



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

I. Species richness, size-structure and production of fishes in Western Port, Victoria

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Received 25 September 1994; revision received 4 May 1995; accepted 19 May 1995

Abstract

Fishes were sampled by seine and gillnet in three different habitat types (seagrass, unvegetated sediment and channel) within Western Port, Victoria, between 1989 and 1990. Approximately twice as many fish species were collected per seine haul from seagrass habitat ($\bar{x} = 8.7$) compared with intertidal unvegetated habitat ($\bar{x} = 4.7$), while relatively few fish species were collected per haul from deeper unvegetated-channel habitat ($\bar{x} = 2.3$). Most fishes associated with seagrass beds were widely distributed within the embayment, with the notable exception of a number of coastal species that occurred in low numbers at a single site (Cowes Bank seagrass) near the entrance to the bay and had presumably drifted as pelagic larvae from reefs outside. Small fishes (<10 g weight) were more abundant in seagrass than in unvegetated habitats; however, relatively few of these animals were juveniles of commercially fished species. Seagrass beds in Western Port were not found to provide a significantly more important nursery habitat for commercial species than unvegetated habitat.

The production of small fishes at different sites was highly correlated with the production of epifauna, particularly crustaceans. We postulate that these factors are causally linked. This hypothesis is supported by seasonal data, which indicate 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. Seagrass beds supported over twice the production of small fishes as unvegetated habitat ($3.82 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ cf. $1.58 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in unvegetated habitat). Because an estimated 178 km^2 of seagrass habitat has been lost from Western Port since 1973, the reduced production of fishes in unvegetated habitat translates to a decline in small fish production of ≈ 630 tonnes AFDW per year. However, falling

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catches of only two commercial fishes, six-spined leatherjackets (*Meuschenia freycineti*) and blue rock whiting (*Haletta semifasciata*), were clearly associated with seagrass loss, with most of the loss of fish production occurring amongst small non-commercial species, particularly syngnathids, clinids and scorpaenids.

Differences in production of small fishes between habitats were not reflected higher in the food chain. Although greater numbers of fishes were collected using small-mesh (64 mm) gillnets from seagrass than unvegetated habitats, these differences were due to variation in the catch of the omnivorous mullet *Aldrichetta forsteri*, the most abundant species, rather than variation in the abundances of piscivorous fish species. No differences were found between catches of fish using large-mesh (108 mm) gillnets placed in different habitats.

Keywords: Australia; Fish; Production; Seagrass; Species richness; Temperate

1. Introduction

The composition and abundance of fish assemblages in shallow coastal waters has been known since the work of Petersen (1918) to be strongly affected by the presence of macrophytes, and relationships between fishes and seagrasses have now been studied at a variety of sites worldwide (Bell & Pollard, 1989). While fish densities in seagrass beds are not always higher than in bare substrata immediately adjacent to the beds (Ferrell & Bell, 1991), seagrasses have been found in most studies to increase species richness of fish assemblages and enhance abundance (Heck & Orth, 1980). Seagrasses thus appear to have a similar positive effect on the species richness and production of fish communities as they have on invertebrate communities (Howard et al., 1989; Edgar et al., 1994), despite the structure of seagrasses having a less obvious benefit to fish than to invertebrates. The structural complexity of seagrass habitats should partly aid fishes by providing concealment from larger predators, but may also be detrimental because it will conceal prey from the majority of fishes which are visual carnivores.

Extensive loss of seagrass beds has occurred in southern Australia this century, with particularly severe declines occurring in Western Port, Victoria, a large embayment 60 km south-east of Melbourne. A total of 70% of the area of seagrass (178 km²) in the bay disappeared between 1973 and 1984 (Shepherd et al., 1989). The present study was initiated to determine the consequences of this loss to the marine fauna, particularly with respect to local fishery production. Seagrass loss was predicted to affect fish catches in three ways: (1) the catch of fishes should be directly affected by habitat transformation because abundance and composition of adult fishes differs between seagrass and unvegetated habitats, (2) seagrass beds are widely considered prime nursery habitat (Pollard, 1984), hence a reduction in the area of seagrass may reduce habitat available for juvenile fish, and (3) detached seagrass contributes to detrital input into the base of the food chain (Klumpp et al., 1989), so the loss of seagrass production may result in a general baywide decline in production of fishes feeding on detritivorous invertebrates and their predators.

The present study was designed primarily to address the first, and to a lesser extent the second of the above predictions, while the third prediction has not been investigated here. In contrast to previous studies, which have concentrated on the composition and abundance of fishes in seagrass relative to unvegetated habitats (e.g. Sogard et al., 1987; Thayer & Chester, 1989), this study attempted to quantify differences in the production of fish assemblages between habitats, and to identify any general production relationships between invertebrates and fishes. Related work on the diets of fishes and trophic relationships between fish and benthos are described in an associated paper (Edgar & Shaw, 1995).

The secondary aim of the study was to investigate whether seagrass beds are important as nursery grounds for commercially-important fish species in the area. A widely-quoted paradigm suggests that seagrass beds are important nursery areas for fishes (see Bell & Pollard, 1989). This hypothesis has, however, 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 flatfishes as are many reefs by juvenile sparids and labrids. The paradigm can be interpreted in a more useful form as a prediction that seagrass beds support a greater abundance, and number of species, of juveniles of commercially-important species than unvegetated habitats in their vicinity. Surprisingly, there are virtually no published studies in which this prediction has been empirically tested at several sites (but see Heck & Thoman, 1984).

