



## The production and trophic ecology of shallow-water fish assemblages in southern Australia

### II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria

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#### Abstract

A total of 5113 fishes belonging to 91 species was collected from seagrass and unvegetated habitats at Western Port for dietary analysis between August 1989 and November 1990, with 720 animals having empty guts. None of the common species was found to have a highly specialised diet. Crustaceans were the dominant component in the diets of the majority (69%) of the 88 species with non-empty guts, with five species (a girellid, a mugilid, a monacanthid and two gobiids) consuming large amounts of algal material, and only one species [the garfish *Hyporhamphus melanochir* (Valenciennes)] ingesting seagrass in any quantity. In general, dietary differences between juveniles and adults of a species were as great as dietary differences between fish belonging to different species when at the same body size. Amongst the crustacean feeders, diets generally changed from predominantly copepods to predominantly peracarids (amphipods, isopods and mysids) at  $\approx 0.1$  g wet body weight, and from predominantly peracarids to predominantly crabs and shrimps at  $\approx 100$  g. Across the range of species examined, there was a close relationship between the size of ingested prey and fish biomass. Prey length averaged 7.5% of predator length. The dominant species in gillnet catches, the mullet *Aldrichetta forsteri* (Cuvier & Valenciennes), possessed an unusual diet because prey were smaller than for other fishes of the same body size and large quantities of algal material were also consumed.

Similar trophic pathways leading to fishes were found in different habitats, with the major linkages being from benthic microalgae and detritus through epifaunal crustaceans to the smaller fishes. The major predators of small fishes were locally-resident species, the rock flathead *Platycephalus laevigatus* Cuvier & Valenciennes in seagrass beds and the sand

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flathead *Platycephalus bassensis* Cuvier & Valenciennes at unvegetated sites. Crustaceans supplied most of the dietary intake for the small fish communities at all sites, with molluscs and polychaetes also important but supplying >25% of food consumed at only two sites. When daily rates of consumption were compared with daily production of food, the production of crustaceans >1 mm sieve size was calculated to be all consumed by fish. The production of the non-crustacean benthos was an order of magnitude higher than that consumed by fish predators. These results indicate that the availability of high quality crustacean prey may limit the production of fishes, and that fishes are likely to compete diffusively for crustacean prey. Additional support for this hypothesis is provided by the observations that the condition of seagrass-associated fish declined, and mortality rates were high, during the autumn season when total fish consumption could not be supported by crustacean production.

**Keywords:** Australia; Consumption; Diet; Fish; Seagrass

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## 1. Introduction

A question of fundamental importance for ecologists is whether communities are limited by a lack of food resources, as would inevitably occur if other processes do not intervene (Malthus, 1966), or whether recruitment failure, predation, competition for non-food resources or environmental-induced catastrophes occur with such frequency that communities rarely reach their food resource limits. Biologists in different fields of fish ecology vary in their attitude towards this question. While biologists working on freshwater systems spend considerable effort trying to distinguish bottom-up from top-down processes (McQueen et al., 1989), marine biologists rarely discuss the importance of food limitation to fish assemblages for contradictory reasons. Correlations between fish production and nutrient enrichment seem so pervasive at mesoscales to fishery biologists and modellers dealing with pelagic stocks that a causal relationship between fish production and food (generally diatom) production is widely assumed (see, e.g. Mann, 1993; although for a contrary opinion see Branch et al., 1987). In other fields, competition for food resources is neglected because of the widespread perception that it is of trivial importance in structuring fish assemblages compared with recruitment, predation, stochastic events and behavioural interactions. For example, in a review of studies dealing with the factors influencing coral reef fish populations, Doherty & Williams (1988) found little evidence for interference competition amongst settling fishes, leading them to suggest that competition is not a strong structuring force; they neglected to consider whether exploitative competition for food is important, although they recognized that very high mortality of fishes occurs immediately after settling on reefs, and that on reefs where fishes are experimentally removed then numbers quickly recover to asymptotic levels. While major differences may exist in the importance of food limitation to fishes in pelagic, reef and soft-sediment habitats, as is suggested by the different approaches of workers in these systems, any such

differences should be explicitly recognised and documented, particularly with reference to spatial scale (see Menge, 1992).

In this study, we investigate the importance of food resources to fishes in seagrass and soft-sediment habitats by quantifying the production of food and relating this to the consumption and production of the local fish community. If food production is much greater than total community consumption by fishes (as postulated by Adams, 1976), then fish consumption should lead to little change in prey availability, and exploitative competition is unlikely. On the other hand, if food production approximately equals consumption by fishes (as postulated by Brook, 1977), then a major increase in fish numbers could not be supported by the resource base, and exploitative competition is probably occurring. To calculate production and consumption, we use the techniques described in Edgar (1990), Edgar & Aoki (1993) and Edgar & Shaw (1995), which enable the size-structure and production of invertebrates and fishes to be estimated with relatively little logistic effort, and by using a new method for rapidly quantifying gut contents.

In addition to the major aim of relating fish consumption to benthic production, this study also investigates the major characteristics of fish diets in seagrass and unvegetated habitats. In particular, we were interested in determining whether the substantial loss of seagrass that has occurred in Western Port during the past two decades (Edgar et al., 1994) has led to major changes in trophic pathways leading to commercial fish species. While the presence of seagrass possibly adds an extra trophic resource to the base of the food web and increases fish production through enhanced food availability (Lubbers et al., 1990), little evidence is available to support or refute this hypothesis.

## **2. Methods**

Sites and sampling methods used for the collection of fishes for dietary analyses are described in Edgar et al. (1994) and Edgar & Shaw (1995). The diets of all fishes collected during the Western Port study were examined (Edgar & Shaw, 1995), except when more than 12 individuals of a species were collected from a site on one sampling date. In these cases, 10 individuals ranging in size from the smallest to the largest were subsampled for gut content analysis.

In the laboratory, foreguts were removed and the contents observed under a dissecting microscope. Gut contents were examined within 2 days of capture for formalin-preserved fish collected by seine and within 24 h for chilled specimens collected by gillnet. The wet weight of foreguts from gillnet collected fish was also measured before and after contents had been removed in order to determine directly the total wet weight of prey items.

