera*) - dominated habitats as nursery areas by commercially important fish". Unpublished report, FRDC, pp. 1-101.

Kanno, Y. (1989) Comparison of age composition, sex ratio and growth rate among populations of herring *Clupea pallasii* in the Far Eastern waters. Nippon Suisan Gakkaishi 55, pp. 583-589.

Ketchen, K.S. (1975) Age and growth of dogfish *Squalus acanthias* in British Columbian waters. J. Fish. Res. Can. 32, pp. 43-59.

Kimmerer, W.J. & A.D. McKinnon (1985) A comparative study of the zooplankton in two adjacent embayments, Port Phillip and Westernport Bays, Australia. Estuar. Coast. Shelf Sci. 21, pp. 145-159.

Klumpp, D.W., R.K. Howard & D.A. Pollard (1989) Trophodynamics and nutritional ecology of seagrass communities. Pp. 394-457, in *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*, ed. A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, Netherlands.

Kneib, R.T. (1992) Population dynamics of the tanaid *Hargeria rapax* (Crustacea: Peracarida) in a tidal marsh. Mar. Biol. 113, pp. 437-445.

Kneib, R.T. & A.E. Stiven (1978) Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina saltmarsh. J. Exp. Mar. Biol. Ecol. 31, pp. 121-140.

Knudsen, E.E. & W.H. Herke (1978) Growth rate of marked juvenile Atlantic croakers, *Micropogon undulatus*, and length of stay in a coastal marsh nursery in southwest Louisiana. Trans. Am. Fish. Soc. 107, pp. 12-20.

Kumagai, S., T. Bagarinao & A. Unggui (1985) Growth of juvenile milkfish *Chanos chanos* in a natural habitat. Mar. Ecol. Prog. Ser. 22, pp. 1-6.

Last, P.R. (1983) Aspects of the ecology and zoogeography of fishes from soft-bottom habitats of the Tasmanian shore zone. Ph.D. Thesis, University of Tasmania.

Lewis, F.G. (1984) Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrata. Mar. Ecol. Prog. Ser. 19, pp. 101-113.

Lewis, F.G. & A.W. Stoner (1981) An examination of methods for sampling macrobenthos in seagrass meadows. Bull. Mar. Sci. 31, pp. 116-124.

Love, M.S. & W.V. Westphal (1981) Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull. 79, pp. 533-545.

Manooch, C.S. & G.R. Huntsman (1977) Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106, pp. 26-33.

Marsden, M.A.H. & C.W. Mallett (1975) Quaternary evolution, morphology and sediment distribution, Westernport Bay, Victoria. Proc. R. Soc. Vict. 87, pp. 107-138.

Marsden, M.A.H., C.W. Mallett & A.K. Donaldsen (1979) Geological and physical setting, sediments and environments, Western Port, Victoria. Mar. Geol. 30, pp. 11-46.

Meredith, W.H. & V.A. Lotrich (1979) Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). Estuar. Coast. Mar. Sci. 8, pp. 99-118.

Miller, P.J. (1961) Age, growth and reproduction of the *Gobius paganellus* L., in the Isle of Man. J. Mar. Biol. Assoc. U.K. 41, pp. 737-769.

Mills, D. (1991) Habitat utilization by fish in a seagrass meadow. Honours thesis, Zoology Department, University of Tasmania.

Möller, P., L. Pihl & R. Rosenberg (1985) Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. Mar. Ecol. Prog. Ser. 27, pp. 109-121.

Möller, P. & R. Rosenberg (1983) Recruitment, abundance and production of *Mya arenaria* and Cardium edule in marine shallow waters, western Sweden. Ophelia 22, pp. 33-35.

Morales-Nin, B. & S. Ralston (1990) Age and growth of *Lutjanus kasmira* (Forskal) in Hawaiian waters. J. Fish Biol. 36, pp. 191-203.

Mulkana, M.S. (1966) The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2, pp. 97-167.

Nakatani, T., H. Koizumi S. Yokoyama, T. Maeda, T. Takahashi & H. Matsushima (1990) Age and growth of pleuronectid flounder *Hippoglossoides dubius* in Funka Bay, Hokkaido. Nippon Suisan Gakkaishi 56, pp. 893-901.

Nelson, W.G. (1979) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38, pp. 225-245.

Nepgen, C.S.de V. (1977) The biology of the hottentot *Pachymetopon blochii* (Val.) and the silverfish *Argyrozona argyrozona* (Val.) along the Cape south-west coast. Sea Fish. Br. Invest. Rep., S.A. Dept Industries 105, pp. 1-35.

Nichols, F. (1977) Infaunal biomass and production on a mudflat, San Francisco Bay, California. pp. 339-357, in *Ecology of Marine Benthos*, ed. B.C. Coull, Univ. S. Carolina Press, Columbia, S.C., USA.

O'Gower, A.K. & J.W. Wacasey (1967) Animal communities associated with *Thalassia, Diplanthera,* and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movements. Bull. Mar. Sci. 17, pp. 175-210.

Orth, R.J., K.L. Heck & J. Van Montfrans (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7A, pp. 339-350.

Oxenford, H.A. & W. Hunte (1981) Age and growth of dolphin, *Coryphaena hippurus*, as determined by growth rings in otoliths. Fish. Bull. 81, pp. 906-909.

Parrish, R.H. , D.L. Mallicoate & K.F. Mais (1985) Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax.* Fish. Bull. 83, pp. 483-496.

Pearson, T.H. & R. Rosenberg (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16, pp. 229-311.

Petrova, Y.G. & V.I. Chekunova (1979) Growth of the Chilean perch. Hydrobiol. J. 15, pp. 41-46.

Pierce, B.E. & K.B. Pierson (1990) Growth and reproduction of the tidepool sculpin *Oligocottus maculosus*. Jap. J. Ichthyol. 36, pp. 410-418.

Pollard, D.A. (1981) Estuaries as valuable contributors to fisheries production. Aust. Fish. 40, pp. 7-9.

Pollard, D.A. (1984) A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. 18, pp. 3-42.

Prince, J.D. & I.C. Potter (1983) Life-cycle duration, growth and spawning times of five species of Atherinidae (Teleostei) found in a Western Australian estuary. Aust. J. Mar. Freshw. Res. 34, pp. 287-301.

Pulfrich, A. & C.L. Griffiths (1988) Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.). S. Afr. J. mar. Sci. 7, pp. 25-36.

Richards, C.E. & M. Castagna (1976) Distribution, growth, and predation of juvenile white mullet (*Mugil curema*) in oceanside waters of Virginia's eastern shore. Chesapeake Science 17, pp. 308-309.

Rigby, B.A. (1984) The ecology of fish inhabiting estuarine seagrass habitats in the Gippsland Lakes, Victoria. M.Sc. Thesis, University of Melbourne, Melbourne, Australia.

Robertson, A.I. (1977) The ecology of King George whiting *Sillaginodes punctatus* (Cuvier and Valenciennes) (Pisces: Perciformes) in Western Port, Victoria. Aust. J. Mar. Freshw. Res. 28, pp. 35-43.

Robertson, A.I. (1978) Trophic interactions among the macrofauna of an eelgrass community. Ph.D. Thesis, University of Melbourne, Melbourne, Australia.

Robertson, A.I. (1980) The structure and organisation of an eelgrass fish fauna. Oecologia 47, pp. 76-82.

Robertson, A.I. (1982) Population dynamics and feeding ecology of juvenile Australian salmon (*Arripis trutta*) in Western Port. Aust. J. Mar. Freshw. Res. 33, pp. 369-375.

Robertson, A.I. (1984) Trophic interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. Aquat. Bot. 18, pp. 135-153.

Robertson, C.H. & R.W.G. White (1986) Feeding patterns of *Nesogobius* sp., *Gymnapistes marmoratus, Neoodax balteatus* and *Acanthaluteres spilomelanurus* from a Tasmanian seagrass meadow. Aust. J. Mar. Freshw. Res. 37, pp. 481-489.

Sainsbury, K.J. & A.W. Whitelaw (1984) Biology of Peron's threadfin bream, *Nemipterus peroni* (Valenciennes), from the North West Shelf of Australia. Aust. J. Mar. Freshw. Res. 35, pp. 167-185.

Sanders, H.L. (1968) Marine benthic diversity: a comparative study. Am. Nat. 102, pp. 243-282.

Schwartz, F.J. (1990) Length-weight, age and growth, and landings observations for sheepshead *Archosargus probatocephalus* from North Carolina. Fish. Bull. 88, pp. 829-832.

Schwinghamer, P. (1981) Characteristic size-distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. 38, pp. 1255-1263.

Schwinghamer, P. (1985) Observations on size structure and pelagic coupling of some shelf and abyssal benthic communities. Pp. 347-359, in *Proceedings of the 19th European Marine Biology Symposium*, ed. P.E. Gibbs, Cambrige University Press, Cambridge, U.K.

Scott, J.K., R. Dybdahl & W.F. Wood (1986) The ecology of *Posidonia* seagrass fish communities in Cockburn Sound, Western Australia. Dept Cons. Environ., Tech. Ser. No. 11, pp. 1-144.

Shepherd, S.A., A.J. McComb, D.A. Bulthuis, V. Neverauskas, D.A. Steffensen & R. West (1989) Decline of seagrasses. Pp. 346-393, in *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*, ed. A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, Netherlands.

Shlossman, P.A. & M.E. Chittenden, Jr. (1981) Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*. Fish. Bull. 79, pp. 649-669.

Silberstein, K., A.W. Chiffings & A.J. McComb (1976) The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on the productivity of *Posidonia australis* Hook. f. Aquat. Bot. 24, pp. 355-371.

Sogard, S.M. (1989) Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. J. Exp. Mar. Biol. Ecol. 133, pp. 15-37.

Sogard, S.M., G.V.N. Powell & J.G. Holmquist (1987) Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. Mar. Ecol. Prog. Ser. 40, pp. 25-39.

Spies, R.B., D.D. Hardin & J.P. Toal (1988) Organic enrichment or toxicity? A comparison of the effects of kelp and crude oil in sediments on the colonization and growth of benthic infauna. J. Exp. Mar. Biol. Ecol. 124, pp. 261-282.

Struhsaker, P. & J.H. Uchiyama (1976) Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull. 74, pp. 9-17.

Szedimayer, S.T., M.P. Weinstein & J.A. Musick (1990) Differential growth among cohorts of Age-0 weakfish *Cynoscion regalis* in Chesapeake Bay. Fish. Bull. 88, pp. 745-752.

Tanaka, S. & K. Mizue (1979) Studies on sharks - XV. Age and growth of the Japanese dogfish *Mustelus manazo* Bleeker in the East China Sea. Bull. Jap. Soc. Sci. Fish. 45, pp. 43-50.

Thistle, D., J.A. Reidenauer, R.H. Findlay & R. Waldo (1984) An experimental investigation of enhanced harpacticoid (Copepoda) abundances around isolated seagrass shoots. Oecologia 63, pp. 295-299.

Thomas, R.M. (1985) Growth rate of the pilchard off south west Africa, 1971-1983. Sea Fish. Res. Inst. Invest. Rep., S.A. Dept Environ. Affairs 128, pp. 1-41.

Thomas, R.M. (1986) Growth of larval pelagic fish in the south-east Atlantic from daily otolith rings in 1982/83 and 1983/84. S. Afr. J. mar. Sci. 4, pp. 61-77.

Tong, L.J. & C.M. Vooren (1972) The biology of the New Zealand Tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider). Fish. Res. Bull., Fish. Res. Div. N.Z. 6, pp. 1-60.

Uchiyama, J.H. & P. Struhsaker (1981) Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, Thunnus albacares, as indicated by daily growth increments of sagittae. Fish. Bull. 79, pp. 151-162.

Van Dolah, R.F. (1978) Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. Ecol. Monogr. 48, pp. 191-217.

Virnstein, R.W. (1977) The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58, pp. 1199-1217.

Vooren, C.M. & R.F. Coombs (1977) Variations in growth, mortality, and population density of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. Fish. Res. Bull., Fish. Res. Div. N.Z. 14, pp. 1-32.

Warlen, S.M & A.J. Chester (1985) Age, growth, and distribution of larval spot, *Leiostomus xanthurus*, off North Carolina. Fish. Bull. 83, pp. 587-600.

Warwick, R.M. & R. Price (1975) Macrofauna production in an estuarine mud-flat. J. Mar. Biol. Assoc. U.K. 55, pp. 1-18.

Watson, G.F., A.I. Robertson & M.J. Littlejohn (1984) Invertebrate macrobenthos of the seagrass communities in Western Port, Victoria. Aquat. Bot. 18, pp. 175-197.

Webb, B.F. & C.J. Grant (1979) Age and growth of jack mackerel, *Trachurus declivis* (Jenyns), from south-eastern Australian waters. Aust. J. Mar. Freshw. Res. 30, pp. 1-9.

Whitlach, R.B. (1981) Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. J. Exp. Mar. Biol. Ecol. 53, pp. 31-45.

Wilk, R.R., J.B. Keene & M.A.H. Marsden (1979) Sediment characteristics in the Embayment Head of Western Port. The impact of swamp drainage and erosion on sedimentation and seagrass deposition. Environmental studies section, Ministry for Conservation, Publication No. 264., pp. 1-59.

Wilkinson, L. (1987) SYSTAT: the system for statistics. 822 pp. SYSTAT, Evanston, Illinois.

Withell, A.F. & J.W. Wankowski (1988) Estimates of age and growth of ocean perch, *Helicolenus percoides* Richardson, in south-eastern Australian waters. Aust. J. Mar. Freshw. Res. 39, pp. 441-457.

Yabuki, K. (1989) Age determination of Yanagimushigarei *Tanakius kitaharai* (Pleuronectidae) from otoliths in the Sea of Japan off Kyoto Prefecture. Nippon Suisan Gakkaishi 55, pp. 1331-1338.