2. Methods

Western Port is a 30-km wide coastal embayment in central Victoria, with a large island (French Island) in the central section and another (Phillip Island) forming the southern boundary of the bay (Fig. 1). Surface water temperatures recorded in a channel at Rhyll during the study ranged from 10 to 22°C annually, with salinities close to fully marine ($>32\text{‰}$). Intertidal mudflat, colonised in places by the seagrasses *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog and *Zostera muelleri* Irmisch ex Aschers, occupies $\approx 40\%$ of the total area of Western Port, with extensive dendritic channels (4–10 m deep) draining the mudflats. Flat embayment plains at 5–10 m depth occupy considerable areas in the southern section of the bay (Marsden et al., 1979).

Small fishes and epibenthic invertebrates were sampled at the same times and sites as a study of benthos described in Edgar et al. (1994) using a 15 m seine net with 3-m drop and 1×1 mm mesh. Netting was carried out from a small dingy by first anchoring the boat at the end of a long (40 m) anchor line and then setting the net over the side of the boat along the circumference of a circle of 40 m radius. The boat was then pulled by hand up the anchor line without dragging the net while 12-m long ropes attached to the two ends of the net were let out. The boat was next retied to the anchor line so that the drag force as the net was pulled would be counterbalanced by the anchor, and a period of at least 2 min allowed to

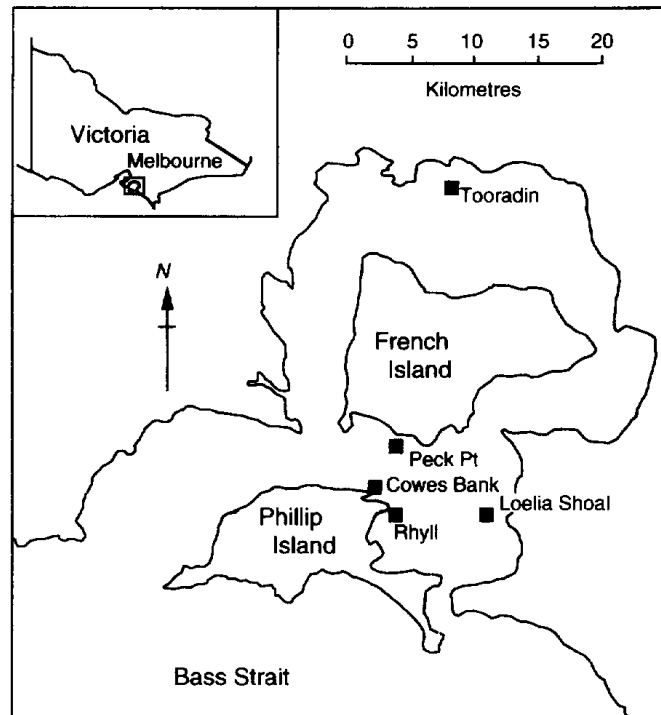


Fig. 1. Map showing the locations of the study sites.

elapse in order to minimise any disturbance to the fish community caused by the deployment of the net. To prevent the base of the net lifting above the seabed, the net ropes were clipped through a shackle attached to a 15 kg weight which was dropped overboard. The ropes, followed by the net, were pulled in through the shackle into the boat. The net ends thus traversed a distance of 12 m across the seabed before lifting into the boat. In depths >2 m the floatline of the net was located below the water surface because the leadline was heavily weighted with chain.

Samples were taken in three habitat types (seagrass, unvegetated intertidal flats and unvegetated channel) at three primary localities (Peck Point, Rhyll and Tooradin) within Western Port, at seagrass and unvegetated sand habitats at Cowes Bank, and on a silty 5-m deep embayment plain at Loelia Shoal. Site in this study refers to a habitat type within a locality, and so 12 sites were examined. Four to seven replicate seine hauls were made at the Peck Point and Rhyll sites at 3 monthly intervals (referred to as different seasons) between August 1989 and November 1990, at the Cowes Bank seagrass site between February 1990 and November 1990, and at the other sites between November 1989 and November 1990. Each site was sampled during daylight within 4 days of the associated benthos sampling date. Seine netting was also carried out in the three Peck Point habitats 2 to 4 h after sunset during each sampling season between August 1989 and August 1990. Three replicate hauls were pulled at these times.

Large fishes were sampled using 50-m monofilament gillnets with 3-m drop and

one 25 m panel of 64-mm mesh and another 25-m panel of 108 mm mesh. These gillnets were set and retrieved at 3 hourly intervals over a 9-h period centred on sunset. During March and September they were thus set from 1:30 p.m. to 4:30 p.m., 4:30 p.m. to 7:30 p.m. and 7:30 p.m. to 10:30 p.m. 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 nets were set at the sites during each sampling season.

Fish collected by seine net were preserved in formalin, and those collected by gillnet were chilled on ice and their gut contents analysed within 24 h in the laboratory. Animals were weighed after their surfaces had been blotted dry, and length to caudal fork (LCF) measured. The distance between fully opened upper and lower jaws (referred to as gape height–GH) was also measured using vernier callipers. If >120 animals of a species were collected from a site then 100–120 individuals were subsampled for weighing and measuring.