In order to compare directly the size-distribution of ingested prey with invertebrate size-classes recorded during the benthos sampling program (i.e. the densities of animals retained by nested sieves of different mesh size, Edgar et al., 1994), both the sieve size-class and identity of individual prey were recorded. Animals were allocated to sieve size-classes by eye using a graticule in the

microscope eyepiece and a reference collection consisting of a mixture of species retained by different-sized sieves. In the case of damaged molluscs, the size of the original animal, and its sieve size-class, was estimated on the basis of shell fragments. The standard length of fishes and carapace lengths of decapods in stomachs were measured when intact; in cases where fishes had been largely digested, the length of the missing sections were visually estimated. The percent occurrence of seagrass, macroalgae, 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 15 major food categories: (1) epifaunal crustaceans, (2) infaunal crustaceans, (3) planktonic crustaceans, (4) epifaunal molluscs, (5) infaunal molluscs, (6) pelagic molluscs, (7) epifaunal polychaetes, (8) infaunal polychaetes, (9) other mobile epifaunal invertebrates, (10) other infaunal invertebrates, (11) demersal fishes, (12) pelagic fishes, (13) sessile invertebrates, (14) algae, (15) seagrass. Infaunal and epifaunal species were distinguished on the basis of the taxonomic categories described in Table 1 of Edgar (1994). The percent occurrence by biomass of these categories in stomachs was determined for each fish by firstly estimating the biomass of mobile invertebrates in guts using their estimated sieve-sizes and the biomass/sieve-size relationships described in Edgar (1990), and by calculating the biomass of ingested fishes and decapods using length/weight relationships calculated from seine-netted fish and decapods from Western Port. These biomass data were combined with the estimated percent occurrence of plants and sessile animals. For example, if epifaunal crustaceans in a gut 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 were calculated to comprise 40, 20 and 40% of the gut contents, respectively. The crustacean component of the diet was further partitioned into different sieve size-classes using information on the numbers and biomass of benthic crustaceans in different sieve size-classes consumed by each fish.

The general relationship between the size of fishes collected from Western Port and mean prey size was determined by initially calculating regression equations relating fish biomass to mean biomass of prey in guts for each of the 48 most abundant fish species (i.e. those with  $\geq 10$  individuals collected). Using these regressions, the mean prey biomass was estimated for each fish species at the median fish size, and these data used to calculate a general regression relating predator to mean prey biomass for the 48 fish species. General relationships between fish biomass and the range in biomass of prey ingested were also calculated. This was done using data on the median biomass of each abundant fish species and the maximum and minimum biomasses of individual items ingested in the pooled gut contents of the five captured fish closest to this median size. In this analysis it was necessary to pool groups of five fish 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 fish having a single prey only in their guts; such animals provided no indication of the range in prey size

Table 1

Mean daily ration (daily consumption/fish biomass) of small fish species as estimated in the Western Port study by Robertson (1984). These data were used for individual fish species

Species	Daily ration (%)
<i>Tetractenos glaber</i>	3.39
<i>Aldrichetta forsteri</i>	2.22
<i>Gymnapistes marmoratus</i>	0.75
<i>Rhombosolea tapirina</i>	1.05
<i>Heteroclinus perspicillatus</i>	1.06
<i>Arenigobius frenatus</i>	3.86
<i>Sillaginodes punctatus</i>	2.94
<i>Diodon nichthemerus</i>	5.06
<i>Favonigobius lateralis</i>	2.26

Mean daily ration of small fish species. These data were combined with those given above to calculate the general mean daily ration for small fishes (=3.1%), a value used in calculations of fish consumption for all species in Western Port other than those listed above

Species	Daily ration (%)
<i>Atherinasoma presbyteroides</i> <sup>1</sup>	1.49
<i>Atherinosoma microstoma</i> <sup>1</sup>	1.69
<i>Nesogobius</i> sp. <sup>2</sup>	3.08
<i>Neoodax balteatus</i> <sup>2</sup>	2.69
<i>Acanthaluteres spilomelanurus</i> <sup>2</sup>	3.40
<i>Atherina breviceps</i> <sup>3</sup>	4.93
<i>Clinus spatulus</i> <sup>3</sup>	5.63
<i>Gilchristella aestuaria</i> <sup>3</sup>	5.66
<i>Psammogobius knysnaensis</i> <sup>3</sup>	4.28
<i>Syngnathus acus</i> <sup>3</sup>	3.76
<i>Caffrogobius multifasciatus</i> <sup>3</sup>	3.48

References shown by superscript are 1: Robertson (1984), 2: Robertson & White (1986), 3: Bennett & Branch (1990).

that 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 total daily consumption by fish of different faunal groups, for example crustaceans ( $C$ ), at the twelve Western Port sites was estimated for each sampling period as:

$$C = \sum_{i=1}^n \frac{W_i \cdot 0.22 \cdot R_i \cdot P_i}{N \cdot H}$$

where  $W_i$  is the wet weight (g) of fish  $i$ ,  $n$  is the total number of fish collected from the site during that quarterly sampling period,  $R_i$  is the estimated daily ration of fish  $i$ ,  $P_i$  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<sup>2</sup> (generally = 20 for seagrass and unvegetated sites and 9 for channel sites, but see Table 5 in Edgar & Shaw,

1995, for other values for common fishes), and 0.22 is the wet weight/AFDW conversion factor. For estimates of the total consumption rates of benthic crustaceans in different size-classes, an additional parameter  $S_i$ , the percentage of the total biomass of crustacean prey belonging to each size-class, was incorporated into the numerator of this equation. The daily ration ( $R$ ) used was that calculated for common fish species in Western Port by Robertson (1984) (see Table 1). Fish species not investigated by Robertson (1984) were assumed to have consumed 3.1% of their body weight per day, the mean value calculated from estimates for 20 small fish species described in the studies by Robertson (1984), Robertson & White (1986) and Bennett & Branch (1990). The diet of each sampled fish whose guts content was not investigated was assumed to be similar to the individual fish of the same species with closest body length in the same season. Calculations of annual consumption were made using the mean daily rate of consumption in each of the four seasons.

### 3. Results

#### 3.1. Gut fullness

The wet weight of gut contents (WW), as directly determined from the difference between the full weight and empty weight of stomach, was initially compared with the estimated AFDW of stomach contents (AFDW), as calculated using the novel method of allocating prey to sieve-size categories. A total of 1164 fish collected by gillnet with non-empty guts were used in this analysis. The regression relating these variables was calculated to be:

$$\ln \text{ AFDW} = -2.86 (\pm 0.20) + 0.99 (\pm 0.02) \ln \text{ WW} \\ (r^2 = 0.58, p < 0.001, \text{ SD of residuals} = 0.96).$$

The exponent in this equation was very close to and not significantly different from 1, indicating that AFDW, as calculated using the new method, was directly proportional to WW, as calculated using the volumetric method ( $\text{AFDW} = 0.53 \times \text{WW}$ ). The difference between these measurements reflects the conversion from AFDW to wet weight ( $\text{AFDW} \approx 0.22 \times \text{wet weight for fish}$ ) and the mean degree of digestion ( $\approx 40\%$  of original weight) of gut contents.