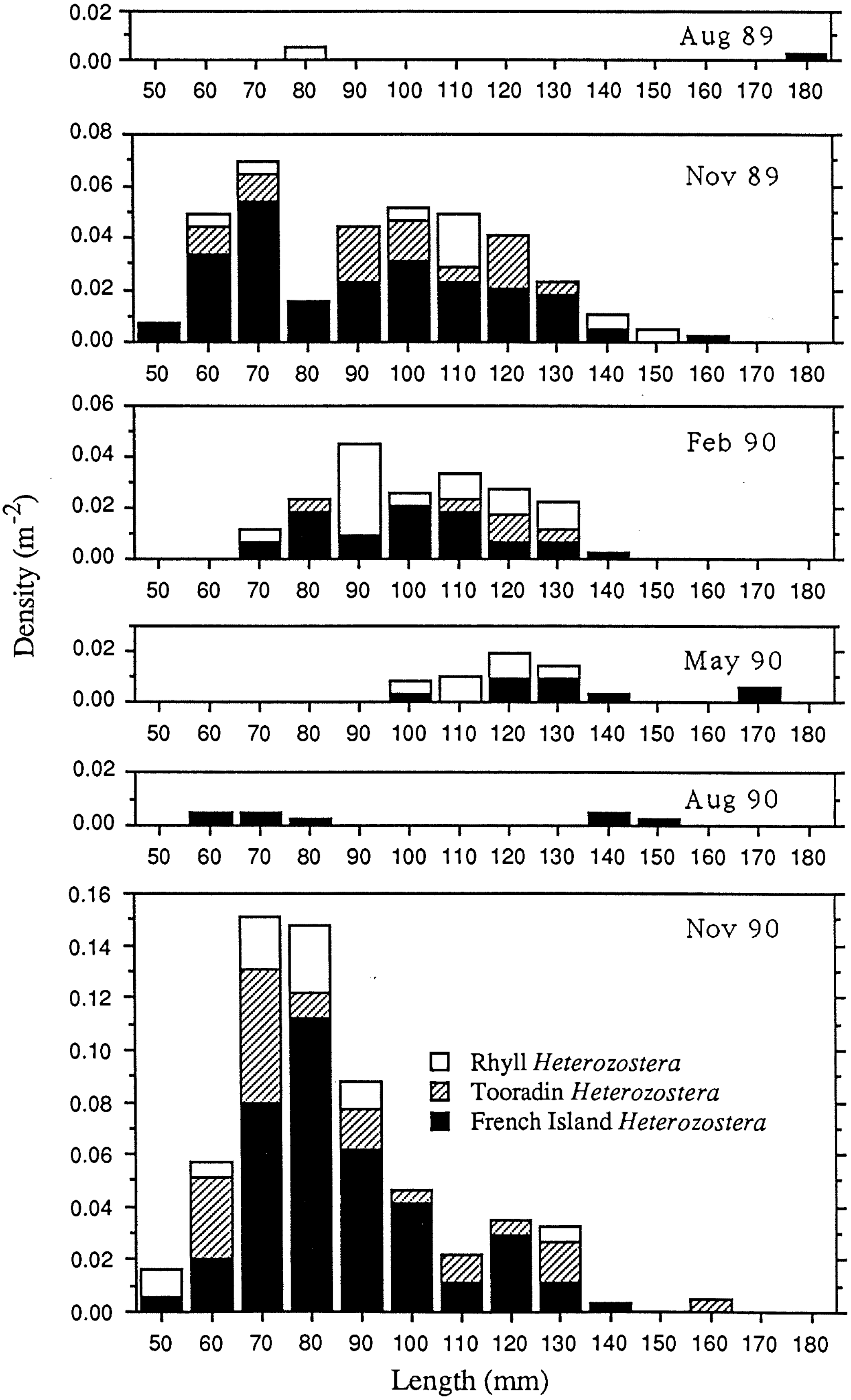
Appendix 1.1. Coefficients for the length/weight equation: ln W = a + b*ln L, where W is wet weight (g) and L is length to caudal fork (mm) for common fishes collected during the Western Port and southern Australian studies. Number of fish (n), minimum length (min) and maximum (max) length (mm) of fish used to calculate these equations are also shown.

Species	a	b	r^2	n	min	max
Mustelus antarcticus Günther	-11.91	2.97	0.969	98	337	1075
Galeorhinus australis (Macleay)	-11.24	2.89	0.909	9	329	428
Urolophus cruciatis (Lacepede)	-9.62	2.69	0.948	15	145	303
Urolophus paucimaculatus Dixon	-11.03	2.91	0.987	8	130	333
Callorhyncus milii Bory de St Vincent	-12.12	3.09	0.969	98	151	700
Spratelloides robustus Ogilby	-15.64	4.00	0.978	50	22	55
Hyperlophus vittatus (Castelnau)	-15.54	3.95	0.974	109	12	86
Sardinops neopilchardus (Steindachner)	-12.83	3.22	0.970	21	36	75
Engraulis australis (Shaw)	-14.97	3.71	0.992	42	12	90
Muraenichthys breviceps Günther	-16.12	3.22	0.937	13	249	430
Pseudophycis bachus (Bloch & Schneider)	-10.95	2.92	0.858	78	219	412
Genypterus tigerinus Klunzinger	-15.41	3.53	0.996	9	246	584
Hyporhamphus melanochir (Valenciennes)	-15.45	3.44	0.997	26	67	388
Atherinasoma microstoma (Günther)	-12.30	3.15	0.996	30	10	66
Atherinasoma presbyteroides (Richardson)	-12.90	3.26	0.990	97	8	94
Craterocephalus honoriae (Ogilby)	-11.37	2.93	0.976	10	31	39
Kestratherina brevirostris Pavlov,Ivantsoff, Last & Crowley	-12.62	3.19	0.993	79	8	68
Kestratherina esox (Klunzinger)	-11.36	2.88	0.998	12	50	94
Kaupus costatus (Waite & Hale)	-15.92	3.33	0.939	10	61	101
Mitotichthys semistriatis (Kaup)	-15.47	3.12	0.971	166	56	222
Stigmatopora argus (Richardson)	-15.11	2.91	0.951	166	37	220
Stigmatopora nigra Kaup	-16.26	3.17	0.944	375	19	156
Vanacampus phillipi (Lucas)	-14.92	3.09	0.981	233	18	143
Vanacampus poecililaemus (Peters)	-15.11	3.11	0.979	10	53	196
Urocampus carinirostris Castelnau	-15.31	3.07	0.940	260	19	96
Centropogon australis (Shaw)	-12.27	3.31	0.977	26	25	65
Gymnapistes marmoratus (Cuvier & Valenciennes)	-11.36	3.07	0.995	195	8	206
Neosebastes scorpaenoides Guichenot	-11.77	3.21	0.999	8	22	48
Platycephalus bassensis Cuvier & Valenciennes	-13.03	3.18	0.994	123	26	561
Platycephalus laevigatus Cuvier & Valenciennes	-11.99	3.01	0.998	137	16	604
Pelates quadrilineatus (Bloch)	-12.69	3.37	0.995	11	9	92
Pelates sexlineatus (Quoy & Gaimard)	-11.37	2.97	0.971	40	13	158
Velambassis jacksoniensis (Macleay)	-11.86	3.17	0.996	27	7	55
Apogon conspersus Klunzinger	-11.83	3.23	0.998	14	27	86
Apogon ruepellii (Günther)	-12.38	3.34	0.995	22	9	95
Siphamia cephalotes Castelnau	-10.93	2.91	0.971	48	4	83
Sillaginodes punctatus Cuvier & Valenciennes	-13.10	3.23	0.999	74	13	369
Pomatomus saltator Linaeus	-12.83	3.28	0.866	31	260	313
Pseudocaranx dentex Bloch & Schneider	-11.89	3.21	0.990	141	53	315
Arripis trutta (Bloch & Schneider)	-11.26	3.04	0.978	45	110	304
Arripis truttaceous Johnston	-9.36	2.69	0.963	114	183	307
Enoplosus armatus (White)	-11.39	3.06	0.999	8	24	93
Aldrichetta forsteri (Cuvier & Valenciennes)	-12.60	3.23	0.997	582	12	371
Shyraena novaehollandiae (Günther)	-13.10	3.12	1.000	8	33	666
Haletta semifasciata (Cuvier & Valenciennes)	-12.57	3.15	0.997	119	37	324
Halichoeres brownfeldii (Whitley)	-11.03	2.87	0.998	10	57	109
Neoodax balteatus (Cuvier & Valenciennes)	-11.88	3.05	0.997	56	12	149

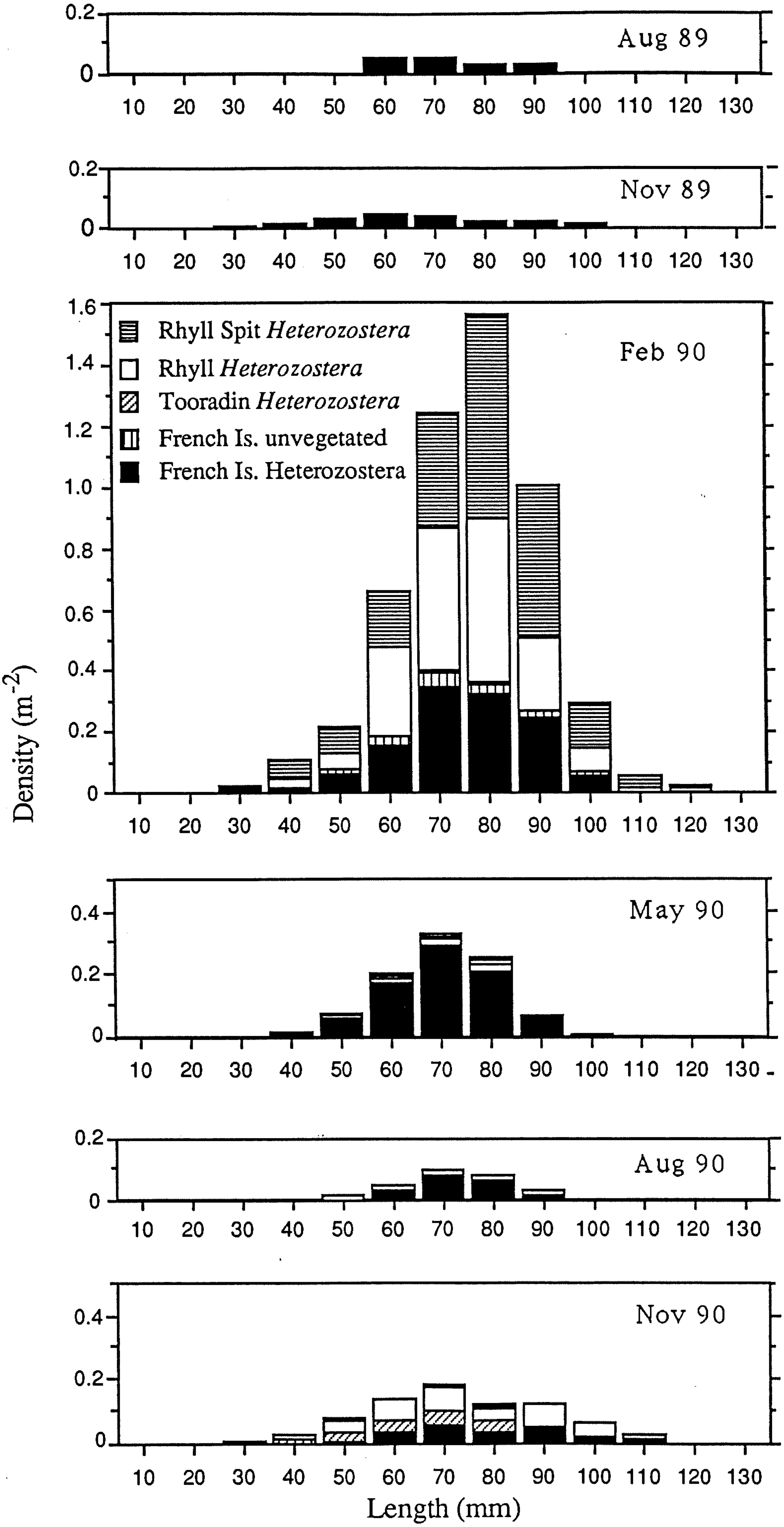
Appendix 1.1 (Cont.)

Species	a	b	r^2	n	min	max
Siphonognathus radiatus (Quoy & Gaimard)	-12.11	2.97	0.997	44	20	159
Parapercis haackei (Steindachner)	-12.44	3.23	0.994	10	12	66
Pseudaphritis bursinus Cuvier	-11.25	2.87	0.982	9	78	155
Cristiceps australis Cuvier & Valenciennes	-11.93	2.99	0.990	49	15	196
Heteroclinus adelaidei Castelnau	-11.82	3.05	0.992	38	15	98
Heteroclinus perspicillatus (Cuvier & Valenciennes)	-12.24	3.13	0.993	262	13	144
Callionymus goodladi (Whitley)	-11.32	2.88	0.997	13	12	173
Arenigobius bifrenatus (Kner)	-11.24	2.80	0.991	55	9	134
Arenigobius frenatus (Günther)	-11.49	2.95	0.991	409	7	146
Bathygobius kreffti (Steindachner)	-11.54	2.99	0.996	10	9	57
Favonigobius tamarensis (Johnston)	-12.06	3.07	0.984	235	7	59
Favonigobius lateralis (Macleay)	-11.98	3.08	0.987	105	10	64
Gobiopterus semivestitus (Munro)	-12.19	3.04	0.961	150	7	31
Nesogobius pulchellus (Castelnau)	-11.86	3.09	0.992	20	11	66
Nesogobius sp. 1	-12.71	3.28	0.995	50	14	89
Nesogobius sp. 4	-13.83	3.70	0.979	12	17	35
Pseudogobius olorum (Sauvage)	-12.29	3.19	0.986	169	8	49
Redigobius macrostoma (Günther)	-12.64	3.36	0.958	14	26	43
Tasmanogobius gloveri Hoese	-12.98	3.37	0.976	9	13	39
Tasmanogobius lasti Hoese	-13.55	3.48	0.994	10	13	34
Cochleoceps spatula (Günther)	-10.59	2.53	0.879	35	28	139
Parvicrepis sp.1	-11.11	2.69	0.947	32	8	32
Ammotretis rostratus Günther	-11.89	3.10	0.997	38	31	271
Rhombosolea tapirina Günther	-11.54	3.04	0.999	85	6	414
Acanthaluteres spilomelanurus (Quoy & Gaimard)	-10.78	2.84	0.993	100	11	122
Bigener brownii (Richardson)	-11.02	2.96	0.997	11	11	216
Brachaluteres jacksonianus (Quoy & Gaimard)	-9.10	2.69	0.987	19	9	43
Meuschenia freycineti (Quoy & Gaimard)	-10.76	2.95	0.999	119	9	334
Penicipelta vittiger (Castelnau)	-10.82	2.86	0.976	39	11	101
Scobinichthys granulatus (Shaw)	-10.89	3.00	0.995	13	14	190
Contusus brevicaudus Hardy	-10.00	2.94	0.995	16	8	263
Tetractenos glaber (Freminville)	-10.21	2.90	0.971	236	95	150
Tetractenos hamiltoni (Gray & Richardson)	-10.36	2.91	0.959	15	81	130
Diodon nicthemerus Cuvier	-8.58	2.70	0.990	114	67	285