2.1. Calibration of fish density data using box traps

In order to allow data collected by seine to be expressed per unit area of seafloor, 1-m² box drop-traps with 600-mm high sheet-metal sides were used at the Rhyll unvegetated site on 27 August 1990 and at the Peck Point seagrass site on 26 November 1990, in the same areas as seven replicate seine hauls had been pulled. Similar box traps have been used effectively and their virtues and deficiencies 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 ≈0.3 m water depth from the front of a small boat as it drifted with the current across the study site. Fish were removed from the traps using small handnets which were moved from side to side within the traps until no further animals had been collected for 2 min. Mean numbers of fish collected in box traps were considered to represent absolute densities for small demersal fish species, and these densities used to calibrate numbers collected per beach seine haul.

2.2. Estimation of fish production

The production of 10 of the 12 most abundant fish species collected by seine was determined from seasonal changes in the modal size of year classes of animals at the different sampling dates (Fig. 2). Seasonal increase in the mode for another common fish species, *Tetractenos glaber*, was not clearly recognizable from its analogous graph, probably because of poor recruitment during the year of study and slow growth of animals at sizes greater than 100 mm. Production of this species was calculated using information on mean daily length increments provided in a study of a Tasmanian population of this species by Bradford (1991),

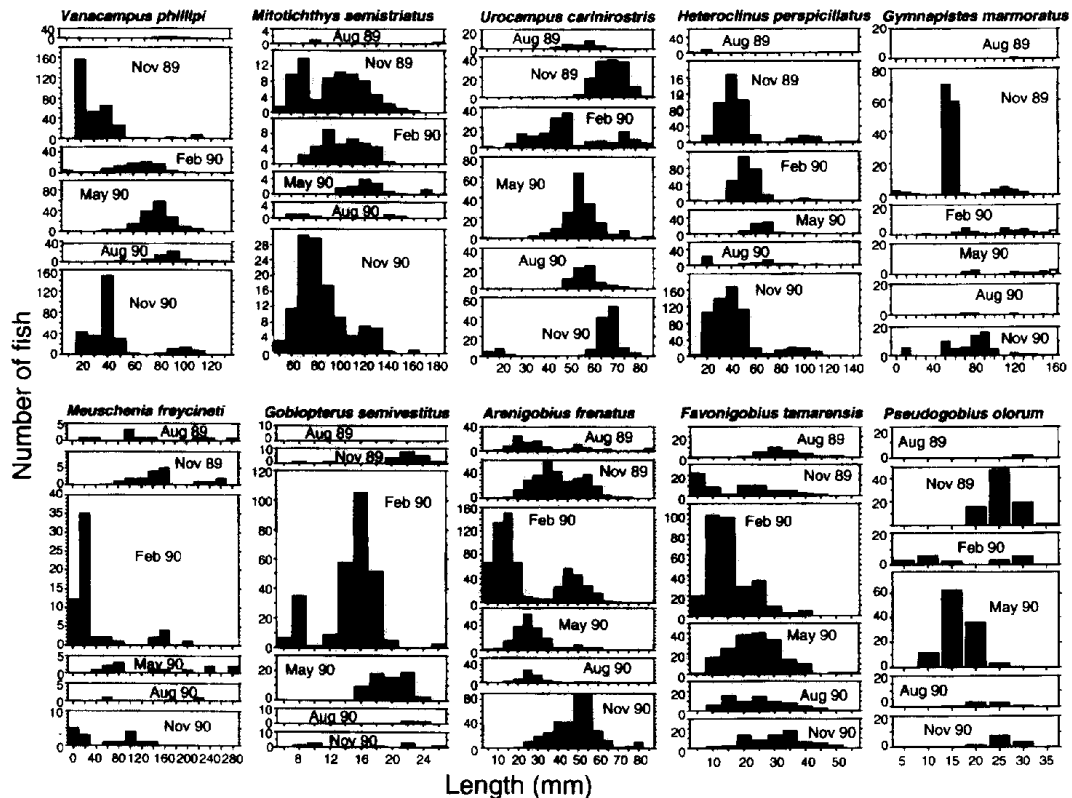


Fig. 2. Number of animals in different length classes collected in different seasons during the study for 10 common fish species.

who found a modal size of 121 mm after 1 yr, 137 mm after 2 yr, 147 mm after 3 yr and 153 mm after 4 yr.

For the syngnathid *Stigmatopora nigra*, the only other common species with indistinguishable modes, and for the rarer species in a sample, production was estimated using a newly-derived 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 (°C). The logged version of this equation, with standard error 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 was calculated using data obtained from the published literature on the biomass, estimated daily somatic production and ambient water temperature for 62 fish species distributed worldwide (Table 1). It relies on the same assumptions, and was formulated using the same method, as a production/biomass regression used for benthic invertebrate data (Edgar, 1990; Edgar et al., 1994). For many of the larger fishes included in the analysis, 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 in the area of study. This regression is slightly less accurate than the macrobenthic invertebrate regression when used for predictive purposes (SD of residuals = 0.33, cf. 0.26 for macrobenthos, Edgar, 1990).