#### 3.2. Diets of fishes

Amongst the 5113 fish collected for dietary analysis from Western Port, 720 animals had empty guts. Crustaceans were the predominant food item in 61 of the 88 (69%) fish species collected with non-empty guts, with eight species feeding mainly on other fish, seven on molluscs, six on polychaetes and one (the boarfish

*Pentaceropsis recurvirostris*<sup>1</sup>) feeding on ophiuroids. None of the animals sampled consumed nematodes in other than trivial quantities. The diets of the 57 most common species are shown in Fig. 1. Only five of the examined species ingested more algae than other dietary components (*Aldrichetta forsteri*, *Acanthaluteres spilomelanurus*, *Pseudogobius olorum*, as shown in Fig. 1, and *Tasmanogobius gloveri* and *Girella tricuspidata*, not shown), with seagrass ingested in large quantities by a single species only (*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 syngnathids and juvenile *Hyporhamphus melanochir*) on plankton, and only one (a goby) on infauna.

The fish predators examined can be divided into two groups, those predominantly feeding on open-water fishes, and those feeding on the smaller demersal fishes (Table 2). The major predators of clupeoid and atherinid fish were the pelagic fish species *Arripis trutta*, *A. truttacea* and *Pomatomus saltator*. The major species feeding on the demersal fishes were locally-resident flathead, *Platycephalus laevigatus* in seagrass habitats and *Platycephalus bassensis* in unvegetated habitats.

Classification of the 57 common fish species by diet indicates that the fish assemblage in Western Port can be subdivided into six trophic categories (see Fig. 1). The major group (Group C in Fig. 1) consisted of 43 species that primarily consumed benthic crustaceans, with one species in this group, *Haletta semifasciata*, also consuming large quantities of epifaunal molluscs. The next largest groups consisted of nine fishes that primarily ingested planktonic crustacea (Group F), followed by seven species with a large component of seagrass or sessile animals in their diet (Group D). Other groups consisted of fish predators (Group A; four species), polychaete feeders (Group B; two species) and molluscivores (Group E; two species).

None of the fishes examined possessed a highly specialised diet, with the possible exception of *Pentaceropsis recurvirostris* which was only collected twice but both animals had fed solely on ophiuroids. Two fishes of the same body mass but belonging to different species were generally more likely to ingest similar prey species than juvenile and adult fish of a single species. Amongst the crustacean feeders, species tended to shift their diets from copepods to amphipods and isopods at  $\approx 0.1$  g wet weight, and to crabs and shrimps at  $\approx 100$  g weight (Fig. 2). The major exception to this pattern was the yellow-eyed mullet *Aldrichetta forsteri*, the most abundant species collected by gillnet. Mullet consumed amphipods when at a size where other species were feeding on decapods, and copepods when at a size where other species were feeding on amphipods.

A close relationship was detected between the log mean wet weight of fish ( $\bar{B}_f$ , measured in g) and the log mean AFDW of ingested prey ( $\bar{B}_p$ , mg) for the

<sup>1</sup> Taxonomic authorities for fishes are listed in Edgar & Shaw (1995), this issue, pp. 53–81.

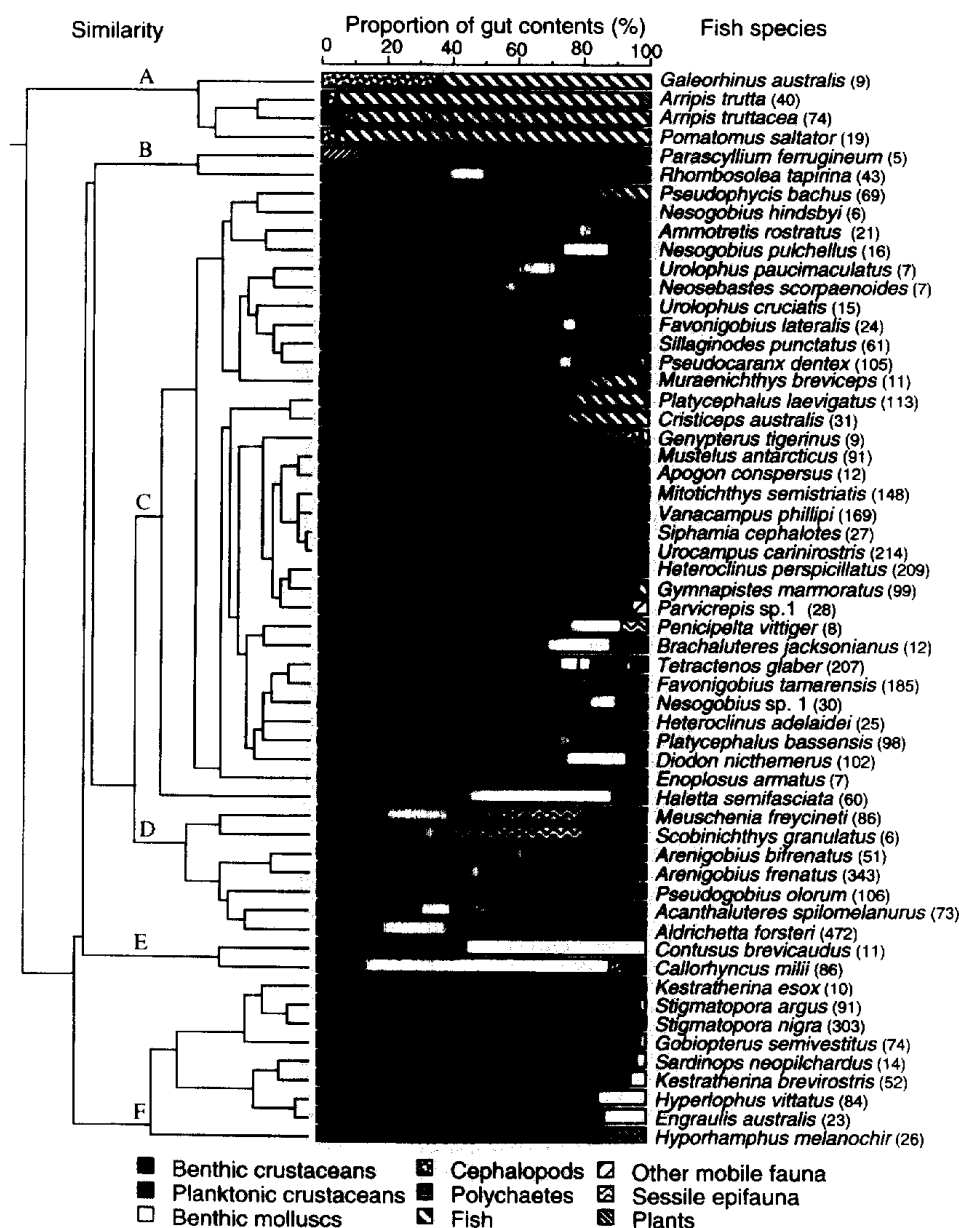


Fig. 1. Proportional abundance of major dietary components in fish guts. Fish species have been classified by diet using cluster analysis based on the mean proportion of total biomass of different dietary components. Similarities between pairs of species were calculated using Euclidean distance which were then grouped using average linkage. Number of guts analysed are shown in parentheses after species name.