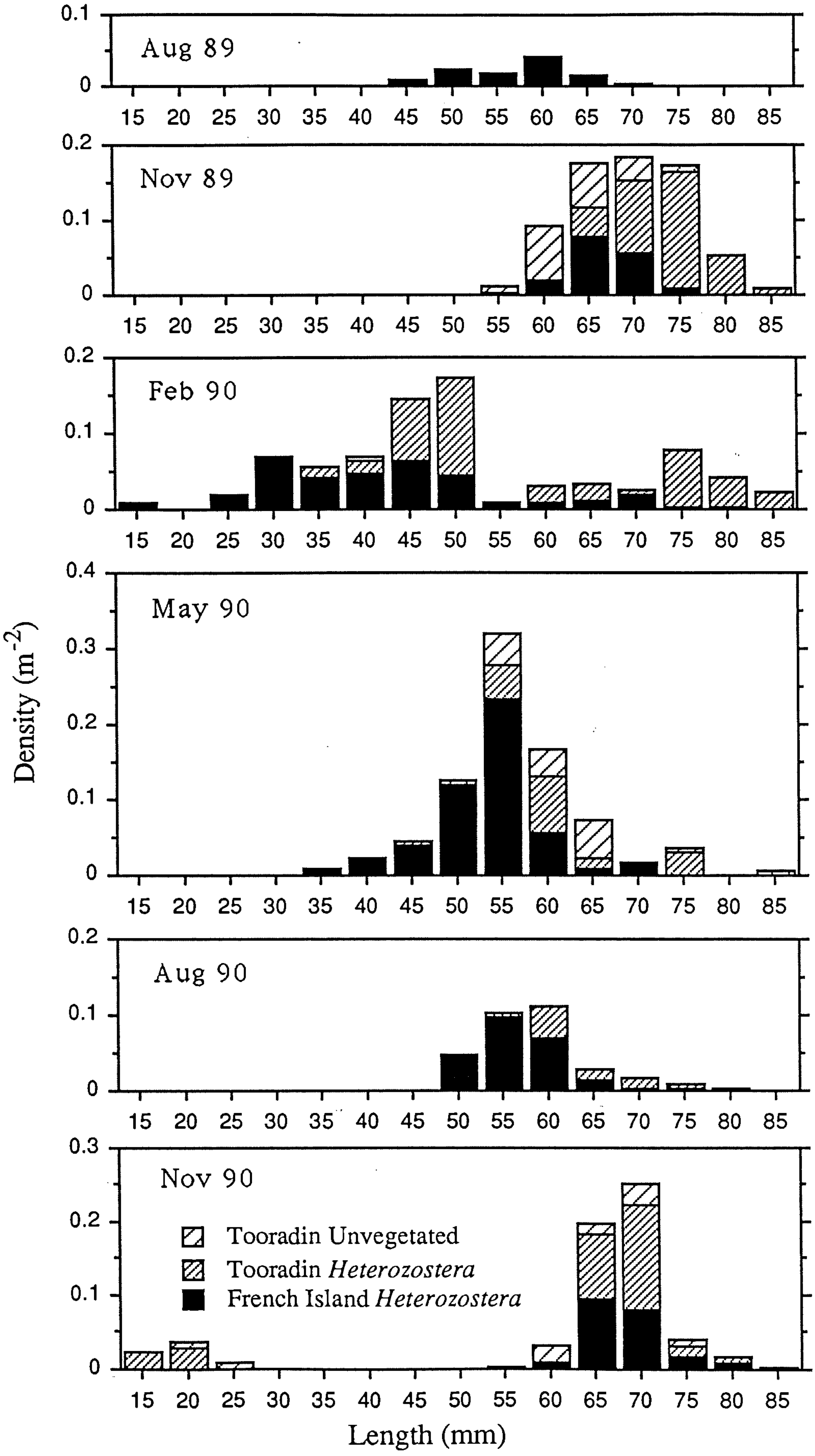
Appendix 1.2.1 Length-frequency distributions of *Mitotichthys semistriatis* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
50
60
70
80
90
100
110
120
130
140
150
160
170
180
Density (m^{-2})
Length (mm)
☐ Rhyll *Heterozostera*
▨ Tooradin *Heterozostera*
■ French Island *Heterozostera*

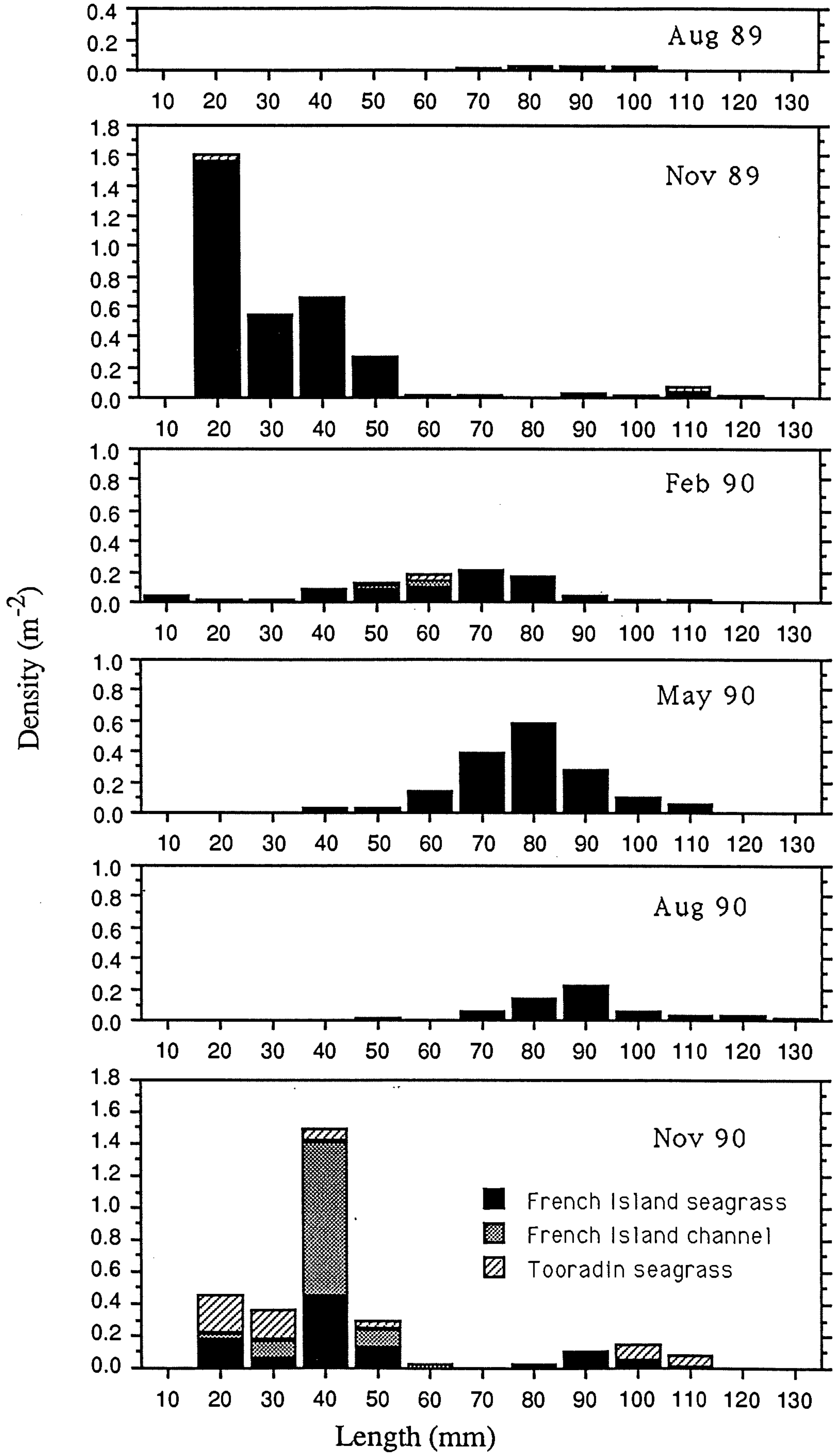
Appendix 1.2.2 Length-frequency distributions of *Stigmatopora nigra* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
▤ Rhyll Spit *Heterozostera*
☐ Rhyll *Heterozostera*
▨ Tooradin *Heterozostera*
◫ French Is. unvegetated
■ French Is. Heterozostera
May 90
Aug 90
Nov 90
Density (m^{-2})
Length (mm)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
10
20
30
40
50
60
70
80
90
100
110
120
130

Appendix 1.2.3 Length-frequency distributions of *Urocampus carinirostris* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
Density (m^{-2})
Length (mm)
0
0.1
0.2
0.3
0.4
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
Tooradin Unvegetated
Tooradin *Heterozostera*
French Island *Heterozostera*

Appendix 1.2.4 Length-frequency distributions of *Vanacampus phillipi* collected in different months and at different sites in Western Port.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Nov 89
Feb 90
May 90
Aug 90
Nov 90
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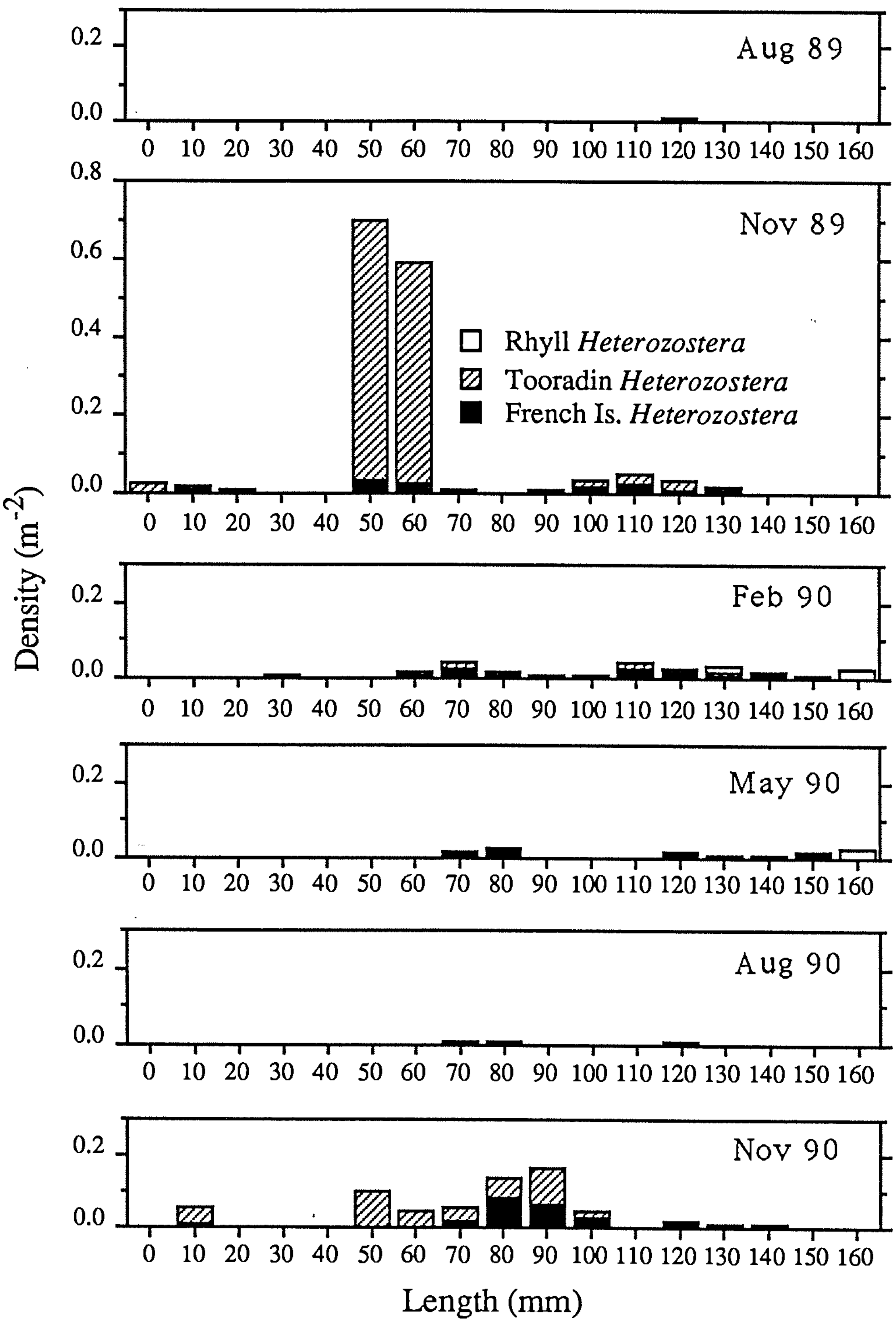
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
10
20
30
40
50
60
70
80
90
100
110
120
130
Density (m^{-2})
Length (mm)
■ French Island seagrass
▩ French Island channel
▨ Tooradin seagrass