Table 1

Daily production of fishes ($\text{g} \cdot \text{day}^{-1}$) of different wet weight (g) and at different water temperatures ($^{\circ}\text{C}$), as estimated from previous studies

Species	Temp.	Wet weight	Production	Study author
<i>Aldrichetta forsteri</i>	22	5.82	0.114	Chubb et al. (1981)
<i>Archosargus probatocephalus</i>	23	221	0.567	Schwartz (1990)
<i>Argyrozona argyrozona</i>	19	98.8	0.179	Nepgen (1977)
<i>Atherinosoma prebysteroides</i>	19	0.407	0.00349	Prince & Potter (1983)
<i>Caranx georgianus</i>	19	1750	4.36	James (1984)
<i>Carcharinus tilstoni</i>	29	3930	6.08	Davenport & Stevens (1988)
<i>Chanos chanos</i>	27	7.34	0.332	Kumagai et al. (1985)
<i>Cheilodactylus macropterus</i>	19.5	319	0.363	Tong & Vooren (1972)
<i>Chelidonichthys kumu</i>	19.5	76.0	0.159	Elder (1976)
<i>Chrysophrys auratus</i>	19.5	1320	2.73	Vooren & Coombs (1977)
<i>Clupea harengus</i>	11	1.65	0.0496	De Silva (1973)
<i>Clupea pallasii</i>	7	52.1	0.146	Kanno (1989)
<i>Coracinus capensis</i>	19	215	0.445	Bennett & Griffiths (1986)
<i>Coryphaena hippurus</i>	27	12300	63.8	Oxenford & Hunte (1981)
<i>Cymatoceps nasutus</i>	23	276	0.375	Buxton & Clarke (1989)
<i>Cynoscion arenarius</i>	16	74.4	0.829	Shlossmann & Chittenden (1981)
<i>Cynoscion nothus</i>	25	24.1	0.465	DeVries & Chittenden (1982)
<i>Cynoscion regalis</i>	25	0.119	0.00961	Szedimayer et al. (1990)
<i>Engraulis capensis</i>	20	0.0952	0.00713	Thomas (1986)
<i>Engraulis mordax</i>	14	5.61	0.0255	Parrish et al. (1985)
<i>Etrumeus micropus</i>	15	14.2	0.0649	Geldenhuys (1978)
<i>Fundulus heteroclitus</i>	25	0.644	0.00441	Kneib & Stiven (1978)
<i>Galeorhinus australis</i>	16	4040	4.44	Grant et al. (1979)
<i>Gobius cobitis</i>	14.5	1.67	0.00784	Gibson (1970)
<i>Gobius paganellus</i>	18	0.493	0.00916	Miller (1961)
<i>Helicolenus lengerichi</i>	9	36.7	0.113	Petrova & Chekunova (1979)
<i>Helicolenus percoides</i>	12	15.0	0.0499	Withell & Wankowski (1988)
<i>Hippoglossoides dubius</i>	9	4.76	0.0183	Nakatani et al. (1990)
<i>Katsuwonus pelamis</i>	24	1860	9.37	Uchiyama & Struhsaker (1981)
<i>Lagodon rhomboides</i>	26	0.676	0.0075	Hansen (1969)
<i>Lates calcarifer</i>	27	3070	3.86	Davis & Kirkwood (1984)
<i>Leionura atun</i>	15	40.4	0.483	Grant et al. (1978)
<i>Leiostomus xanthurus</i>	10	0.00128	0.000086	Warlen & Chester (1985)
<i>Lesueurigobius friesii</i>	12	0.203	0.00251	Gibson & Ezzi (1978)
<i>Liza subviridis</i>	21	65.6	0.158	Al-Daham & Wahab (1991)
<i>Lutjanus campechanus</i>	28	34.4	0.541	Holt & Arnold (1982)
<i>Lutjanus kasmira</i>	22	110	0.207	Morales-Nin & Ralston (1990)
<i>Menidia menidia</i>	18	3.00	0.0380	Conover & Ross (1982)
<i>Micropogon undulatus</i>	17	0.0714	0.00546	Knudsen & Herke (178)
<i>Mugil cephalus</i>	27	72.0	0.547	Grant & Spain (1975)
<i>Mugil curema</i>	25	9.78	0.379	Richards & Castagna (1976)
<i>Mustelus munaço</i>	20	591	0.892	Tanaka & Mizue (1979)
<i>Nematolosa vlaminghi</i>	19	63.4	0.113	Chubb & Potter (1986)
<i>Menipterus peronii</i>	27	83.4	0.272	Sainsbury & Whitelaw (1984)
<i>Oligocottus maculosus</i>	11.5	1.30	0.00356	Pierce & Pierson (1990)
<i>Pachymetopon blochii</i>	19	11.8	0.0463	Pulfrich & Griffiths (1988)
<i>Pagrus pagrus</i>	20	145	0.436	Manooch & Huntsman (1977)
<i>Pomatoschistus microps</i>	14	0.500	0.00470	Healey (1972)

Table 1 (continued)

Species	Temp.	Wet weight	Production	Study author
<i>Pseudopleuronectes americanus</i>	22	0.401	0.0108	Mulkana (1966)
<i>Rhombosolea plebeia</i>	15	3.47	0.0901	Colman (1978)
<i>Sardinops neopilchardus</i>	21	3.66	0.0384	Blackburn (1949)
<i>Sardinops ocellata</i>	15	0.856	0.0336	Thomas (1985)
<i>Scomberomorus cavalla</i>	28	0.00511	0.00165	DeVries et al. (1990)
<i>Sebastes serranoides</i>	15	131	0.260	Love & Westphal (1981)
<i>Sprattus sprattus</i>	14	1.65	0.0496	De Silva (1973)
<i>Squalus acanthias</i>	12	235	0.248	Ketchen (1975)
<i>Stolephorus purpureus</i>	22	0.277	0.00804	Stuhsaker & Uchiyama (1976)
<i>Tanakius kitaharai</i>	10	3.47	0.0170	Yubuki (1989)
<i>Tautolabrus adspersus</i>	15	9370	50.4	Dew (1976)
<i>Trachurus declivus</i>	16	243	0.461	Webb & Grant (1979)
<i>Trachurus trachurus</i>	16	21.0	0.0871	Geldenhuys (1973)
<i>Trisopterus esmarkii</i>	14	10.5	0.110	Gordon (1977)

Wet weights of fishes included in Table 1 and those collected during the Western Port study 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 (Robertson, 1978). Mean surface water temperatures measured at high tide in Rhyll in August 1989, November 1989, February 1990 and May 1990 were 11°C, 16°C, 22°C and 16°C, respectively. These temperature data were applied in production calculations for all sites.