abundant species ( $\log \bar{B}_p = -2.40 + 0.98 \times \bar{B}_f$ ,  $R^2 = 0.77$ ,  $n = 48$ ,  $p < 0.001$ ; Fig. 3). The corresponding relationship between gape height and prey biomass also had a high correlation coefficient, albeit slightly lower ( $R^2 = 0.72$ ), and the relationship between fish total length and prey biomass was less well defined again ( $R^2 = 0.61$ ) because very small prey were ingested by long narrow fishes such as pipefish. The



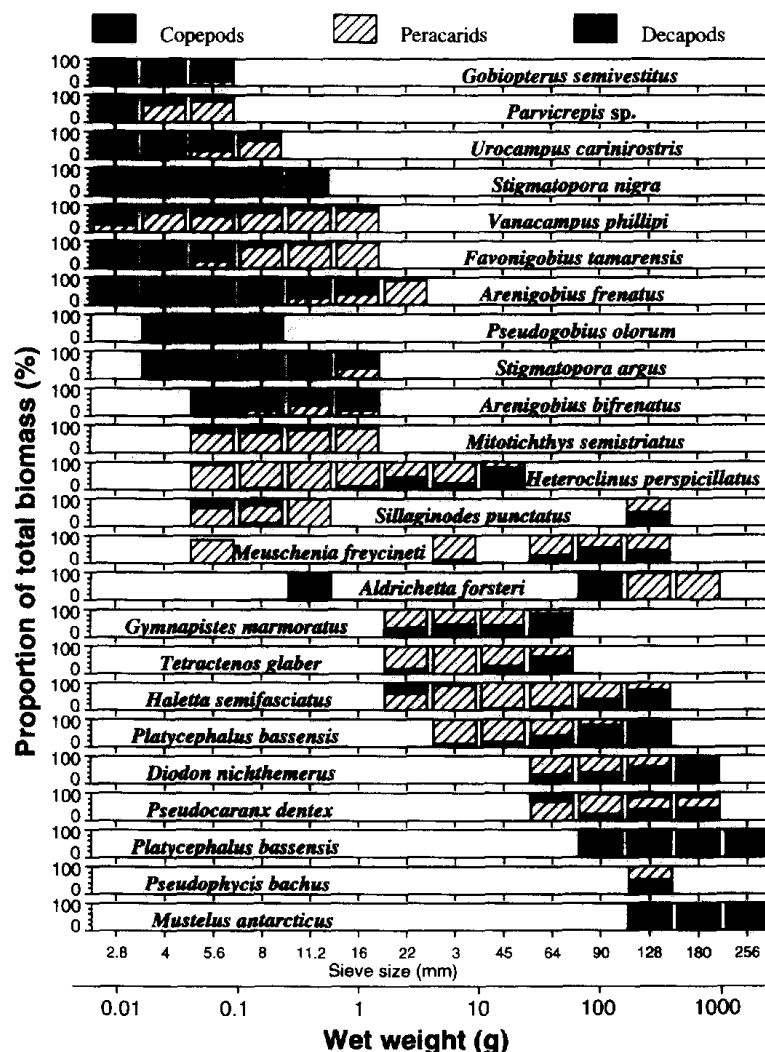


Fig. 2. Percent of total crustacean biomass in the guts of fishes of different size that consisted of copepods, peracarids (amphipods, isopods, tanaids, cumaceans and mysids) and decapods. Size is expressed using two different scales, wet weight of fishes and sieve size-class. The latter represents the measured range in biomass of benthic animals retained by sieves of different mesh size (Edgar, 1990) and has been included to allow comparisons with benthic invertebrate data (see, e.g. Fig. 8 in Edgar et al., 1994; Edgar & Shaw, 1995).

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 consumed prey at an estimated AFDW of 8.27 mg, which, if body mass is proportional to length cubed and AFDW is 22% of fish 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

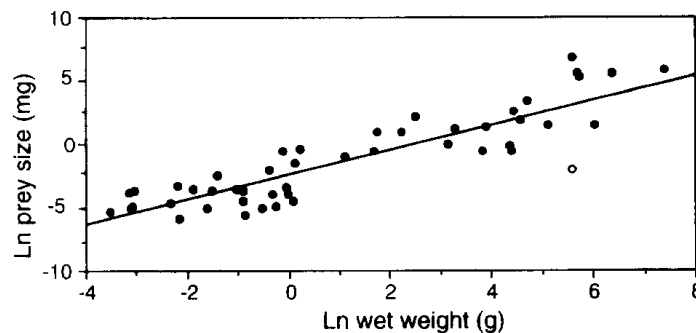


Fig. 3. Relationship between log wet weight of fishes (g) and log mean ash-free dry weight of prey (mg) in guts for 48 fish species collected in Western Port. Data point for yellow-eyed mullet is shown by open circle.

the yellow-eyed mullet (see Fig. 3). This species consumed much smaller prey than would be expected from the general regression; fish weighing 100 g 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 fish and the log maximum ( $U$ ) and minimum ( $L$ ) AFDW of ingested prey ( $\log U = -0.71 + 1.04 \bar{B}_f$ ,  $R^2 = 0.74$ ,  $n = 45$ ,  $p < 0.001$ ;  $\log L = -4.52 + 0.78 \times \bar{B}_f$ ,  $R^2 = 0.72$ ,  $p < 0.001$ ). Although the regression coefficient in the fish weight/minimum 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).

### 3.3. Trophic relationships between fish and benthos

Estimates of the rate of annual consumption of crustaceans, polychaetes and molluscs by small fish at each site are shown in Table 3. Crustaceans, predominantly epifaunal species, were the major food source for fish at all sites. Sponges, bryozoans and ascidians contributed substantially to total fish consumption at only one site, Peck Point seagrass, a site where a high biomass of sessile animals was attached to seagrass plants. Seagrass was also ingested at a relatively high level at this site, probably largely as an incidental item attached to the sessile animals. Algae was consumed in moderate quantities at the other two primary seagrass sites, Rhyll and Tooradin.