Appendix 1.2.5 Length-frequency distributions of *Gymnapistes marmoratus* collected in different months and at different sites in Western Port.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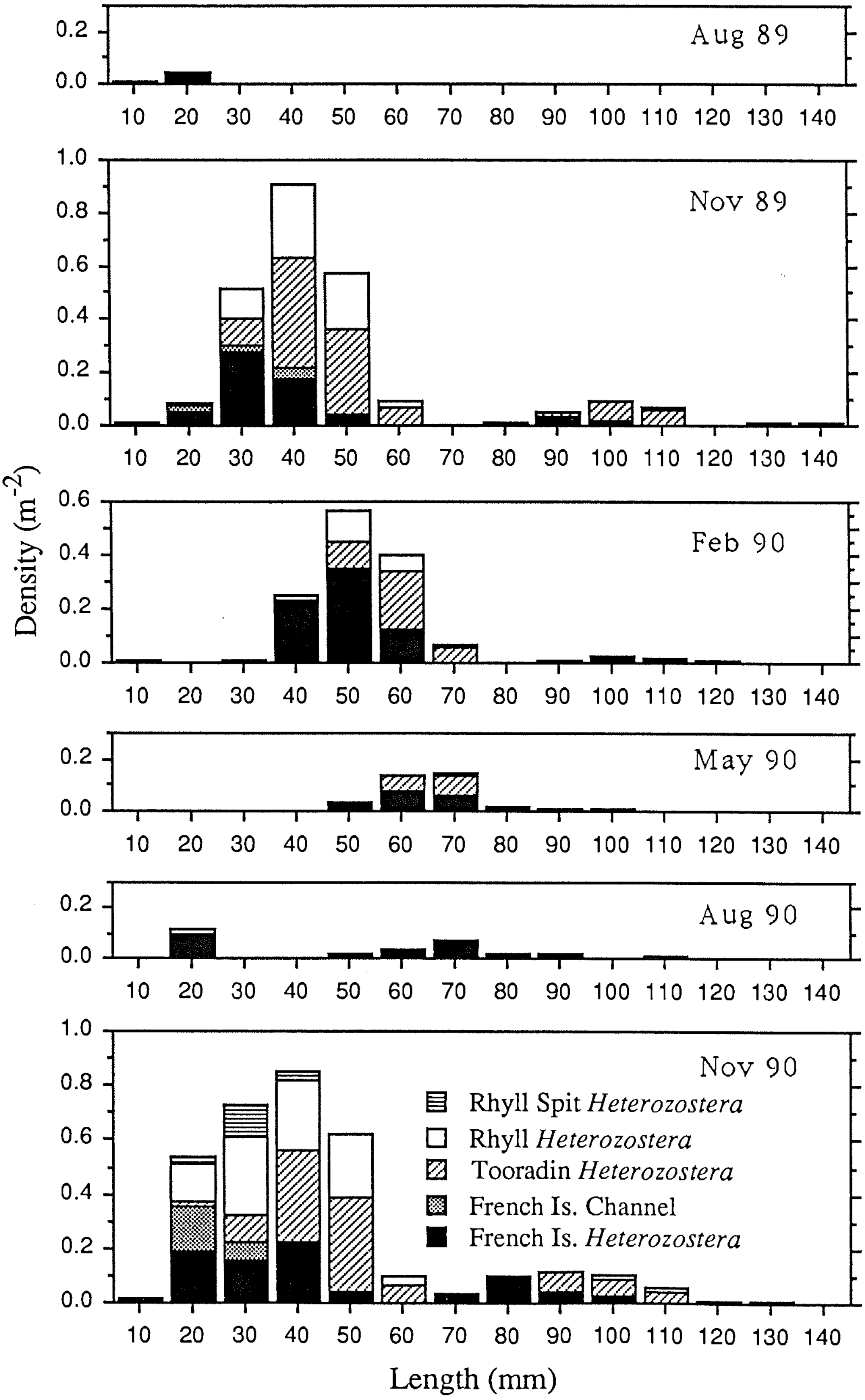
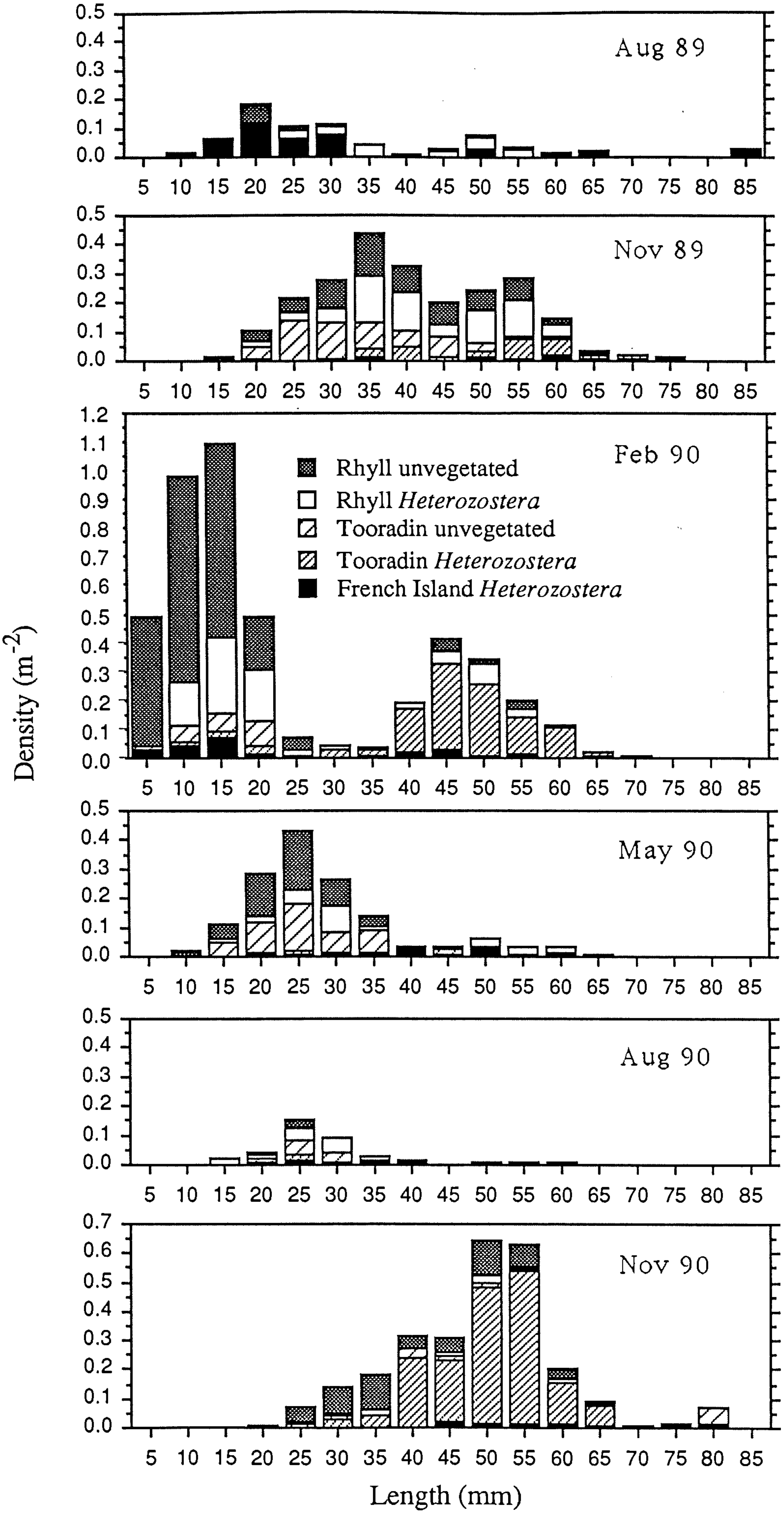
Nov 89
Feb 90
May 90
Aug 90
Nov 90
0.0
0.2
0.4
0.6
0.8
Density (m^{-2})
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160
Length (mm)
☐ Rhyll *Heterozostera*
▨ Tooradin *Heterozostera*
■ French Is. *Heterozostera*

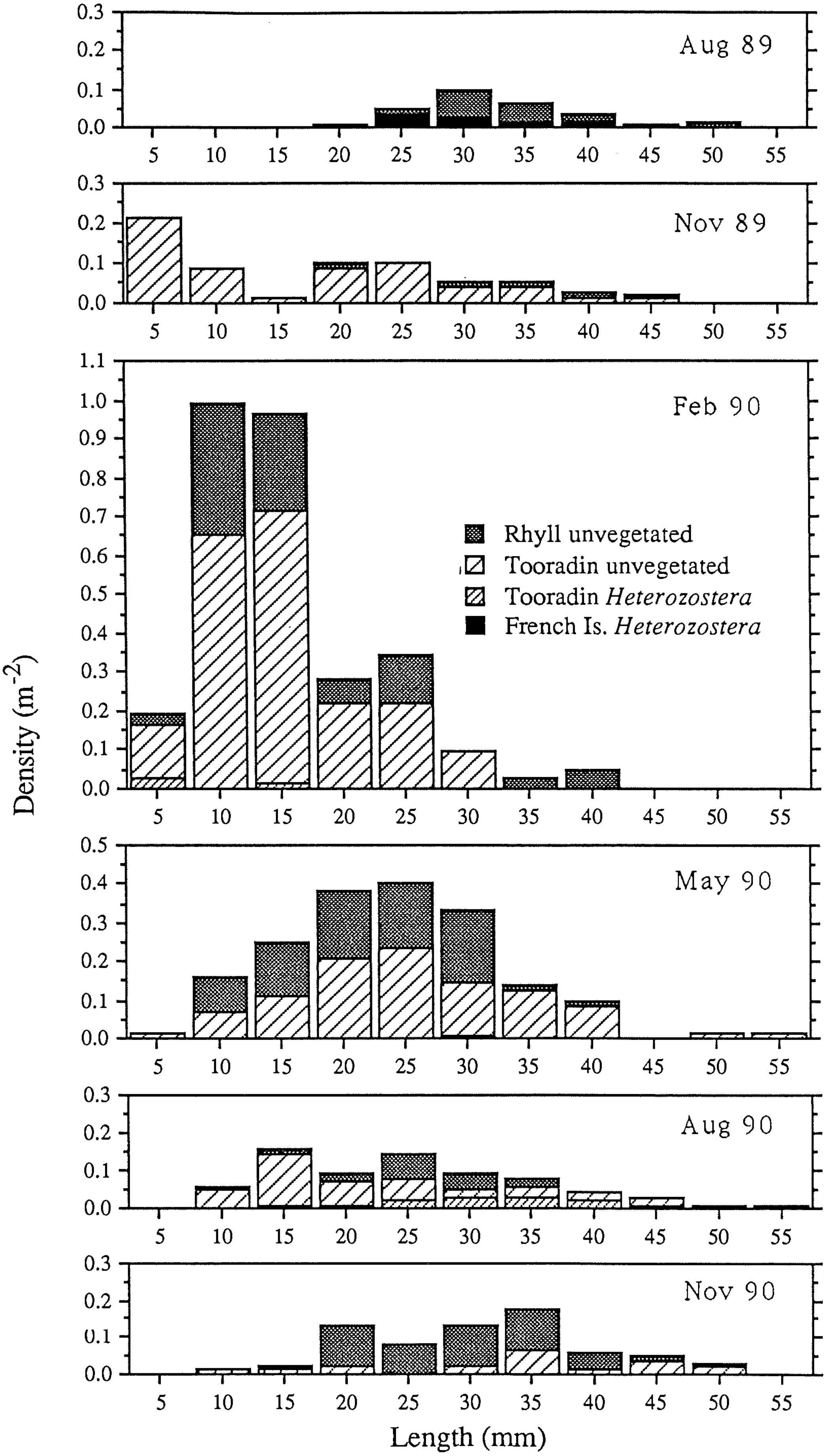
Appendix 1.2.6 Length-frequency distributions of *Heteroclinus perspicillatus* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
Density (m^{-2})
Length (mm)
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
Rhyll Spit *Heterozostera*
Rhyll *Heterozostera*
Tooradin *Heterozostera*
French Is. Channel
French Is. *Heterozostera*

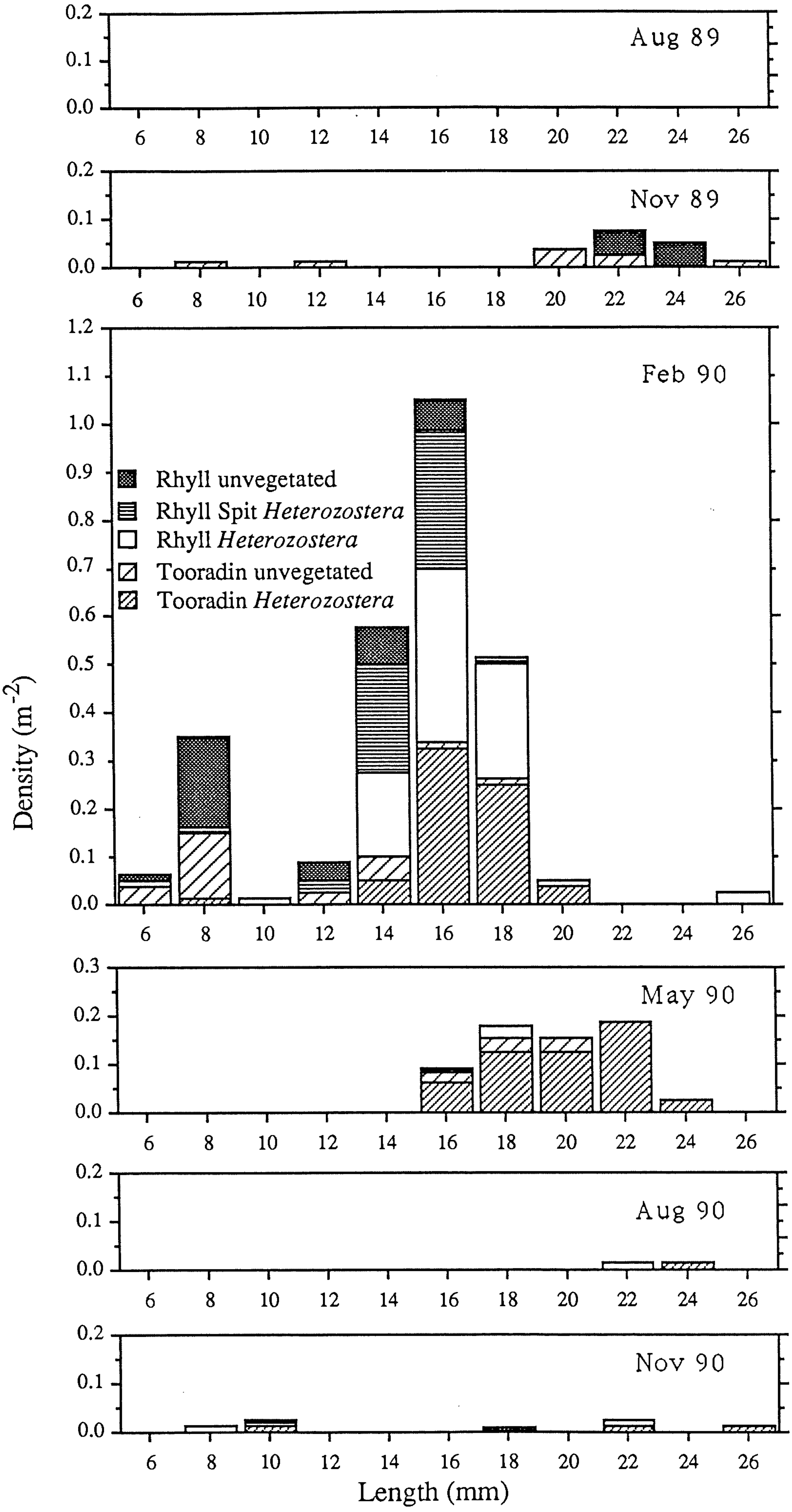
Appendix 1.2.7 Length-frequency distributions of *Arenigobius frenatus* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
Rhyll unvegetated
Rhyll *Heterozostera*
Tooradin unvegetated
Tooradin *Heterozostera*
French Island *Heterozostera*
Density (m^{-2})
Length (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85

Appendix 1.2.8 Length-frequency distributions of *Favonigobius tamarensis* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
Rhyll unvegetated
Tooradin unvegetated
Tooradin *Heterozostera*
French Is. *Heterozostera*
Density (m^{-2})
Length (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
5
10
15
20
25
30
35
40
45
50
55