2.3. Data analyses

The number of animals (abundance) and number of species (species richness) collected per seine net haul were analysed using ANOVA. Habitat and season were considered fixed factors and locality a random factor, with data used in analyses being those collected at the three primary localities on the four sampling occasions between November 1989 and August 1990. Abundance and species richness of fish collected at night were also compared to daylight catches using data from Peck Point obtained between November 1989 and August 1990. The analysis used was a three-way ANOVA with habitat, season and time of day fixed factors. Abundance data were log-transformed to accommodate heteroscedasticity assumptions of ANOVA, species richness data did not require transformation.

3. Results

3.1. 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 total numbers collected at each site are listed in Table 2, and seasonal change in the size-distributions of 10 common species

Table 2
Total number of fishes collected by seine from different sites in Western Port

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

Table 2 (continued)

Species	Site															Total
	PH	PU	PC	RH	RU	RC	TH	TU	TC	LS	CBH	CBU	PHN	PUN	PCN	
<i>Acanthopogonius laticifer</i> (Kaup)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Apogon conspersus</i> Klunzinger	1	0	0	7	0	0	0	0	0	0	1	0	5	0	0	14
<i>Siphonina cephalotes</i> Castelnau	58	0	2	2	1	0	0	0	0	0	9	0	11	0	0	83
* <i>Sillaginodes punctatus</i> Cuvier & Valenciennes	5	7	2	0	2	0	11	8	0	0	3	0	10	5	0	53
* <i>Pseudocaranx dentex</i> Block & Schneider	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
* <i>Arripis trutta</i> (Bloch & Schneider)	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
* <i>Girella tricuspidata</i> (Quoy & Gaimard)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Enoplosus armatus</i> (White)	3	0	0	2	0	0	0	0	0	0	1	0	1	0	0	7
<i>Dactylophora nigricans</i> (Richardson)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
* <i>Aldrichetta forsteri</i> (Cuvier & Valenciennes)	0	0	0	2	1	0	0	1	0	0	4	10	0	2	0	20
<i>Sphyræna novæhollandiæ</i> (Günther)	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3
<i>Dotabrus aurantiacus</i> (Castelnau)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
* <i>Haletta semifasciata</i> (Cuvier & Valenciennes)	32	0	0	6	0	0	0	0	0	0	8	0	11	0	1	58
<i>Neodax balteatus</i> (Cuvier & Valenciennes)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
<i>Cristiceps australis</i> Cuvier & Valenciennes	10	0	1	11	0	0	3	0	0	0	50	1	5	0	1	82
<i>Heteroclinus adelaidæ</i> Castelnau	10	0	0	0	0	0	1	0	0	0	9	0	9	0	0	29
<i>Heteroclinus forsteri</i> (Castelnau)	0	0	0	0	0	0	0	0	0	0	4	0	48	0	0	52
<i>Heteroclinus perspicillatus</i> (Cuvier & Valenciennes)	422	7	3	191	13	8	273	0	1	0	20	3	108	0	6	1085
<i>Arenigobius bifrenatus</i> (Kner)	0	0	0	0	2	0	2	89	11	0	0	0	34	0	0	138
<i>Arenigobius frenatus</i> (Günther)	45	10	1	308	631	0	428	237	13	0	3	0	80	1	5	1762
<i>Callogobius depressus</i> (Ramsay & Ogilby)	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	4
<i>Favonigobius tamarensis</i> (Johnston)	1	3	14	5	251	0	17	349	81	0	0	4	18	2	9	754
<i>Favonigobius lateralis</i> (Macleay)	0	2	2	0	2	2	0	7	0	0	1	0	0	0	0	16
<i>Gobiopsis semivestitus</i> (Munro)	13	1	14	63	31	5	101	39	5	0	37	2	20	4	3	338
<i>Nesogobius hindshyi</i> (McCulloch & Ogilby)	0	0	0	0	0	1	0	0	0	0	4	1	0	0	0	6
<i>Nesogobius pulchellus</i> (Castelnau)	0	2	0	2	0	0	5	0	0	0	3	0	3	0	0	15
<i>Nesogobius</i> sp. 1	3	45	0	0	0	0	0	4	0	0	0	1	0	2	0	55
<i>Nesogobius</i> sp. 2	0	0	0	0	0	1	0	0	0	0	3	2	0	0	0	6

Table 2 (continued)