Between 7 and 48% of the total production of benthos >125 mm sieve size (see Edgar et al., 1994) was consumed by fishes at the sites investigated (Table 4). The proportion of secondary production consumed by fishes was nearly twice as high in the primary channel habitats ( $\approx 31\%$ ) as in seagrass and shallow unvegetated habitats ( $\approx 15\%$ ). The proportion of crustacean production consumed by fishes was extremely high at all sites (an average of 90% for the primary sites), with

Table 3  
Estimated annual consumption ( $\text{g AFDW} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) of different faunal groups by small fishes at the sites studied in Western Port

Habitat	Dietary group										
	Crustacea			Mollusc	Polychaete	Fish	Sessile fauna	Algae	Scagrass	Other	Total
	Epifauna	Infauuna	Plankton								
Peck Point seagrass	12.9	0.6	1.1	1.9	2.5	0.4	2.3	0.5	0.9	0.1	23.2
Rhyll seagrass	16.2	*	0.6	1.9	3.4	*	*	3.4	*	0	25.4
Tooradin seagrass	9.1	*	0.1	1.3	1.7	0.4	*	4.6	0.4	*	17.6
Mean primary seagrass	12.7	0.2	0.6	1.7	2.5	0.3	0.8	2.8	0.4	*	22.1
Peck Point unvegetated	3.1	0.1	0.1	0.3	1.1	0.5	*	*	0	0.1	5.3
Rhyll unvegetated	7.8	*	*	1.6	1.1	0.1	0.1	2.1	0	0.2	13.1
Tooradin unvegetated	15.0	0.2	0.1	1.1	1.3	0	0	0.4	0	*	27.7
Mean primary unvegetated	8.6	0.1	0.1	4.2	1.2	0.2	0.1	0.8	0	0.1	15.4
Peck Point channel	11.2	0.1	*	*	2.9	1.6	*	*	*	1	16.9
Rhyll channel	16.7	1.6	*	12	6.6	0.3	0	0	0	0	37.4
Tooradin channel	8.9	0.8	*	0.6	1.2	0	0	0.2	0	*	11.8
Mean primary channel	12.2	0.8	*	4.3	3.6	0.6	*	0.1	*	0.3	22.0
Cowes Bank seagrass	20.0	0.1	1.4	0.5	1.6	0.9	*	0.2	0.1	*	24.7
Cowes Bank unvegetated	4.2	2.3	*	0.6	0.6	0	*	*	0	*	7.8
Loelia Shoal	3.2	0.8	0	*	0.1	0	0	0	0	0	4.1

\* indicates dietary groups that were ingested in quantities  $<0.05 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

Table 4

The percentage of the total annual production of benthos (>125-mm sieve size; see Figs. 8 and 9 in Edgar et al., 1994) that is consumed by small fishes

Habitat	Proportion consumed (%)			P/C (%)
	Total	Crustacea	Other	
Peck Point seagrass	11	49	3.3	16.4
Rhyll seagrass	16	97	4.3	14.6
Tooradin seagrass	10	28	3.5	22.5
Mean primary seagrass	12	58	3.7	17.8
Peck Point unvegetated	7	34	2.5	12.7
Rhyll unvegetated	8	69	2.2	13.5
Tooradin unvegetated	37	156	19.1	8.3
Mean primary unvegetated	17	86	7.9	11.5
Peck Point channel	24	90	7.7	10.1
Rhyll channel	50	141	30.5	6.9
Tooradin channel	20	147	3.6	12.7
Mean primary channel	31	126	13.9	9.9
Cowes Bank seagrass	45	174	5.5	13.7
Cowes Bank unvegetated	25	81	5.4	10.9
Loelia Shoal	15	56	0.5	17.1

Total benthic invertebrates, crustacean and non-crustacean taxa (other) are listed separately. Also shown are fish production/fish consumption ratios (P/C), which indicate the proportion of food consumed that is incorporated into fish biomass for small-fish assemblages in different habitats.

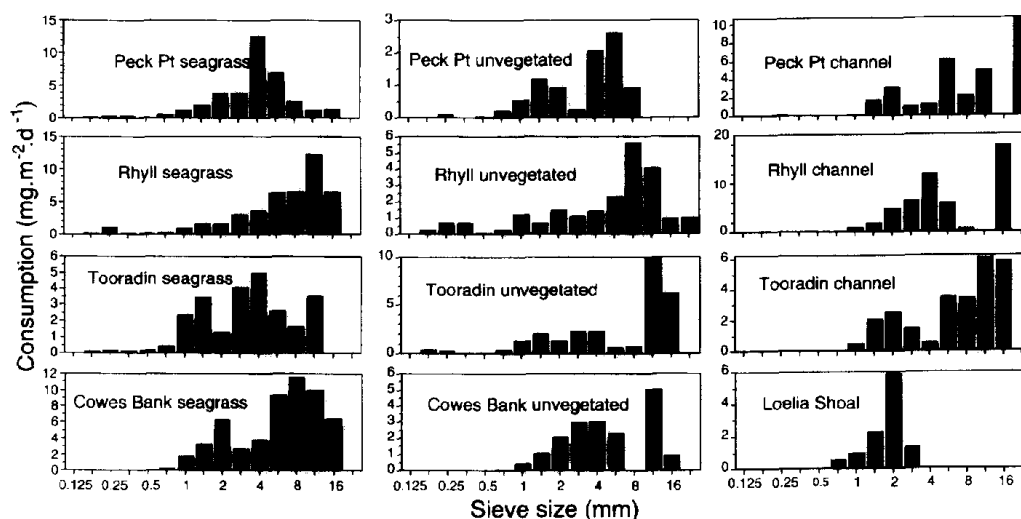


Fig. 4. Mean estimated rates of consumption by the small-fish assemblage of crustaceans in different sieve size-classes at different sites.

other major faunal groups contributing in only a minor way to community fish consumption (generally <10%).

Consumption of crustaceans by small fishes was concentrated on prey in the 1 to 16 mm sieve-size range (Fig. 4), with highest consumption in most habitats in the 4 to 11.2 mm sieve-size range. The mean size of animals ingested at Loelia Shoal was, however, much smaller than for other sites, presumably because very few prey >5.6 mm sieve size were present at that site (Edgar et al., 1994).

When the production of crustaceans (Fig. 9 in Edgar et al., 1994) is compared with rates of macrocrustacean consumption by small fishes, all crustacean production >1 mm sieve-size was estimated to be cropped by fishes (Fig. 5) but very little of the production of crustaceans <0.5 mm sieve-size was consumed. No clear differences in the size-range of ingested prey were evident between fish assemblages associated with different habitats (Fig. 5).

Within the seagrass habitat, fish consumption was lower than crustacean production in August and November (consumption/production = 86 and 50%, respectively), with the reverse situation occurring in February (198%) and May (133%). Estimates of the ratio of consumption to production can exceed 100% in these calculations because consumption estimates do not indicate real rates of consumption but the rates of consumption for fishes of a given size as averaged over a year. Fishes presumably ingest prey at rates higher than these averages in spring to counterbalance the relatively low rates possible in autumn. In unvegetated and channel habitats there were no clear seasonal trends in the ratio of fish consumption to production.