Appendix 1.2.9 Length-frequency distributions of *Gobiopterus semivestitus* collected in different months and at different sites in Western Port.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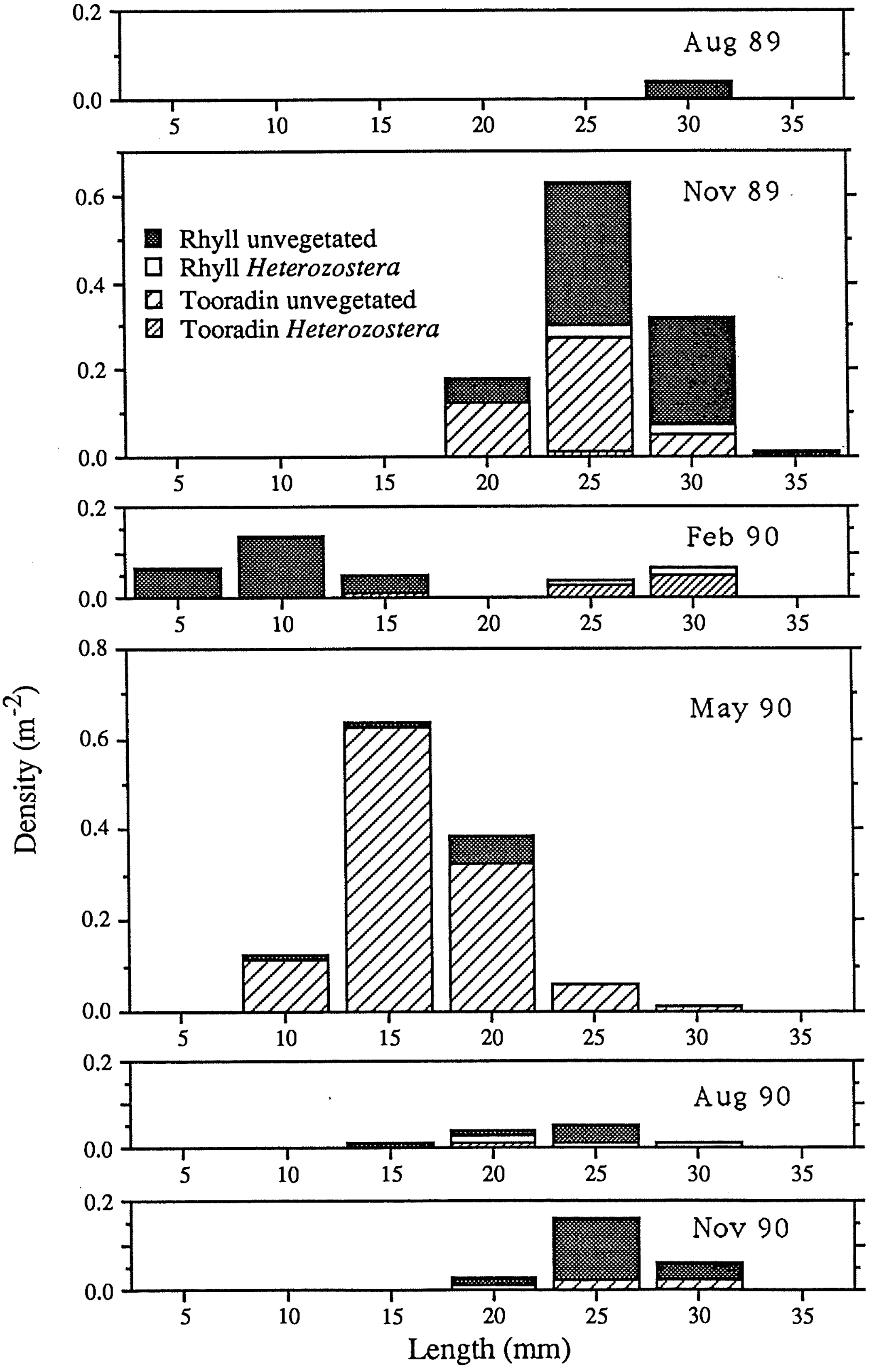
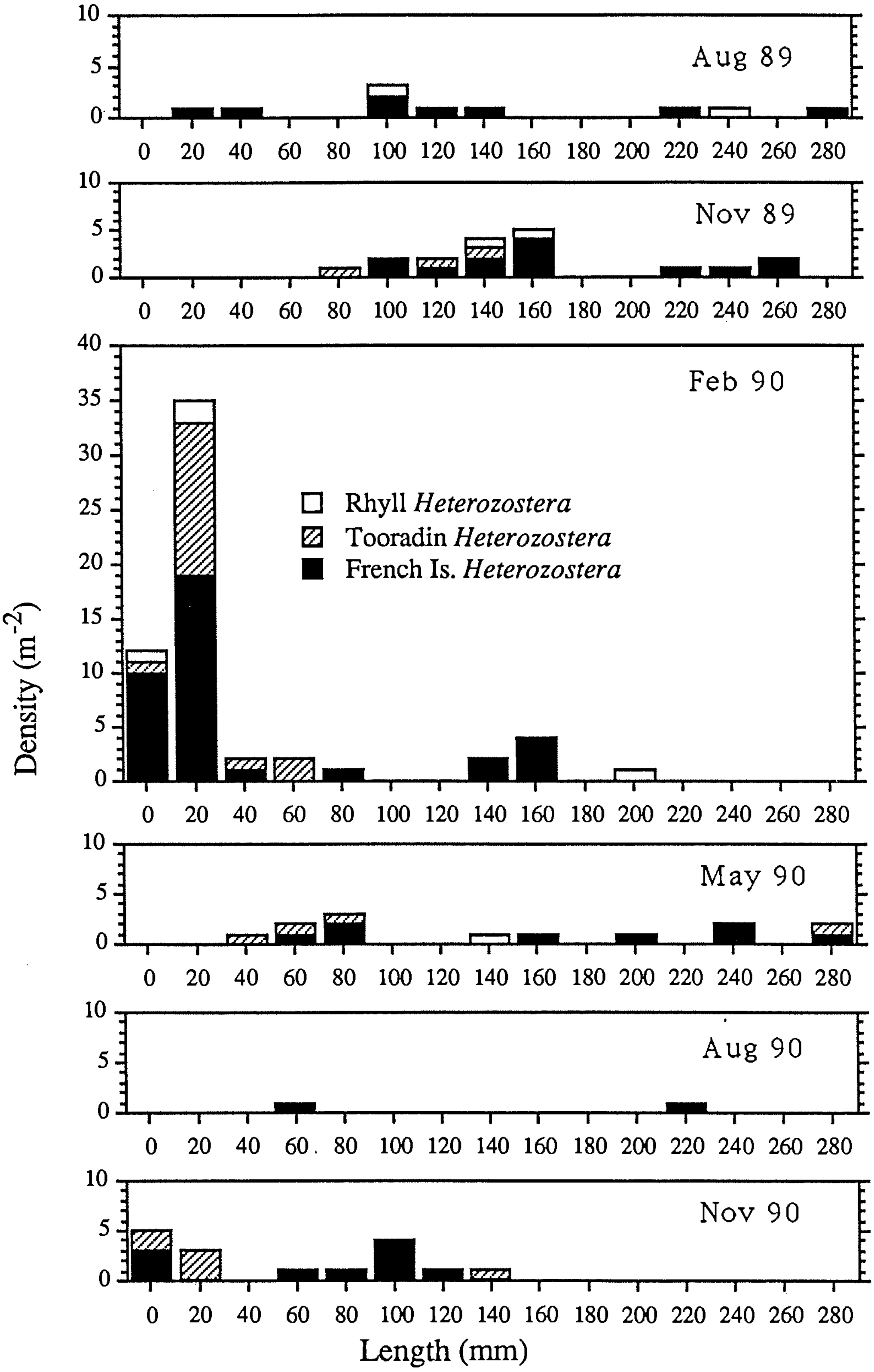
Nov 89
Feb 90
May 90
Aug 90
Nov 90
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
6
8
10
12
14
16
18
20
22
24
26
Rhyll unvegetated
Rhyll Spit *Heterozostera*
Rhyll *Heterozostera*
Tooradin unvegetated
Tooradin *Heterozostera*
Density (m^{-2})
Length (mm)

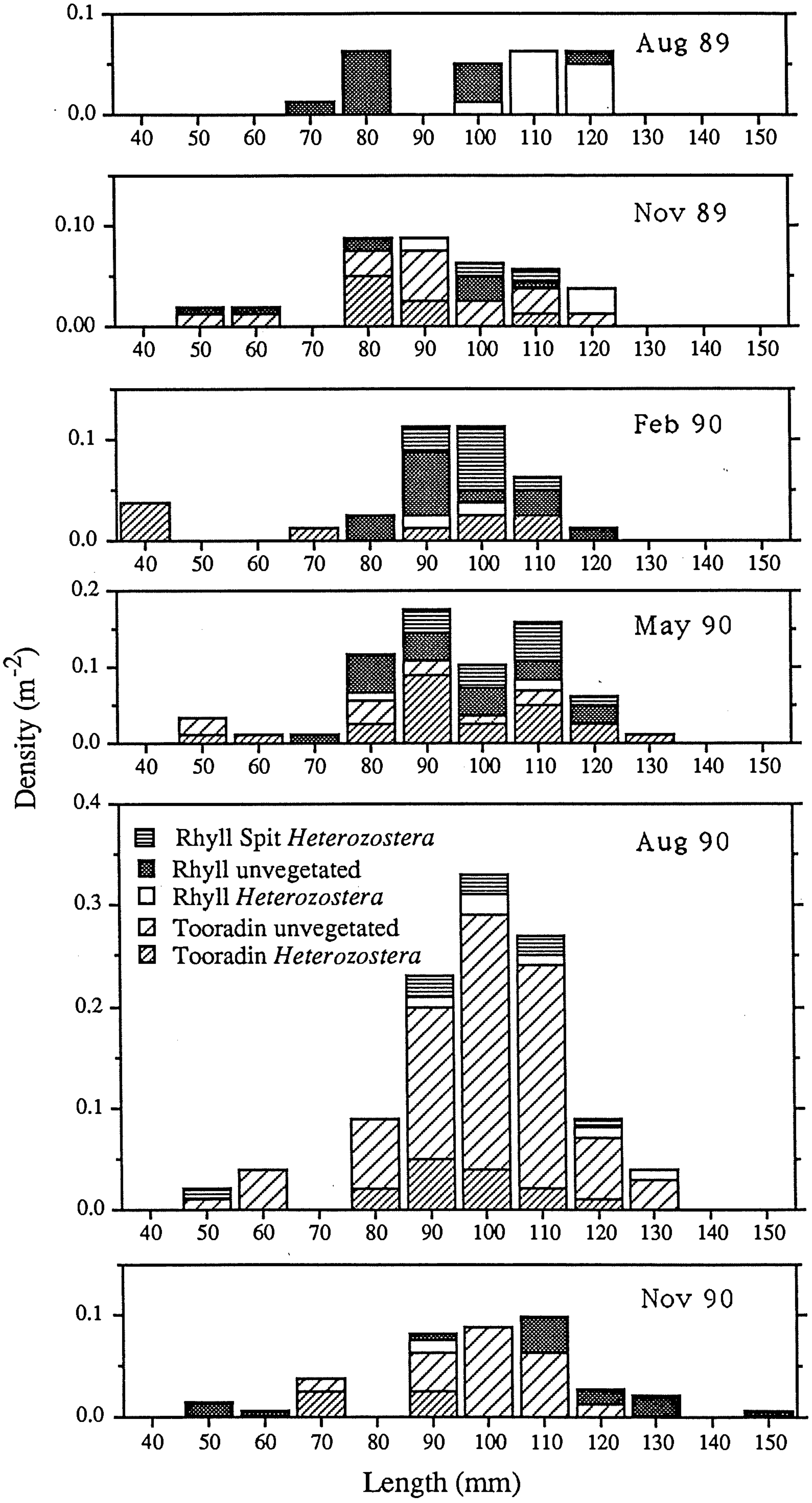
Appendix 1.2.10 Length-frequency distributions of *Pseudogobius olorum* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
▩ Rhyll unvegetated
☐ Rhyll *Heterozostera*
☐ Tooradin unvegetated
▨ Tooradin *Heterozostera*
Density (m^{-2})
0.0
0.2
0.4
0.6
0.8
5
10
15
20
25
30
35
Length (mm)

Appendix 1.2.11 Length-frequency distributions of *Meuschenia freycineti* collected in different months and at different sites in Western Port.


Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
□ Rhyll *Heterozostera*
▨ Tooradin *Heterozostera*
■ French Is. *Heterozostera*
Density (m^{-2})
Length (mm)
0
5
10
15
20
25
30
35
40
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280

Appendix 1.2.12 Length-frequency distributions of *Tetractenos glaber* collected in different months and at different sites in Western Port.



Aug 89
Nov 89
Feb 90
May 90
Aug 90
Nov 90
0.0
0.1
0.00
0.10
0.2
0.3
0.4
40
50
60
70
80
90
100
110
120
130
140
150
Density (m^{-2})
Length (mm)
Rhyll Spit *Heterozostera*
Rhyll unvegetated
Rhyll *Heterozostera*
Tooradin unvegetated
Tooradin *Heterozostera*

Appendix 2.

OFFPRINT FROM

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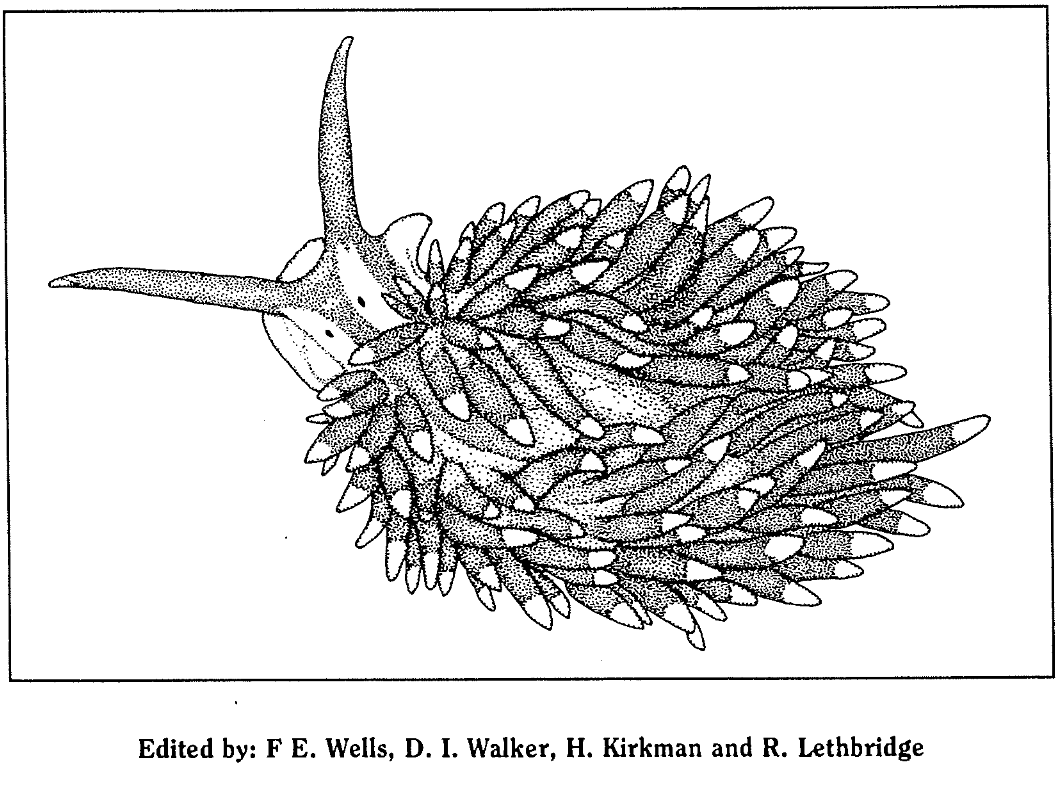
THE
MARINE FLORA AND FAUNA
OF ROTTNEST ISLAND, WESTERN AUSTRALIA



Edited by: F E. Wells, D. I. Walker, H. Kirkman and R. Lethbridge

Australian Marine
Sciences Association

WESTERN AUSTRALIAN MUSEUM

Inter-relationships between sediments, seagrasses, benthic invertebrates and fishes in shallow marine habitats off south-western Australia

by
Graham J. Edgar*
and
Craig Shaw

Zoology Dept, University of Melbourne, Parkville, Victoria 3052, Australia
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Abstract

Fishes, invertebrates and sediments were sampled in *Posidonia* and unvegetated habitats at two locations in each of the Rottnest Island, Cockburn Sound and Albany regions of southern Western Australia. Sediment particle sizes were more heterogeneous and the level of organic matter was higher in seagrass habitats at the three most sheltered locations, while at more exposed sites little difference was apparent in sediment characteristics between vegetated and sand habitats. The species richness, abundance, biomass and estimated production of benthic invertebrates and demersal fishes were greater in vegetated than unvegetated habitats at all locations; however, large numbers of hardyheads and sprats were collected in two sandy habitats (Parker Point and Princess Royal Harbour), greatly elevating total fish production at those sites. Macrofaunal species richness and biomass remained relatively constant between the six *Posidonia* sites studied (a range of 101-124 species per habitat; 10.2-22.3 g AFDW m^{-2}). These faunal parameters nevertheless varied substantially between unvegetated habitats, with species richness varying over a fourfold range (17-68 species per habitat) and production varying over a 30-fold range (0.5-16.0 g AFDW m^{-2}) between sites. Fish and invertebrate production were much higher in the sheltered compared with the exposed unvegetated sites. The size-distribution of macrofauna showed a regular pattern at the different *Posidonia* sites, with peaks in production consistently occurring at 1 to 1.4 mm sieve size. Total production of benthic invertebrates was highly correlated with total demersal fish production, being ≈12 times greater across all sites. Fish are postulated to be attracted to sites with abundant prey of appropriate size.