Species	Site															Total
	PH	PU	PC	RH	RU	RC	TH	TU	TC	LS	CBH	CBU	PHN	PUN	PCN	
<i>Pseudogobius olorum</i> (Sauvage)	0	0	1	15	53	0	8	134	1	0	0	0	1	0	0	213
<i>Tasmanogobius gloveri</i> Hoese	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Kathetostoma laevis</i> (Bloch & Schneider)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Parvicrepis</i> sp.	0	0	0	9	1	0	0	0	0	0	68	0	0	0	0	78
<i>Arnoglossus bassensis</i> Norman	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
* <i>Annotretis rostratus</i> Günther	0	4	0	0	0	0	0	10	3	0	0	2	0	1	0	20
* <i>Rhombolela tapirina</i> Günther	0	5	1	0	0	1	0	6	0	0	0	0	1	1	0	15
<i>Acanthaluteres spilomelanurus</i> (Quoy & Gaimard)	61	0	0	16	0	0	0	0	0	0	14	0	8	0	0	99
<i>Brachaluteres jacksonianus</i> (Quoy & Gaimard)	4	0	0	4	0	0	0	0	0	0	4	0	0	0	0	12
<i>Eubalichthys gunnii</i> (Günther)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
* <i>Meuschenia freycineti</i> (Quoy & Gaimard)	42	1	0	3	0	0	28	0	0	0	1	0	13	0	0	88
<i>Penicipelta vittiger</i> (Castelnau)	3	0	0	4	0	0	3	0	0	0	1	0	0	0	0	11
<i>Scorbinichthys granulatus</i> (Shaw)	3	0	0	0	0	0	0	0	0	0	1	0	2	0	0	6
<i>Arcania aurita</i> (Gray)	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
<i>Contusus brevicaudus</i> Hardy	0	0	1	1	5	0	0	2	1	0	8	0	0	0	0	18
<i>Contusus richiei</i> (Freminville)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Tetractenos glaber</i> (Freminville)	10	17	1	24	51	0	53	131	13	0	9	36	10	14	0	369
<i>Diodon nichememus</i> Cuvier	18	1	2	6	0	3	2	2	3	0	0	0	12	1	0	50
Total animals captured	3368	298	224	2425	1166	69	1571	1190	201	55	1629	116	2262	47	93	14714
Total commercial species captured	84	19	10	18	9	13	42	31	13	21	104	26	44	13	8	455
Number of species	32	21	26	31	23	22	25	23	18	4	44	19	34	16	20	75
Number of commercial species	4	5	7	6	5	6	5	6	3	3	9	5	7	6	4	17
Number of seine hauls	31	25	25	25	29	21	21	22	21	21	19	22	16	17	16	331

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 (CUB), Peck Point seagrass night (PHN), Peck Point unvegetated night (PUN), Peck Point channel night.

* Commercially-important species.

shown in Fig. 2. Most species were small, non-commercially important species of gobies (Gobiidae), pipefish (Syngnathidae) and weedfish (Clinidae). Total numbers of commercially-important fishes were consistently higher in seagrass than unvegetated habitats at all locations (Table 2), due to the relatively large numbers of leatherjackets (*Meuschenia freycineti*), garfish (*Hyporhamphus melanochir*) and clupeoids (*Engraulis australis* and *Sardinops neopilchardus*) collected amongst seagrass. The significance of this relationship could not be tested because of the patchy distribution of these species, and consequent high heterogeneity of variances. Juveniles of the commercially-important species appeared to be 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 (Edgar & Shaw, unpubl. data), showing a clear change in habitat with increasing age. The number of commercially-important species collected from different sites varied from three to nine, with approximately equal numbers of species collected from each habitat type (Table 2).

The mean number of fish species collected per seine haul was found using SNK tests following ANOVA (see Table 3) to be significantly greater ($\alpha = 0.05$) in seagrass habitat ($\bar{x} = 8.7$) than in unvegetated intertidal ($\bar{x} = 4.7$) and channel ($\bar{x} = 2.3$) habitats. Fish species richness differed substantially between different localities, with significant higher order interactions also detected by ANOVA (Table 3). The number of fish species collected from channel habitats increased more rapidly with additional sampling than samples from seagrass or intertidal unvegetated habitats (Fig. 3). While nearly four times as many species were collected per seine haul from seagrass habitats as from channel habitats, the total number of fish species collected from seagrass habitats at the three primary localities was not markedly greater than that collected from channel habitats (44 species from 77 daytime hauls cf. 35 from 46 hauls). Thus, fish in channel habitats were more heterogeneously distributed than fish in shallow habitats, a similar pattern to that found for macrofauna (Edgar et al., 1994).

Table 3

Results of three-way ANOVA (fixed factors: season and habitat, random factor: locality) using data on the log-transformed abundance and total number of fish species collected per seine haul at primary locations

Factor	Hypothesis	df	Log abundance		No. of species	
			SS	F	SS	F
Habitat (H)	H/HL	2	152.9	5.3	1086	9.5*
Locality (L)	L/E	2	6.1	5.5**	49.1	6.5**
Season (S)	S/LS	3	80.1	11.3**	410	9.7*
Habitat * locality (HL)	HL/E	4	57.4	25.8***	228	15.1***
Habitat * season (HS)	HS/HLS	6	12.2	1.3	136.2	2.0
Locality * season (LS)	LS/E	6	14.2	4.2*	84.6	3.7*
Habitat * locality * season (HLS)	HLS/E	12	18.9	2.8**	137.2	3.0**
Error (E)		122	67.9		461.9	

* $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$.