Associated with the seasonal change in available food in seagrass habitat was a change in the condition of a number of fish species. Six of the eight most common seagrass-associated fishes were found to have poorest condition in May (Fig. 6), while for the other two species, *Mitotichthys semistriatus* and *Heteroclinus perspicillatus*, May was the second poorest month for fish condition. The four

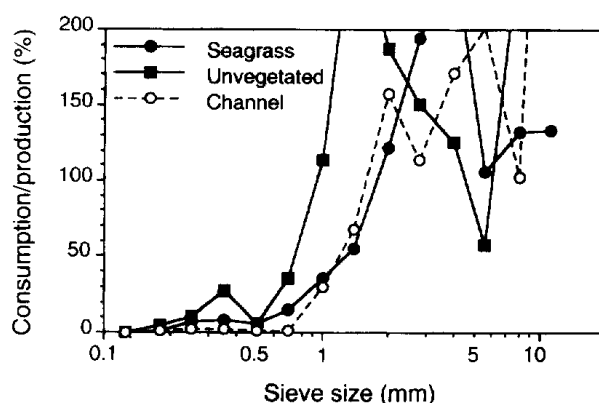


Fig. 5. Mean ratios of consumption of crustaceans by fishes/crustacean production for different sieve size-classes in different habitats. Standard error bars for different habitats overlap at all size-classes so are not shown, nor are values greater than 200% that result from disproportionately low denominators in the calculated ratio.

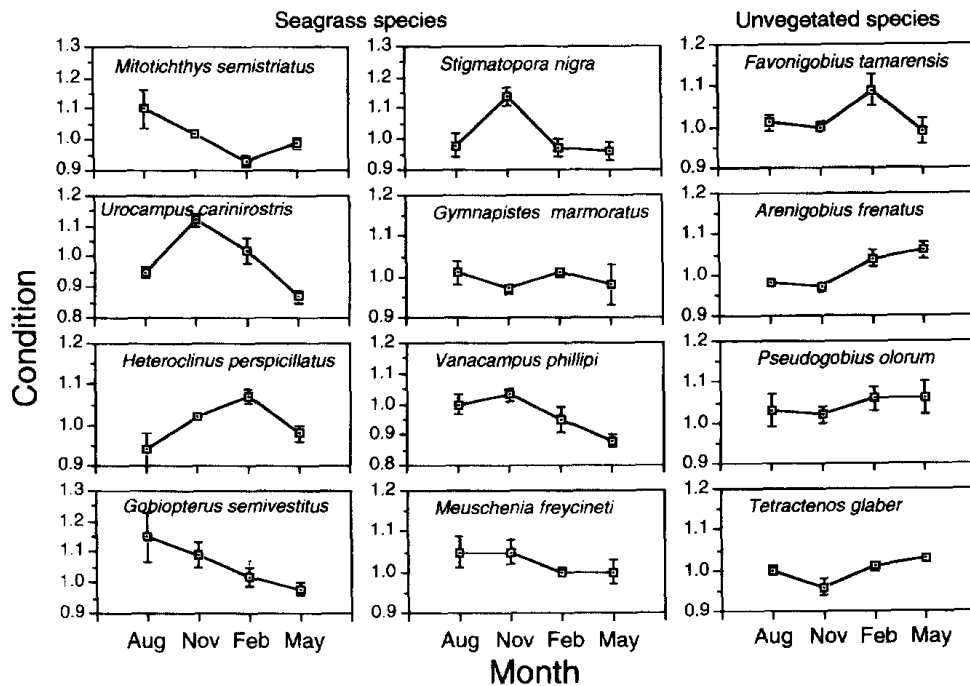


Fig. 6. Condition of the twelve most common species collected by seine in different seasons. Condition was calculated for each fish as  $WW/WW$ ; where  $WW$  is the wet weight of the fish and  $WW$  is the mean wet weight of fish of the same length as determined from the general regression equation relating fish length to wet weight for all fish of that species collected during the study. Standard error bars are shown.

most common fishes in unvegetated habitats did not show consistent seasonal trends (Fig. 6).

## 4. Discussion

### 4.1. Gut content analysis

Our method of gut analysis has several advantages over the more commonly used volumetric methods: (1) data include information on the size-distribution of ingested prey, and are obtained in a form that is directly comparable to data obtained using benthos sampling techniques, (2) data can be readily converted from abundance into biomass by using appropriate scaling factors (Edgar, 1990), and (3) the new procedure is extremely rapid, with most fish taking  $\approx 10$  min to process. Procedures that lack our subjective step of allocating animals to size-class by eye will be more accurate than our method per fish, but at the cost of considerable extra sorting time or the missing of rarer prey items. Because of the variability in gut contents between individual animals, a more accurate assessment of diet should result from studying the gut contents of, for example, 10 individuals

than from five individuals whose gut contents were each determined slightly more accurately.

The method of gut content analysis used here differs only slightly from the method described by Berg (1979) where animals are allocated to sieve size-classes by direct sieving and counting rather than by eye. Direct sieving is more time-consuming and will result in the partial fragmentation of prey items, and the inadvertent allocation of broken and partially digested fragments to small sieve size-classes.

The major problem with the new procedure, as with other techniques, is its sensitivity to digestion and gut passage rates differing amongst prey species. The importance of prey with indigestible structures and slow passage rates may be considerably overestimated. If, for example, mollusc fragments are detectable for 3 times as long in fish guts as crustacean fragments, then the biomass of molluscs in stomachs will be overestimated by a factor of 3 compared with crustacean biomass. At present, the significance of this bias is impossible to assess as we have not conducted studies of passage rates of individual prey items.

#### 4.2. Diet and feeding of fishes

The fish assemblage in Western Port showed similar general dietary patterns to fish assemblages elsewhere. In this and all other studies of southern Australian seagrass fish communities (Burchmore et al., 1984; Rigby, 1984; Robertson, 1984; Robertson & White, 1986; Scott et al., 1986), and in the great majority of studies worldwide (Kikuchi, 1974; Pollard, 1984; Huh & Kitting, 1985; Whitfield, 1988), crustaceans were found to be the major item in fish diets. Bell & Harmelin-Vivien (1983) found that crustaceans were the most important food type for 68% of species in a Mediterranean seagrass bed, compared to 69% in Western Port. Furthermore, as at most other sites (Klumpp et al., 1989), few fish species were capable of directly utilizing plant material. However, while the number of omnivorous species was low in Western Port, several species in this trophic category were abundant, including the dominant species in gillnet catches, *Aldrichetta forsteri*.

Most fishes had broadly overlapping diets at the level of prey species, with locally common species of amphipod ingested by many of the small fish species present at each site. For example, the amphipods *Paradexamine churinga* Barnard and *Tethygeneia* sp. were consumed by the majority of fishes at seagrass sites (Edgar & Shaw, unpubl. data). No evidence was found for a shift in diet between closely related fish species to avoid competition. The variation in diet within sibling species pairs (*Arripis* spp., *Stigmatopora* spp. and *Arenigobius* spp.), for example, was very low (Fig. 3), and no greater than the variation within each of these species at different sites or on different sampling occasions. Because species possessed such widely overlapping diets, we have not calculated the dietary overlap between pairs of species, as is often done in studies of fish (e.g. Robertson, 1980; Huh & Kitting, 1985). If fishes are competing diffusively for limited resources, as suggested below, then each of the dietary components

ingested by a fish may also be a food resource for several other species. Therefore, although a species may have low pairwise dietary similarities with all other locally-resident species, this does not preclude competition for food because the assemblage of other species may together utilise virtually all of its prey.