Introduction

Numerous studies have been conducted during the past twenty years in which the extent to which various physical parameters (*e.g.*, depth, biomass of macrophytes, water temperature, salinity, sediment characteristics) influence the distributions of marine fishes and benthic invertebrates is described (*e.g.*, Heck and Whetstone, 1977; Poore and Rainer, 1979; Poore, 1982; Lewis, 1984).

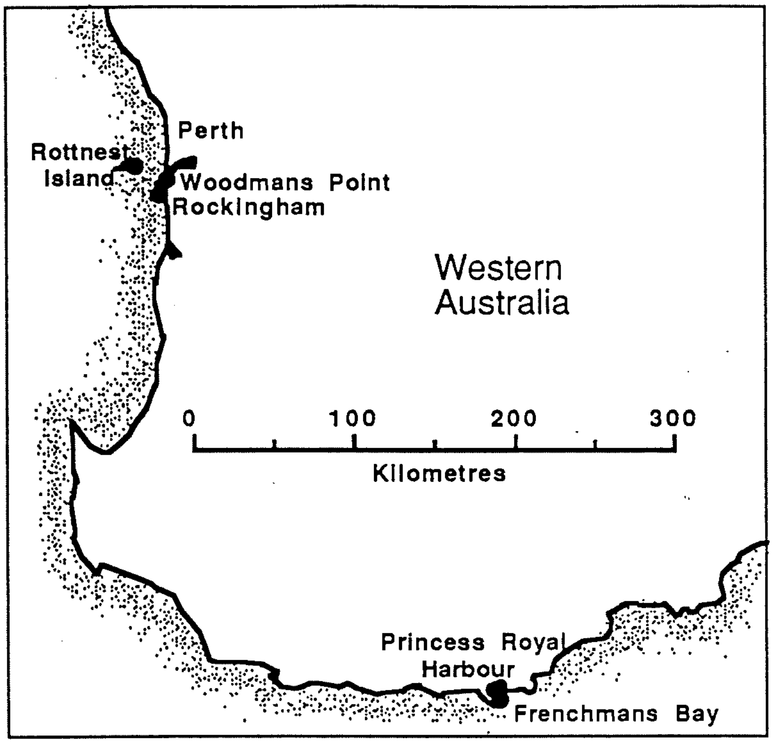

Figure 1. The south-western Australian coast showing location of the study sites.

Although virtually no studies have investigated whether fishes are attracted to sites with abundant benthic prey, interactions between fishes and invertebrates have also been investigated in studies concerned with the impact of fish predation on the abundance of benthic invertebrates (*e.g.*, Heck and Orth, 1980; Heck and Thoman, 1981; Nelson, 1981; Orth *et al.*, 1984; Wilson, 1989). If the marine environment is at all comparable with freshwater environments, then fishes should exert a general influence on the abundance and size-distribution of invertebrate prey species (*e.g.*, see Brooks and Dodson, 1965; Sprules, 1972; Crowder and Cooper, 1982).

As part of a larger investigation into the influence of seagrass on the trophic structure of fish and benthic invertebrate communities in southern Australia, we describe in this paper the patterns of fish and invertebrate production at shallow-water sites off south-western Australia. The major physical features measured in this study were sediment characteristics because sediments exert a strong direct influence on the distribution of animals (Whitlach, 1981). Because the size of sediment particles is correlated with wave energy (Allen, 1971), particle size also provides an approximate index of wave exposure, another major factor known to affect inshore animals (see, *e.g.*, Gibbons, 1988). Water depth, water temperature and salinity were not examined but kept approximately constant between sites. The biotic variables examined were fish and invertebrate density. Seagrass biomass did not vary significantly between vegetated sites. Particular emphasis has been placed on identifying the size-distribution of fish and invertebrate assemblages in our study because intraspecific interactions between different size-classes were found to be less important than interspecific interactions within a size-category for many fishes in Western Port, Victoria (Edgar & Shaw, unpublished data).

Methods

Samples were collected from paired vegetated (*Posidonia* spp.) and unvegetated habitats in shallow depths (<5 m) at the following six sites during January 1991 (Figure 1): Thomsons Bay (Rottnest Island), Porpoise Bay/Parker Point (Rottnest Island), Woodmans Point (Cockburn Sound), Rockingham (Cockburn Sound), Princess Royal Harbour (Quaranup Point, near Albany) and Frenchmans Bay (near Albany). Vegetated and unvegetated habitats were located within 1 km of each other at each site, except for the south-east Rottnest Island samples where suitable habitats for seining could only be found 3 km apart (Porpoise Bay - *Posidonia* habitat; Parker Point - unvegetated habitat). The meiofauna was sampled at each site using 5 replicate 50 mm diameter cores pushed by a diver into the substratum to a depth of 100 mm, and macrofauna using 150 mm diameter cores pushed to the same depth. Both corer types were constructed from PVC tubing with 125 µm mesh over the end caps. Core samples were transferred into plastic bags and preserved with formalin. In the laboratory, samples were washed through a stacked series of sieves (meiofauna - 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2 mm; macrofauna 1, 1.4, 2, 2.8, 4, 5.6, 8, 11.2, 16 mm) using the methods described by Edgar (1990a). Epifauna and infauna collected on each sieve were then sorted into species (macrofauna) or larger taxonomic categories (meiofauna) and counted.

The quantity of organic material and ash in sediments in each habitat were measured by amalgamating sediments collected from replicate meiofaunal cores, and then weighing the sediments retained by different sieves (<0.063, 0.63, 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6, >8 mm sieve size-categories) after drying at 60°C for at least 2 d. Sediments were ashed at 550°C for 2 h after the dry weight had been measured, and reweighed to enable the percentage of ash and organic material to be determined. The biomass of live seagrass leaves, rhizomes and debris collected from macrofaunal core samples were also measured after drying at 60°C for at least 2 d.

Fishes were sampled using a small beach seine (15 m long, 3 m drop, 1 mm mesh) that was set in a straight line from the back of a runabout, and then pulled through a standardized distance of 12 m onto the anchored boat. The weight line was heavier than the float line, hence the net sank below the water surface in depths >2 m. The area swept by the net was measured (±SD) to be 77±10 m^2. Trials using the same sampling methods in Western Port, Victoria, indicated that the capture efficiency of the seine for small fish species varied from 12% to 63%, with an overall mean efficiency of 26% (Edgar & Shaw, unpublished data). The numbers collected in each haul were therefore converted to numbers per m^2 by dividing by 20 (=77x0.26). In the laboratory, fishes were weighed, and length to caudal fork (LCF) recorded. If >120 animals of a species were collected for a habitat and site then 100-120 individuals were subsampled for weighing and measuring.

Estimates of the daily production of benthic invertebrates for each habitat were calculated using the mean weight of animals retained by sieves of different size as determined by Edgar (1990a), and the equation $P = 0.0049*B^{0.80}T^{0.89}$ which relates daily macrobenthic production P (µg/d) to ash-free dry weight B (µg) and water temperature T (°C) (Edgar, 1990a). Water temperature varied little between sites and was standardized at 20°C, the approximate water temperature at all sites in January. Fish production was estimated using the measured wet weights of animals collected in samples, a wet weight/ash-free dry weight (AFDW) conversion factor of 0.22, and a general equation $P = 0.00051 * B^{0.69} T^{1.04}$ which relates daily fish production P (g AFDW/d) to ash-free dry weight B (g) and water temperature T (°C). This equation was calculated using the same method as for the benthic invertebrate production/biomass regression (Edgar, 1990a), from data in the literature on the biomass, production and ambient water temperature for 62 fish species (Edgar & Shaw, unpublished data). In order to compare fish production data with benthic invertebrate data, fishes were categorised by AFDW into the same sieve sizes as invertebrates. This was done by extrapolating the invertebrate regression relating sieve size and AFDW (Edgar, 1990a) to a maximum of 90 mm sieve-size, and by then determining the range in AFDW of animals falling into each size-class. Because far fewer fish were collected than invertebrates, sieve-size classes for fishes were twice as large as for invertebrates (i.e., 2 and 2.8 mm sieve size fish were amalgamated into one size-class (2.8 mm), as were fish of 4 and 5.6 mm (5.6 mm), 8 and 11.2 mm (11.2), etc.).

Results

Habitat analyses

Sediments at all sites were dominated by particles in the 178µm and 250µm sieve size-classes (Figure 2). The size-distribution of particles was more heterogeneous in seagrass habitats than sand habitats, with greater proportions of both fine and large particles. The quantity of organic material in seagrass bed sediments was also much greater than for unvegetated sediments at Rockingham, Princess Royal Harbour and Frenchmans Bay, but, somewhat surprisingly, showed little difference between habitats at the three other more-exposed sites (Figure 2).

The dry weight of above ground seagrass at all sites was ≈700 g m^{-2}, varying from 525±304 m^{-2} (±SD) at Frenchmans Bay to 997±456 m^{-2} at Thomsons Bay. The differences in biomass of seagrass between the six *Posidonia* sites were not found to be significant (one-way ANOVA: d.f. = 5/24, SS = 250/1360, F = 0.88, P = 0.51).

Benthic Invertebrates

In order to determine whether the two different corers produced similar estimates of benthic animal densities for animals in the size range where these methods overlapped, a 2-way ANOVA (sites and core size) was performed using invertebrate density estimates for 1, 1.4 and 2 mm size-classes (Table 1). The 150 mm corer was found to produce significantly lower estimates of faunal densities for animals at 1 mm sieve-size, but not for animals at 1.4 or 2 mm sieve-size. Consequently, densities of animals were calculated in this study using data from the 50 mm cores for animals ≤1 mm sieve size, using data from the 150 mm cores for animals ≥2.8 mm sieve size,

Table 1. Results of three two-way ANOVAs (factors: core size and site) using density data for animals of 2 mm, 1.4 mm and 1 mm sieve size.

		Sieve size								
		2.0 mm			1.4 mm			1.0 mm		
Factor	df	SS	F	P	SS	F	P	SS	F	P
Core size	1	0.003	0.003	0.96	0.265	0.298	0.587	23.576	34.998	0.000
Site	11	153.05	12.649	0.000	197.16	20.121	0.000	163.48	22.061	0.000
Core size x site	11	7.112	0.588	0.835	15.819	1.614	0.107	7.109	0.959	0.489
Error	96	105.6			85.515			64.671		

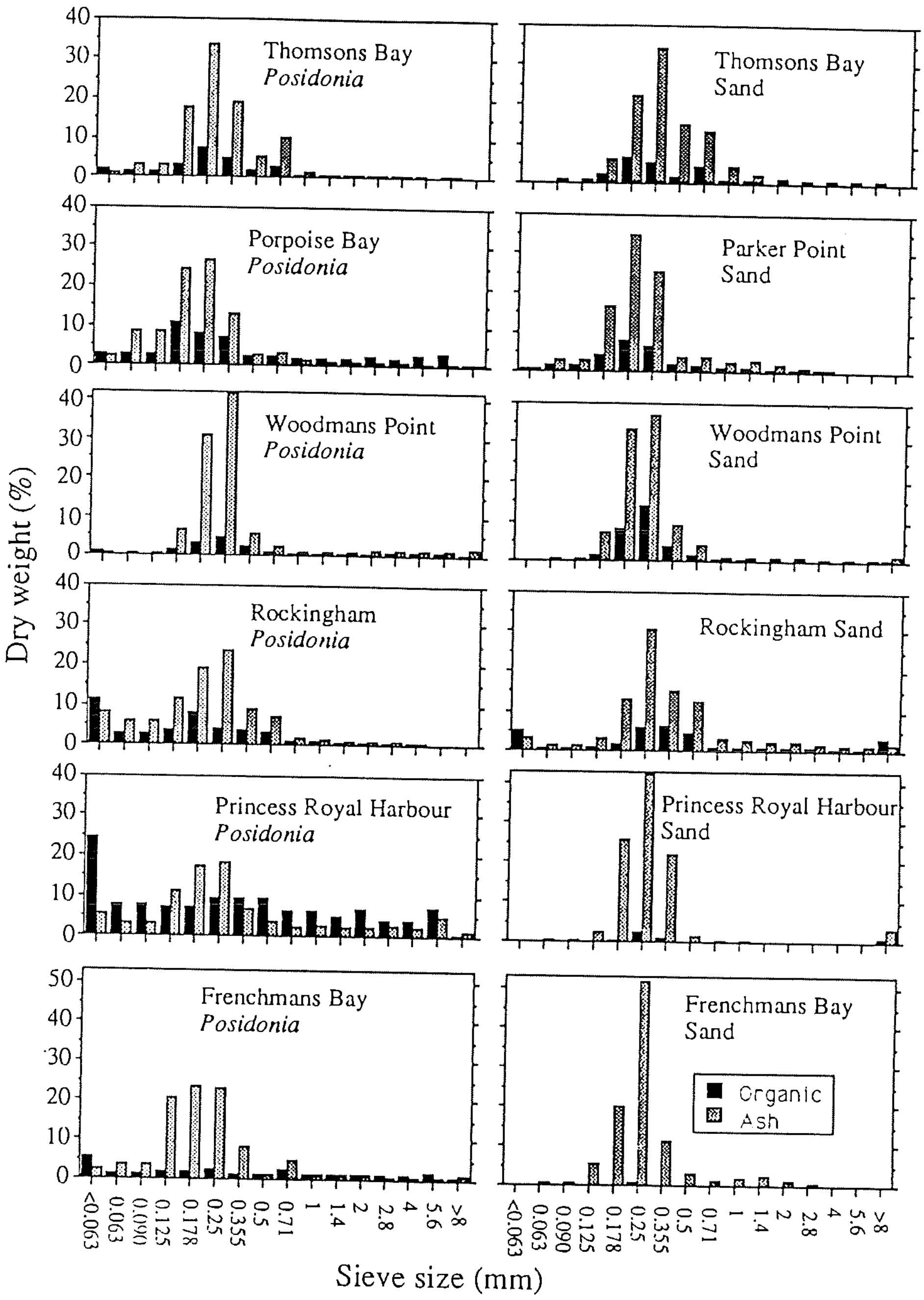

Figure 2. Sediment grain size distributions at the sites studied. The organic content of sediment has also been shown after multiplying by a factor of 10 for display (*i.e.*, for the <0.063 mm sieve size class in *Posidonia* habitat at Princess Royal Harbour, organic material and ash comprised 2.5% and 5%, respectively, of the total dry weight of samples).

and as the mean of data from the two core types for animals of 1.4 and 2 mm sieve size. Very large, significant differences in faunal densities were detected between sites for each of the three sieve sizes examined (Table 1).