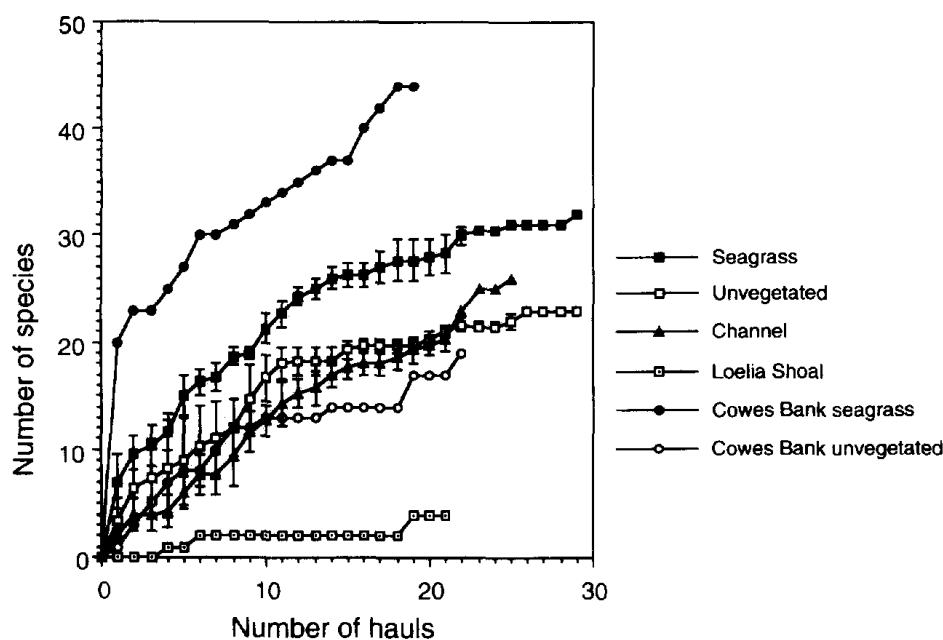


Fig. 3. Cumulative number of species of fish collected with increasing number of seine hauls at different Western Port sites. Because little difference was detected in these curves between the three primary sites for each habitat, the mean (\pm SE) number of species collected is shown for primary seagrass, unvegetated and channel sites.

The site with the greatest number of fish species was Cowes Bank seagrass (Table 2, Fig. 3). 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 (Table 4) indicated that significantly more

Table 4

Results of three-way ANOVA (fixed factors: months, habitat, time of day) using data on the log-transformed abundance and total number of fish species collected per seine haul at primary locations

Factor	df	Log abundance		No. of species	
		SS	F	SS	F
Habitat	2	203.5	223.5***	1483	169.6***
Season	2	32.4	23.7***	218	16.6***
Time	1	0.45	0.99	18.8	4.29*
Habitat * season	6	6.9	2.52*	75.3	2.87*
Habitat * time	2	1.8	2.01	5.7	0.65
Season * time	3	12.5	9.12***	65.8	5.02**
Habitat * season * time	6	7.9	2.90*	63.2	2.41*
Error	67	30.5		293	

* $0.01 < p < 0.05$. ** $0.001 < p < 0.01$. *** $p < 0.001$.

fish species were collected during the night ($\bar{x} = 6.0$) than during the day ($\bar{x} = 5.4$), although time of day had only a minor influence on species richness when compared to differences between habitats (seagrass: $\bar{x} = 11.0$; unvegetated; $\bar{x} = 2.1$, channel: $\bar{x} = 2.5$). No species were found that moved on a diel basis between habitats (see Table 2).

Total abundance of fish collected per seine haul at primary locations varied significantly between locality and season, and a very high habitat \times locality interaction was found which obscured overall differences between habitats (Table 3). Whether seines were hauled at night or during the day had no significant effect on overall numbers collected (Table 4). Interaction effects were, however, detected that involved time of day (Table 4). These interaction effects together contributed only a small proportion (7%) of the total variation in numbers of fish collected by seine.

3.2. 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 (\pm SD) of seabed swept by the net was $77 \pm 10 \text{ m}^2$ in water of 1 m depth and was considerably lower in water of 5 m depth ($36 \pm 8 \text{ m}^2$) due to the net lifting from the bottom earlier. When the numbers of common fishes collected per seine haul were compared with the absolute densities as determined using box traps (Table 5), the proportion of total fish collected as the seine passed (i.e. the efficiency) varied from 63% for the pipefish *Mitotichthys semistriatus* to 12.3% for the burying goby *Arenigobius frenatus*. The mean efficiency of the net in the Peck Point seagrass habitat was 28% compared to 20% in the Rhyl unvegetated habitat. The overall efficiency

Table 5

Mean abundances (\pm SE) of common fishes collected per seine haul, mean densities (\pm 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 Rhyl unvegetated habitats in November 1990

	Seine abundance	Drop net density (m^{-2})	Correction factor	Net efficiency (%)
Peck Point seagrass				
<i>Siphamia cephalotes</i>	4.9 ± 1.7	0.13 ± 0.09	37	49
<i>Vanacampus phillipi</i>	11.9 ± 1.7	1.07 ± 0.55	11	14
<i>Mitotichthys semistriatus</i>	19.4 ± 3.8	0.40 ± 0.26	49	63
<i>Urocampus carinirostris</i>	6.7 ± 1.0	0.20 ± 0.05	34	44
<i>Sigmatopora nigra</i>	28.7 ± 5.9	0.80 ± 0.23	36	47
<i>Heteroclinus perspicillatus</i>	27.1 ± 5.5	1.07 ± 0.18	25	33
Total	115.4 ± 16.0	5.33 ± 0.93	22	28
Rhyl unvegetated				
<i>Aenigobius frenatus</i>	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

when numbers in both habitats were combined was 25.6%, which is equivalent to dividing the total numbers of fish collected by seine by 20 ($=77 \times 0.256$) to produce estimates per m^2 . Numbers of fish collected per seine haul therefore have been converted to numbers per m^2 by dividing by 20 for fish species not listed in Table 5 collected from seagrass and unvegetated habitats, and by dividing by 9 ($=36 \times 0.256$) for fish collected in the deeper channel habitat where the net swept a smaller area.