Despite the shallowness of Western Port, the extent of coupling between benthic and open-water food webs was relatively low. Most of the larger pelagic fishes fed on smaller planktivorous fishes (Table 2), and these in turn fed primarily on holoplanktonic prey. The larger bottom-dwelling fishes, on the other hand, mainly captured smaller demersal fishes and mobile epifaunal invertebrates, with the epifaunal invertebrates represented largely by grazers of periphyton or detritus (Zimmerman et al., 1979; Kitting et al., 1984; Morgan & Kitting, 1984; Howard et al., 1989). Only one common fish, the monacanthid *Meuschenia freycineti*, had a large fraction of the diet consisting of sessile suspension-feeding invertebrates, which in turn are linked to phytoplankton and the open-water food web.

The strongest coupling between benthic and open-water ecosystems was caused by pelagic trevally (*Pseudocaranx dentex*) feeding on benthic crustaceans, and by a considerable proportion ( $\approx 20\%$ ) of the diet of planktivorous clupeoids being supplied by meroplanktonic shrimp and crab larvae during summer. Counterbalancing this were the demersal pipefish *Stigmatopora nigra* and *Stigmatopora argus*, which obtained half their dietary intake from planktonic calanoid copepods.

#### 4.3. Sources of error in consumption estimates

Our estimates for total fish consumption in seagrass habitats ( $\approx 20 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) agree well with estimates made in an earlier study in Western Port conducted by Robertson (1984) ( $\approx 12 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ), particularly given that several of the smaller fish species (including all pipefishes) were excluded from the earlier study. The excess of crustacean consumption over crustacean production for some sites nevertheless indicates the presence of an error in our estimates. Cropping rates were excessively high in channel habitats, in the seagrass habitat at Cowes Bank and in the unvegetated habitat at Tooradin. At these sites, consumption rates were probably overestimated due to the presence of non-resident animals, such as fishes that had moved into channels after feeding elsewhere at high tide. This effect was particularly noticeable at the unvegetated Tooradin site, where very large numbers of the tetraodontid *Tetractenos glaber* were collected that had been feeding on seagrass-associated amphipods, isopods and decapods.

Another potential source of error is that the benthos sampling process may miss particular localised patches with very high densities of invertebrate prey. The total area of substratum sampled at each site was  $\ll 0.01\%$  of the total habitat area, consequently the presence of small patches (say 1% of the total area of substratum) with extremely high densities of invertebrates would be unlikely to be detected, resulting in an underestimation of mean prey estimates for the habitat. This source of error was indicated by the guts of some fishes collected in channel habitats containing high numbers of particular isaeid and ampeliscid amphipod

species that were rarely collected during benthic sampling. Such sampling biases are potentially large but are not often mentioned in the literature. In our study, they are most likely to bias the invertebrate data collected from the channel and, to a lesser extent, the unvegetated habitats; benthic samples collected from seagrass beds were relatively homogeneous (Edgar et al., 1994) so there is little likelihood that particular patches with extremely high densities of prey occurred there.

In contrast to this patchiness error, which will overestimate prey consumption rates, total fish consumption may be underestimated because of poor data on the consumption rates of the mullet *Aldrichetta forsteri*. Gillnet sampling indicated that mullet were abundant but must have largely evaded the seine net. Because they consumed many of the same species of harpacticoid copepod and amphipod as the small fishes used to calculate consumption rates, total fish consumption of benthos will be underestimated. Amongst the other larger fishes collected by gillnet, only the trevally *Pseudocaranx dentex* included a large proportion of grazing and detritivorous invertebrates in its diet.

Calculations of the consumption rates by shrimps and crabs of smaller invertebrates have also not been included in this study, consequently the consumption rates of fishes provided here cannot be used to estimate overall consumption rates by predators of benthos. While total consumption by small decapods may be large (Howard, 1984), most of the invertebrates ingested by decapods were <1 mm sieve size (G. Edgar, unpubl. data) so were largely outside the size range of the prey of fishes. Small decapods may well influence the total population size of crustaceans and molluscs in the 0.25 to 1 mm sieve size range.

#### 4.4. Trophic relations between fishes and benthic invertebrates

Small fishes in Western Port were estimated to consume  $\approx 20\%$  of the total production of meiofaunal and macrofaunal invertebrates. This estimate lies within the range of values calculated in the three previous studies of food consumption by small fish communities, where total consumption of epibenthic fishes (and in one case also decapods) was estimated to account for between 10 and 75% of benthic invertebrate production (Robertson, 1984; Möller et al., 1985; Bennett & Branch, 1990). These estimates were used to infer that an excess of benthic production is available to fishes, and that prey consumed by any fish will not greatly alter the availability of food for other animals, so the likelihood of competition for food resources is slight. However, when the production of animals that are inaccessible to small fishes because they occur infaunally or are of small size is removed from calculations, fishes are found to consume virtually all available benthic production. All of the production of macrobenthic crustaceans, the most important food resource, was calculated to be cropped by fishes in Western Port. A doubling in the numbers of fishes in the area could therefore only be supported by the benthos if fishes could either (1) increase their assimilation efficiencies so that growth and mortality rates were not affected by the decrease in ingestion rates, or (2) reduce their dependence on crustacean prey

by switching to other faunal groups. The first of these possibilities is unlikely, given the already high fish production/fish consumption ratios (Table 4) which would need to approach 30% if the total production of fish doubled with no increase in benthic production. Moreover, for fishes to maintain production when food intake is halved, assimilation efficiencies would need to more than double because the amount of energy required for respiration purposes would decline little when food intake decreased.

The likelihood that fishes can switch to non-crustacean prey types will depend largely on the species involved. Crustacean specialists such as *Mitotichthys semistriatus* are unlikely to be able to change diet, so their population numbers are probably limited in Western Port because of the restricted crustacean production available. Other species with broad diets, for example *Aldrichetta forsteri* and *Meuschenia freycineti*, can possibly switch to other groups. However, the absence of fishes with a purely herbivorous diet indicates that even the species that can ingest both plant and animal material probably require a certain fraction of animal material in their diets to compensate for the high C:N ratios of plants (see Klumpp et al., 1989). Interestingly, while few of the fish species in Western Port consumed algae in any quantity, three of the omnivorous species (*Aldrichetta forsteri*, *Arenigobius frenatus* and *Pseudogobius olorum*) were amongst the most abundant. Similar patterns have been found in other studies, with the most common fishes often having unusually broad diets (Bennett & Branch, 1990). The high densities of these species are possibly related to their diets because algal and low-quality animal supplements should allow populations to be less dependent on the limited crustacean production available. As well as ingesting a wide variety of prey, the mullet *Aldrichetta forsteri* also selected much smaller prey than other fish species with the same body size, so the dominance of this species in gillnet catches may also be due to mullet targeting the more productive invertebrates low in the food chain (i.e. grazing and detritivorous molluscs and peracarid crustaceans) rather than the carnivorous crabs and shrimps selected by other fish species of a similar body size.