The number of invertebrate species collected using 150 mm cores differed substantially between vegetated and unvegetated habitats (two-way ANOVA, factors: habitat and site, d.f.=1/48, F=195.5, $p<0.001$), being approximately 4 times greater in the seagrass habitats (Figure 3). Significant differences were also detected in species richness per core between sites (two-way ANOVA, d.f.=5/48, F=11.2, $p<0.001$), with no significant site/habitat interaction (d.f.=5/48, F=1.072, p=0.387). Very little variation was found in the total number of species collected from the six *Posidonia* sites, with similar numbers of crustacean, mollusc and polychaete species at all sites (Figure 3). The species composition did, however, vary greatly between the seagrass sites, with, for example, amphipods in the genera *Elasmopus, Aora, Mallacoota, Tethygeneia* and *Xenocheira* being the most abundant animals at Princess Royal Harbour, while amphipods in the genera *Amphithoe, Corophium* and *Paradexamine*, the tanaid *Leptochelia* cf *ignota* and the mollusc *Diala* sp. were most abundant at Rockingham.

Estimated invertebrate production was much greater in seagrass habitats than bare habitats, with the exceptions of the two most sheltered sites, Rockingham and Princess Royal Harbour, where high faunal production occurred on the sand (Figure 4). The high faunal production in sandy habitats at Princess Royal Harbour was primarily due to the large bivalve *Katelysia rhytiphora* Lamy and considerable numbers of an unidentified 1 mm diameter gastropod, and at Rockingham to the large polychaete *Nephtys* sp. and high densities of harpacticoid copepods and nematodes.

Invertebrate production varied greatly between the six *Posidonia* sites, with highest levels of production occurring at Rockingham and Princess Royal Harbour (Figure 4). The estimated production of different faunal size-classes nevertheless varied in a consistent pattern at all vegetated sites; animals of 2.8 to 4 mm sieve size were disproportionately low in abundance at all sites, while animals of 0.5 to 1.4 mm sieve size were responsible for high levels of secondary production. Large (>1 mm) invertebrates were rare at unvegetated sites, except at Rockingham and Princess Royal Harbour. Secondary production of invertebrates (>125 µm) was very highly correlated with the proportion of particles <63 µm in the sediment ($n=12, r^2=0.72, p<0.001$), and to a slightly lesser extent with the proportion of organic matter ($r^2=0.56, 0.001<p<0.01$).

Fishes

A total of 48 species of fish was collected by seine (Table 2). Adult specimens of all of the common seagrass fishes were collected, so none of these species can be considered to utilize the coastal seagrass beds solely as nursery habitats.

Many more fishes were collected from seagrass beds than from sandy habitats, except at Princess Royal Harbour and Parker Point where large numbers of the free-swimming hardyhead *Atherinasoma presbyteroides* were collected. Considerable variation was found in the number of fish collected between replicate seines, consequently estimates of fish production showed large standard errors (Figure 5). Fish production varied greatly between habitats and between sites, with maximal production occurring in the 11.2 and 22.5 sieve size classes at nine of the twelve habitats (Figure 5). The presence of *A. presbyteroides* greatly elevated the estimates of total fish production at Princess Royal Harbour and Parker Point. *Atherinasoma presbyteroides* and the blue sprat *Spratelloides robustus* occurred in large schools near the water surface and fed largely on planktonic food resources, hence would not be expected to interact greatly with benthic

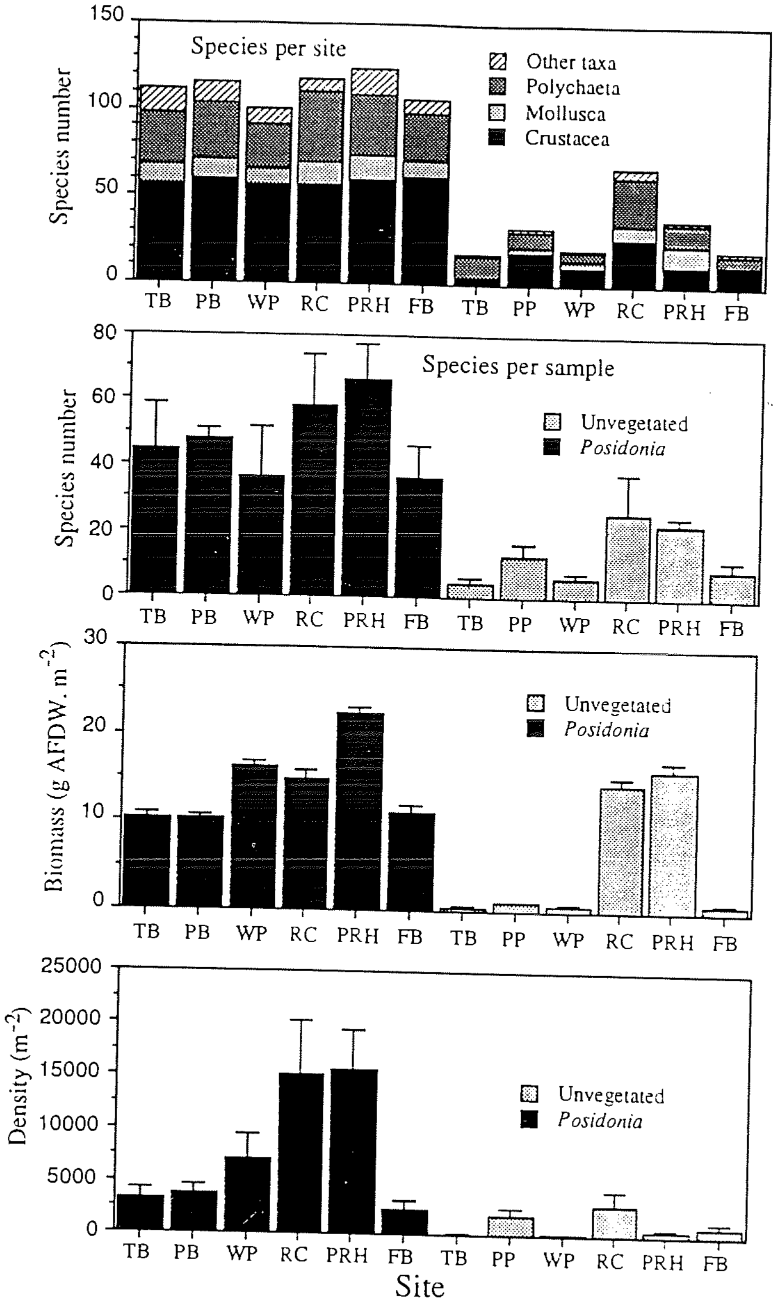

Figure 3. Species richness, density and estimated biomass of macrobenthic fauna at the sites studied: TB Thomsons Bay; PB Porpoise Bay; PP Parker Point; WP Woodmans Point; RC Rockingham; PRH Princess Royal Harbour; FB Frenchmans Bay. Error bars indicate SE.

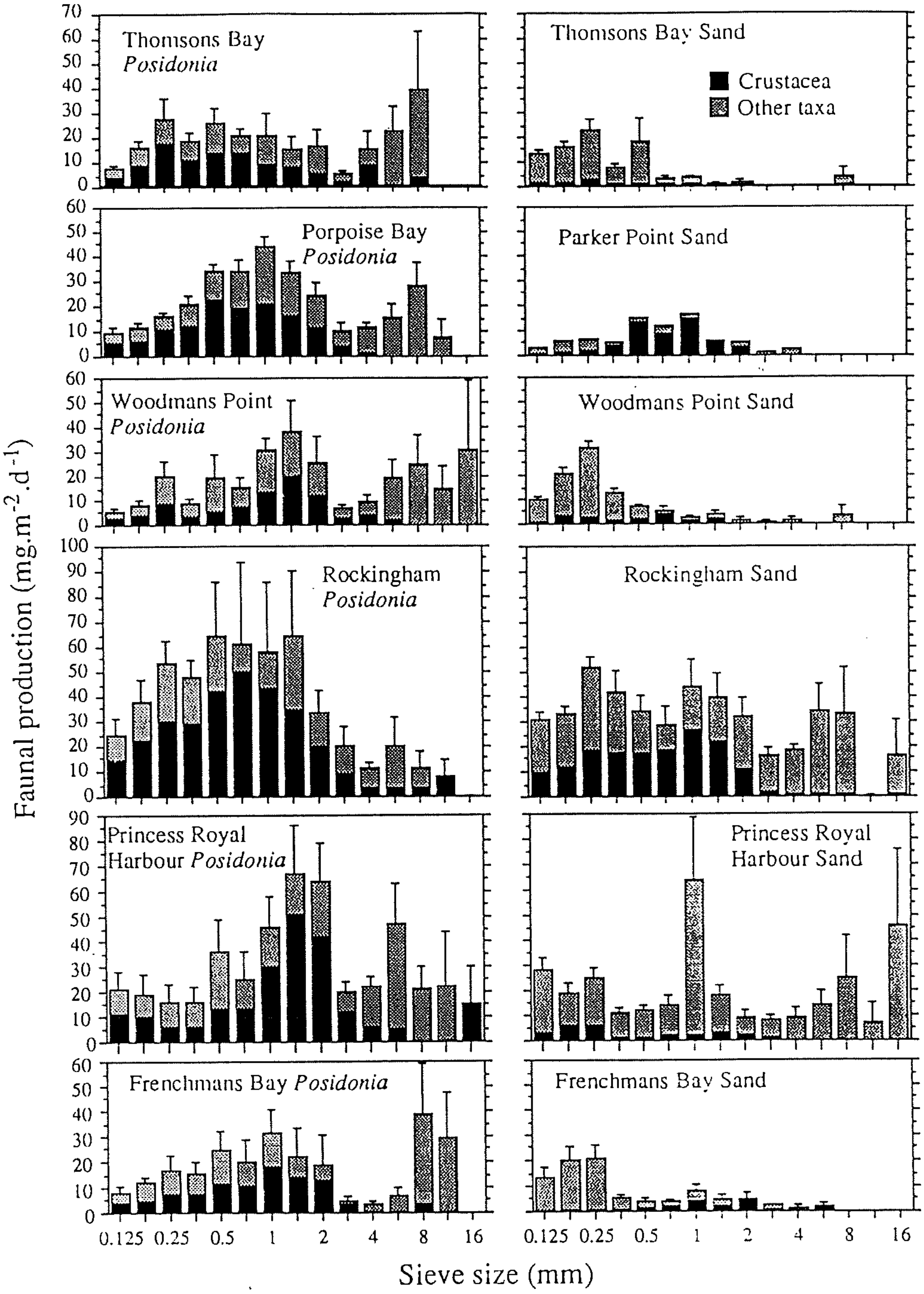

Figure 4. Estimated invertebrate production of different sieve size classes at the sites studied. Error bars indicate SE.

Table 2. Abundances of fish species collected by seine at different sites. TBP Thomsons Bay *Posidonia*; TBU Thomsons Bay unvegetated; PBP Porpoise Bay *Posidonia*; PPU Parker Point unvegetated; WPP Woodmans Point *Posidonia*; WPU Woodmans Point unvegetated; RCP Rockingham *Posidonia*; RCU Rockingham unvegetated; PRHP Princess Royal Harbour *Posidonia*; PRHU Princess Royal Harbour unvegetated; FBP Frenchmans Bay *Posidonia*; FBU Frenchmans Bay unvegetated.

Fish species							Site					
	TBP	TBU	PBP	PPU	WPP	WPU	RCP	RCU	PRHP	PRHU	FBP	FBU
Spratelloides robustus Ogilby			76	71	19				7	1	115	
Cochleoceps spatula (Günther)			2		19		12				3	
Parvicrepis sp.			1		13		1					
Atherinasoma presbyteroides (Richardson)				1494	144				1629	2150		
Filicampus tigris (Castelnau)				1								
Histiogamphelus cristatus (Macleay)		1										
Leptoichthys fistularius Kaup									1			
Mitotichthys c.f. *meraculus* (Whitley)		1										
Stigmatopora argus (Richardson)	3		1		10		13		1		1	
Vanacampus poecililaemus (Peters)							22					
Gymnapistes marmoratus (Cuvier)							27		6			
Maxillicosta scabriceps Whitley							1					
Laeviprora inops (Jenyns)						1						
Laeviprora laevigatus (Cuvier)									1			
Onigocia spinosa (Temmink & Schlegel)								1				
Pelates sexlineatus (Quoy & Gaimard)							26					
Apogon ruepellii (Günther)			1		585		3638					
Siphamia cephalotes (Castelnau)									1			
Vincentia conspersa (Klunzinger)									1			
Sillago bassensis Cuvier		1										
Enoplosus armatus (Shaw)					1							
Threpterius maculosus Richardson									1			
Dotalabrus aurantiacus (Castelnau)									1			
Halichoeres brownfeldii (Whitley)	9											
Notolabrus parilus (Richardson)									1			
Haletta semifasciata (Valenciennes)					4		37		20		3	
Neoodax balteatus (Valenciennes)					1		35		211			
Odax acroptilus (Richardson)			2									
Siphonognathus argyrophanes Richardson											1	
Siphonognathus radiatus (Quoy & Gaimard)	17		13		16		1	7			38	
Parapercis haackei (Steindachner)								12				
Schizochirus sp.						1						
Cristiceps australis Valenciennes									1			
Heteroclinus adelaidei Castelnau					2		4		2			
Callionymus goodladi (Whitley)				1		3		45				
Favonigobius lateralis (Macleay)								13		23		
Gobiopteris semivestitus Whitley								16				
Nesogobius pulchellus (Castelnau)							1		3			
Nesogobius sp.		1						4				
Leptoscopid sp.		3				1						1
Pseudorhombus jenynsii (Bleeker)										1		
Bigener brownii (Richardson)							40					
Brachaluteres jacksonianus (Quoy & Gaimard)		1					2					
Meuschenia freycineti (Quoy & Gaimard)							1		3			
Penicipelta vittiger (Castelnau)			8		2		59		23			
Scobinichthys granulatus (Shaw)	1		3		1						1	
Aracana aurita (Shaw)			1									
Contusus brevicaudus Hardy												1
Total	30	8	108	1567	817	6	3920	98	1913	2175	162	2

invertebrates. All other fish species collected during the study were associated with the seabed. If the two water-column fishes are excluded from analyses, fish production is significantly correlated with benthic invertebrate production ($n=12$, $r^2=0.58$, $0.001<p<0.01$). Fish production was also greatest at the most sheltered sites, consequently the correlation between fish production and the proportion of small particles in the sediment is also significant ($r^2=0.64$, $p<0.001$).

Discussion

The species richness, abundance and production of benthic fishes and invertebrates were all generally at least three times higher in *Posidonia* beds than in sandy habitats. Our results were therefore consistent with previous comparative investigations of vegetated and unvegetated habitats where species richness and abundance have been found to be much higher in vegetated habitats (*e.g.*, Wells *et al.*, 1985; Sergeev *et al.*, 1988; Bell and Pollard, 1989; Howard *et al.*, 1989; Edgar, 1990b; Lubbers *et al.*, 1990; Hutchings *et al.*, 1991). The presence of a seagrass canopy nevertheless explained only part of the variation in invertebrate production; secondary production at the two most sheltered unvegetated sites was greater than in seagrass habitats at Thomsons and Frenchmans Bays.