All three previous studies that compared the production of benthos with the consumption of fish assemblages (Robertson, 1984; Möller et al., 1985; Bennett & Branch, 1990) were aimed at determining the importance of fishes in regulating benthic animal populations through predation, rather than the importance of benthic animals in influencing fish production through competition for limited food resources. Instead of studying either of these potential processes in isolation, the emphasis on patterns of faunal size-structure in this and the associated studies was largely intended to identify which of these two processes was predominant. If the distribution of invertebrates is independent of the distribution of fishes but fishes are dependent on benthic prey, then the graph describing fish consumption rates of different size crustacean prey (Fig. 4) should show high levels of consumption by fishes of prey at the size of modes in crustacean production (Fig. 9 in Edgar et al., 1994) because fishes are attracted to prey of that size (i.e. a positive correlation should be evident). Alternatively, if the distribution of fishes is independent of the distribution of benthic invertebrates but invertebrate

numbers are affected by fish consumption, then the graph describing fish consumption rates of different size crustacean prey (Fig. 4) should show high levels of consumption of prey at the size of depressions in crustacean production because fishes are removing prey of that size (i.e. a negative correlation should be evident). When the fish consumption and crustacean production plots are compared, there is no strong nor general relationship. Correlation coefficients relating fish consumption to crustacean production in the 1- to 8-mm sieve-size range, the size at which relationships should be strongest, are positive at six sites (maximum  $r = 0.70$  at Peck Point unvegetated) and negative at the other six (minimum  $r = -0.70$  at Cowes Bank unvegetated). This lack of a clear relationship can be interpreted in three ways: (1) fish consumption is independent of prey availability, (2) real patterns are not evident from the graphs because variance in the data is too high or the data are incomplete, or (3) there is a two-way interaction between fish consumption and prey availability. The first of these possibilities is unlikely because most crustacean production is consumed at the different sites, so fishes would be expected to have a large effect on the population dynamics of their prey species. We also consider the second of these possibilities unlikely, but recognize that the large number of approximations combined in calculations and the lack of information on the consumption rates of *Aldrichetta forsteri* will cause our estimates to include an unknown but possibly substantial error term (see Edgar & Shaw, 1995). Most of the error will, however, be systematic and should not affect the relative production or consumption rates of animals in one size-class compared to the adjacent size-classes. The most likely conclusion from a comparison of the fish consumption and crustacean production graphs is, therefore, that there is a two-way interaction, and that the production of benthos positively influences the production of fishes and that the production of fishes negatively influences the benthos.

It has been postulated in several other studies that the production of grazing and detritivorous invertebrates is restricted by competition for limited food (Alongi & Tenore, 1985; Wilson, 1989; Edgar, 1993). If food limitation does occur amongst benthos, then it perhaps seems unreasonable to propose that fishes regulate population sizes amongst grazers and detritivores and that fishes are also food-limited. Indeed, the concept of trophic cascades is based on food-limited trophic levels alternating with predation-limited ones (Vadas, 1989) rather than adjacent trophic levels both being food limited. Nevertheless, trophic levels are rarely discrete (Strong, 1992), hence it remains possible for population sizes of both predators and prey to be limited by a lack of available food, providing that fishes are consuming only a subset of invertebrate resources.

We consider that the simplest hypothesis to explain the results is that total benthic invertebrate production remains approximately constant regardless of fish consumption, but that fluctuations in fish consumption rates will influence the species composition and size structure of the benthic assemblage. As the predatory pressure on prey increases, the proportion of production available to fishes in the form of epifaunal crustaceans is predicted to decrease, with a corresponding increase in the production of small-sized, infaunal and inverte-

brates with antipredator defences (Edgar & Aoki, 1993). Thus, the relationship between benthic invertebrates and fishes is postulated to be a dynamic one, with fishes having a large influence on the population dynamics of individual prey species but not total secondary production, and the partitioning of secondary production into high- and low-quality food influencing the population dynamics and total production of fishes.

At sites with pronounced seasonal variability in environmental conditions, such as Western Port, consumption by fishes will rarely be at equilibrium with faunal production because of the lag between recruitment of fishes and recruitment of invertebrates. Hence, although benthic invertebrates are postulated to respond rapidly to increased seagrass, epiphyte and microphytobenthos production in spring, fishes respond to the increased invertebrate production by recruiting after a lag of 1–3 months. They then do so in such numbers that by late summer fish production cannot be sustained by the crustacean fraction of the benthos, particularly in seagrass beds where much of the habitat itself is also declining. Much of the fish population then either emigrates or is lost directly as a result of starvation or, more likely, by predators removing starving fish which may tend to forage more (see Morgan, 1988) and have depressed avoidance responses (see Yin & Blaxter, 1987). This hypothesis is supported by the observation that the condition of fishes in seagrass habitat was lowest during the autumn period of high fish numbers, high fish mortality, declining habitat and low food availability.

The environmental factor primarily responsible for these seasonal oscillations is most likely to be levels of light at the seabed. Light will strongly affect primary production which in turn will affect production of invertebrates (Edgar, 1991), particularly in the seagrass habitat where seasonal fluctuations in production and consumption were most evident. Very little light penetrated to the seagrass beds in winter because of high turbidity (PAR levels were an average of 5% of surface values at 1 m depth at low tide at Rhyll in August 1990, G. Edgar, unpubl. data) and because intertidal seagrass beds were submersed under 1–3 m of water during the 6 h of strongest sunlight in the middle of the day in that season. During the winter months only neap low tides occur in the middle of the day and intertidal seagrass beds become exposed to the atmosphere only at night.

Whether the seasonal hypothesis described above is essentially correct or not, the results of our study clearly indicate that there is no large oversupply of food for fishes in Western Port, and that further work should be carried out to investigate the carrying capacities of benthic habitats and the possibility that competition for crustacean production is a primary factor structuring small fish communities. The deductive approach used here is, of course, only an initial step in determining the importance of resource limits for fishes. Inductive experiments are also required, although experiments that produce enlightening results will be extremely difficult to design. Such experiments should be field based because the strong relationships between fish production, stocking density and food supply that form the basis for management in the aquaculture industry already indicate the importance of food resources in artificial environments. The major difficulty in the design of the field experiments will be to distinguish between food addition

acting to increase fish production (a population response), and food addition acting to increase fish aggregation (a behavioural response).

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