The number of species of macrofauna collected from *Posidonia* habitats varied little between sites. Almost twice as many species were collected per sample from the southern Western Australian sites as was collected from Cliff Head, a subtropical site 300 km north of Rottnest Island where a mean of 23 species per sample were collected using square corers with approximately similar dimensions (Edgar, 1990b). The macrofaunal species richness of *Posidonia* habitats investigated here also appears to be slightly higher than species richness reported from studies conducted elsewhere in Australia (Rainer and Fitzhardinge, 1981; Collett *et al.*, 1984; Wells *et al.*, 1985; Sergeev *et al.*, 1988; Hutchings *et al.*, 1991), although this result may be due to the different sampling procedures used in the various studies. This difference is indicated by comparing our results for Quaranup, Princess Royal Harbour, with the results of the study by Hutchings *et al.* (1991) at a site in the same area. Hutchings *et al.* (1991) did not distinguish between amphipod species, the most diverse order of animals, and consequently recognized much lower total numbers of species (65 cf. 124). Our estimates of macrofaunal densities were also much higher than Hutchings *et al.* (15607 cf. 1413 m^{-2}), possibly because our samples were sorted under a microscope rather than by eye, whereas our biomass estimate did not include ascidians and was comparatively low (22.33 c.f. 78.5 $g.m^{-2}$).

The species of fishes collected in Princess Royal Harbour were comparable to those collected using a beam trawl by Kirkman *et al.* (1991), except that we collected high numbers of the small open-water species *Atherinasoma presbyteroides* and *Spratelloides robustus* which largely avoided the beam trawl. In contrast to most studies of seagrass fishes (see Kikuchi and Pérès, 1977; Kikuchi, 1980; Bell and Pollard, 1989), we did not discover any fish species that utilized the coastal seagrass beds as juveniles only. Coastal seagrass beds therefore appear to be important to commercial fisheries in south-western Australia more by enhancing fish production rather than in acting as nursery sites for species. Estuaries (Lenanton, 1977, 1978) and detached macrophyte accumulations (Lenanton *et al.*, 1982; Lenanton and Caputi, 1989) are probably more important than the coastal seagrass beds as nursery environments in southern Western Australia.

Seagrass beds, particularly in the more-sheltered areas, greatly modify the sedimentary environment (Fig. 2; see also Figs 4 and 5 in Walker *et al.*, 1991). The proportion of large particles was higher in seagrass habitats than bare areas because epiphytic mollusc and foraminiferan shells

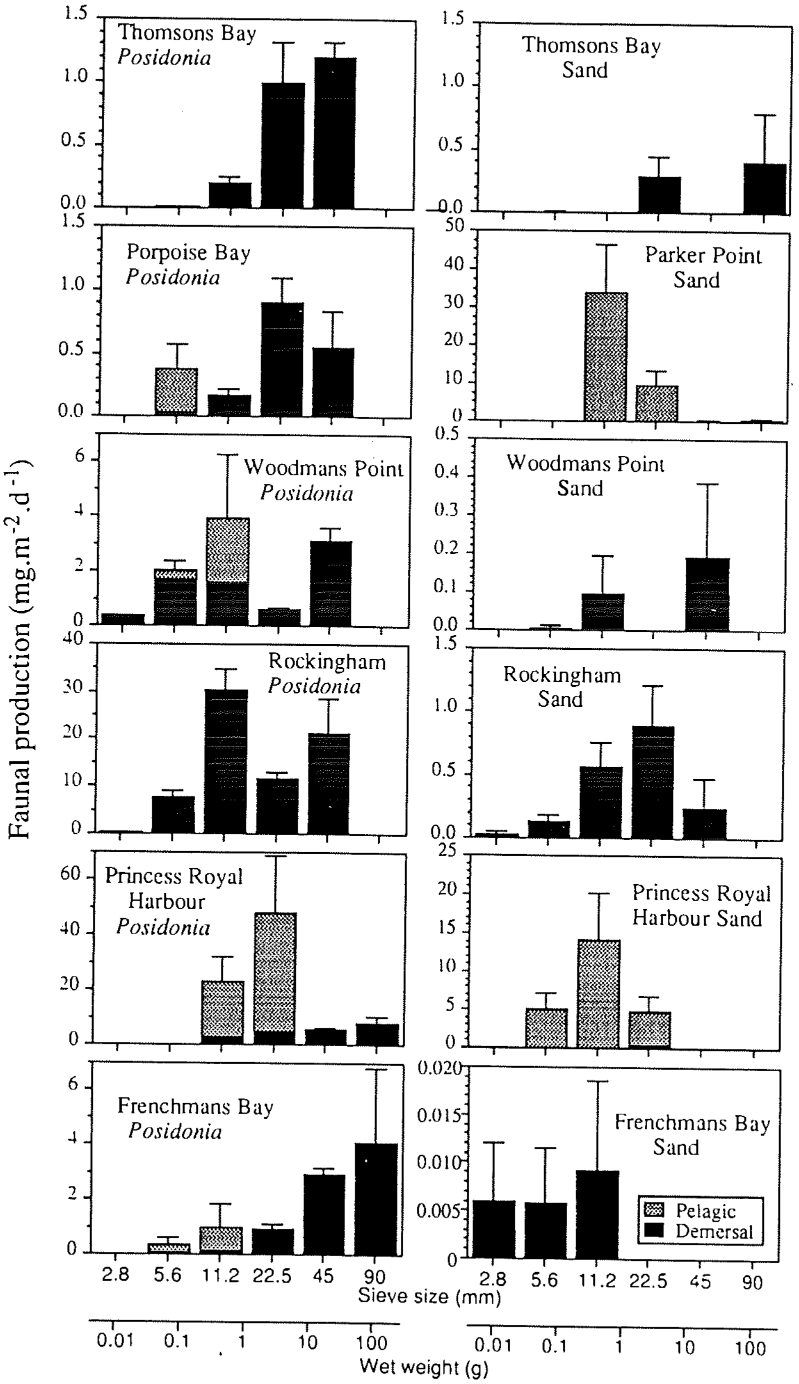

Figure 5. Estimated production of pelagic (atherinid and clupeoid) and demersal (other) fishes belonging to different sieve size classes at the sites studied. Error bars indicate SE.

accumulated under plants, and the proportion of fine particles also increased primarily because seagrass plants act as baffles to water flow, causing fine suspended particles to be deposited (Nowell and Jumars, 1984). The proportion of organic matter in sediments was also much greater in sheltered seagrass beds (Rockingham and Princess Royal Harbour) than unvegetated habitats, largely as a result of plant material decaying *in situ*. At more exposed sites (*e.g.*, Thomsons Bay and Woodmans Point), seagrass debris has presumably been transported away from seagrass beds by wave action because no major difference in sediment characteristics was detected between vegetated and unvegetated habitat types.

The strong interactions between seagrass biomass, percentage of organic matter in sediments and water movement (as indicated by its correlate, the percentage of fine particles in sediments, see Allen, 1970) make it difficult to infer the relative importance of each of these factors. Benthic invertebrate production and benthic fish production were both found to be highly correlated with these three factors, and with each other. The high correlation between fish production and other factors was somewhat surprising given that the variability in the data caused by the one-off sampling at each site, and the patchiness of fish distributions. Invertebrate production is probably positively related to the organic content of sediments because increased food resources are available to deposit feeders in organically-enriched sediments (Pearson and Rosenberg, 1978; Mann, 1988; Spies *et al.*, 1988), but may also be higher in sheltered habitats because diatoms and other food organisms can best colonise stable sediment surfaces.

The question of whether fish respond directly to the shelter of habitats or to the high productivity of invertebrates in sheltered environments remains contentious (Bell and Pollard, 1989), and can unequivocally be determined only by manipulative methods. Our data nevertheless suggest that fish are attracted to sites with high invertebrate productivity. This association is indicated not only by the close correlation between fish and invertebrate productivity, but also by comparing the animal size/productivity relationships for benthic fishes and benthic invertebrates (Figs 3 and 4). Fishes predominantly feed on prey with a mean size of ≈5% of fish body length (Edgar and Shaw, unpublished data), consequently any peak in the fish productivity/sieve size relationship should be reflected by a deformation in the invertebrate productivity/sieve size relationship at 5% of the fish productivity/sieve size peak. This deformation is predicted to be positive (*i.e.*, at a maximum) if fish are attracted by prey, because fish will travel in larger numbers to sites with high densities of the optimal size prey they can consume. In contrast, if the density of fishes is independent of the density of invertebrates then a trough in the size/productivity relationship for benthic invertebrates is predicted because fish will be removing a disproportionate amount of prey from the benthic community at this size. Our data indicate that the size peak in demersal fish productivity occurs at most sites at 11.2-22.5 mm sieve size, with a general peak in benthic invertebrate productivity at 1-1.4 mm sieve size. These results suggest that fish are attracted to sites where prey of the most appropriate size for ingestion are abundant. Although fish did not have a discernible negative effect on invertebrate production, the high levels of fish production clearly indicate that demersal fishes are able to utilize a large proportion of the production of the benthos. Invertebrate production was estimated to be only ≈12 times the production of fishes.

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Literature Cited

Allen, J.R.L. 1970. Physical processes of sedimentation; an introduction. Earth Science Series, No. 1. Allen and Unwin, London.

Bell, J.D. and Pollard, D.A. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. Pp. 565-609. In: Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.

Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of the plankton. Science 150: 28-35.

Collett, L.C., Hutchings, P.A., Gibbs, P.J. and Collins, A.J. 1984. A comparative study of the macro-fauna of *Posidonia australis* seagrass meadows in New South Wales. Aquatic Botany 18: 111-134.

Crowder, L.B., and Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Edgar, G.J. 1990a. The use of the size-structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. Journal of Experimental Marine Biology and Ecology 137: 195-214.

Edgar, G.J. 1990b. The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. Journal of Experimental Marine Biology and Ecology 137: 215-240.

Gibbons, M.J. 1988. The impact of wave exposure on the meiofauna of *Gelidium pristoides* (Turner) Kuetzing (Gelidiales: Rhodophyta). Estuarine Coastal and Shelf Science 27: 581- 593.

Heck, K.L. and Orth, R.J. 1980. Seagrass habitats: the roles of structural complexity, competition and predation in structuring associated fish and macroinvertebrate assemblages. Pp. 449-464. In: Kennedy, V.S. (Ed.) Estuarine perspectives. Academic Press, New York.

Heck, K.L., Jr., and Thoman, T.A. 1981. Experiments on predator- prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology 53: 125-134.

Heck, K.L., Jr., and Whetstone, G.S. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. Journal of Biogeography 4: 135-142.

Howard, R.K., Edgar, G.J. and Hutchings, P.A. 1989. Faunal assemblages of seagrass beds. Pp. 536-564. In: Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.

Hutchings, P.A., Wells, F.E., Walker, D.I. and Kendrick, G.A. 1991. Seagrass, sediment and infauna - a comparison of *Posidonia australis, Posidonia sinuosa* and *Amphobilis antarctica* in Princess Royal Harbour, south-western Australia. II. Distribution, abundance and composition of the macrofauna. Pp. 611-633. In: Wells, F.E., Walker, D.I., Kirkman, H. and Lethbridge, R. (Eds). Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth.

Kikuchi, T. 1980. Faunal relationships in temperate seagrass beds. Pp. 153-173. In: Phillips, R.C. and McRoy, C.P. (eds). Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York.

Kikuchi, T. and Pérès, J.M. 1977. Animal communities in seagrass beds : a review. Pp. 147-193. In: McRoy, C.P. and Helfferich, C. (eds). Seagrass ecosystems : a scientific perspective. Marcel Dekker, New York.

Kirkman, H., Humphreys, P. and Manning, R. 1991. Macrofaunal assemblages of seagrasses and bare sand in Princess Royal Harbour and King George Sound, Albany, south-western Australia. Pp. 533-563. In: Wells, F.E., Walker, D.I., Kirkman, H. and Lethbridge, R. (Eds). Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth.

Lenanton, R.C.J., 1977. Aspects of the ecology of fish and commercial crustaceans of the Blackwood River estuary, Western Australia. Fisheries Research Bulletin, Western Australia 19: 1-72.

Lenanton, R.C.J., 1978. Fish and exploited crustaceans of the Swan-Canning estuary. Department of Fisheries and Wildlife, Western Australia, Report No. 35: 1-36.

Lenanton, R.C.J. and Caputi, N. 1989. The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. Journal of Experimental Marine Biology and Ecology 128: 165- 176.

Lenanton, R.C.J., Robertson, A.I., and Hansen, J.A. 1982. Nearshore accumulations of detached macrophytes as nursery areas for fish. Marine Ecology-Progress Series 9: 51-57.

Lewis, F.G. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrata. Marine Ecology-Progress Series 19: 101-113.

Lubbers, L., Boynton, W.R. and Kemp, W.M. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology- Progress Series 65: 1-14.

Mann, K.H. 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnology and Oceanography 33: 910-930.

Nelson, W.G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Marine Ecology-Progress Series 5: 141-149.

Nowell, A.R.M. and Jumars, P.A. 1984. Flow environments of aquatic benthos. Annual Review of Ecology 15: 303-328.

Orth, R.J., Heck, K.L. and van Montfrans, J. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7(4A): 339-350.

Pearson, T.H., and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review 16: 229-311.

Poore, G.C.B. 1982. Benthic communities in the Gippsland Lakes, Victoria. Australian Journal of Marine and Freshwater Research 33: 901-915.

Poore, G.C.B. and Rainer, S.F. 1979. A three-year study of benthos of muddy environments in Port Phillip Bay, Victoria. Estuarine and Coastal Marine Science 9: 477-497.

Rainer, S.F. and Fitzhardinge, R. 1981. Benthic communities in an estuary with periodic deoxygenation. Australian Journal of Marine and Freshwater Research 32: 227-243.

Sergeev, V.N., Clarke, S.M. and Shepherd, S.A. 1988. Motile macrofauna of seagrasses, *Amphobilis* and *Posidonia*, and unvegetated sandy substrata in Holdfast Bay, South Australia. Transactions of the Royal Society of South Australia 112: 97-108.

Spies, R.B., Hardin, D.D. and Toal, J.P. 1988. Organic enrichment or toxicity? A comparison of the effects of kelp and crude oil in sediments on the colonization and growth of benthic infauna. Journal of Experimental Marine Biology and Ecology 124: 261-282.

Sprules, W.G. 1972. Effects of size-selective predatory and food competition on high altitude zooplankton communities. Ecology 53: 375-386.

Walker, D.I., Hutchings, P.A. and Wells, F.E. 1991. Seagrass, sediment and infauna - a comparison of *Posidonia australis, Posidonia sinuosa* and *Amphobilis antarctica* in Princess Royal Harbour, south-western Australia. I. Seagrass biomass, productivity and contribution to the sediments. Pp. 597-610. In: Wells, F.E., Walker, D.I., Kirkman, H. and Lethbridge, R. (Eds). Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth.

Wells, F.E., Rose, R.A. and Lang, S. 1985. An analysis of benthic marine invertebrate communities in subtidal seagrass and sand habitats in Shark Bay, Western Australia. Records of the Western Australian Museum 12: 47-56.

Whitlach, R.B. 1981. Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit- feeding species diversity. Journal of Experimental Marine Biology and Ecology 53: 31-45.

Wilson, W.H. 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. Journal of Experimental Marine Biology and Ecology 132: 221- 245.