3.3. Production and size-structure of small fish assemblages

The total estimated production of small fish at different sites varied over a 5-fold range, from $0.67 \text{ g AFDW} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Peck Point unvegetated to $3.96 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Tooradin seagrass (Table 6). The levels of fish production differed little between the three primary vegetated sites. Mean fish production at the primary sites was $3.82 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in seagrass, $1.58 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in unvegetated and $1.93 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in channel habitat. By comparison, mean densities of fish varied over a 50-fold range at different sites (Table 6), and the variation in densities within a habitat was much greater than the corresponding values for production.

The highest fish densities were recorded in all habitats during the February sampling period, and numbers consistently declined during the autumn and winter months to reach minimum levels in August (Table 7; Fig. 2). The decline was most acute in the seagrass habitat, where densities in August were less than 10% of the numbers in February. Annual change in estimated production in different habitats was much less pronounced than the change in fish densities. Within the primary seagrass habitats estimated production varied over a 5-fold annual range, whereas in the unvegetated and channel habitats only a 2-fold range in annual production was found. The relatively large annual variation in fish density and

Table 6

Estimated densities, biomass, annual somatic production and P/B ratios of small-fish assemblages at different sites in Western Port

Site	Density (m^{-2})	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)	P/B
Peck Point seagrass	6.08	1.99	3.80	1.91
Peck Point unvegetated	0.84	0.37	0.67	1.82
Peck Point channel	0.83	1.39	1.71	1.23
Rhyll seagrass	6.07	2.58	3.70	1.43
Rhyll unvegetated	2.65	0.94	1.77	1.88
Rhyll channel	0.36	2.46	2.58	1.05
Tooradin seagrass	3.03	1.67	3.96	2.37
Tooradin unvegetated	2.96	2.15	2.30	1.07
Tooradin channel	1.23	1.01	1.50	1.49
Cowes Bank seagrass	4.94	2.37	3.39	1.43
Cowes Bank unvegetated	0.28	0.70	0.85	1.21
Loelia Shoal	0.11	0.44	0.70	1.59

Table 7

Mean abundance and estimated daily production of small-fish assemblages in different seasons and habitats at primary locations. Mean seagrass leaf biomass is also shown

Habitat	November 1989	February 1990	May 1990	August 1990
Fish density (m^{-2})				
Seagrass	4.14 (1.17)	12.03 (7.46)	2.95 (2.52)	1.12 (0.85)
Unvegetated	1.56 (1.48)	4.22 (1.72)	2.11 (1.49)	0.70 (0.89)
Channel	0.89 (1.030)	1.50 (0.84)	0.50 (0.19)	0.34 (0.28)
Fish production ($\text{mg AFDW} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)				
Seagrass	12.71 (6.92)	17.3 (7.54)	7.81 (1.19)	3.02 (1.41)
Unvegetated	4.84 (2.04)	2.83 (1.32)	4.47 (2.87)	4.85 (7.75)
Channel	3.61	2.9 (1.38)	1.64 (0.6)	1.42 (0.94)
Seagrass biomass ($\text{g DW} \cdot \text{m}^{-2}$)				
Seagrass	412 (120)	388 (296)	138 (56)	125 (87)

Values in parentheses indicate standard deviation of the mean for three primary locations.

production in seagrass habitat corresponded with changes in the habitat; seagrass biomass was also relatively high during the summer period (Table 7; also Edgar et al., 1994).

Annual fish production was not significantly correlated ($\text{df} = 11$, $r^2 = 0.17$, $p < 0.05$) with annual macrofaunal production (as shown in Table 5 of Edgar et al., 1994). However, fish production (F) was significantly related to both macroepifaunal production (E) ($F = 1.73 + 0.21 \times E$, $r^2 = 0.52$, $0.01 < p < 0.05$) and macrocrustacean production (C) ($F = 0.08 + 0.68 \times C$, $r^2 = 0.56$, $0.01 < p < 0.05$), the two major components of macrofaunal production eaten by fishes (see Edgar & Shaw, 1995).

The size-distribution of fish assemblages differed between habitats (Fig. 4). At seagrass sites, small fish less than 10 g wet weight were more abundant and productive ($>20 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) than in the other habitats. In channel habitats most fish production was contributed by fish >100 g whereas in unvegetated habitats most production was contributed by fish at an intermediate size.

3.4. Abundance of large fishes

The numbers of the different fish species collected by gillnet are shown in Table 8, and the mean number of fish collected from different sites using 64-mm and 108-mm mesh gillnets in Figs. 5 and 6. The total number of fishes collected by 64-mm gillnet varied significantly between habitats over a 3-fold range (three-way ANOVA: $\text{df} = 2/8$, $F = 39.63$, $p < 0.001$; Fig. 5). This variation was due to differences in the number of yellow-eyed mullet (*Aldrichetta forsteri*) collected in different habitats; the number of fishes other than mullet remained constant amongst habitats at ≈ 3 fishes per net at the primary sites ($\text{df} = 2/8$, $F = 3.41$, $p > 0.05$). Most of the abundant species collected in gillnets apart from mullet were species that feed largely on other fishes.

In contrast to the large difference in number of fishes collected from different

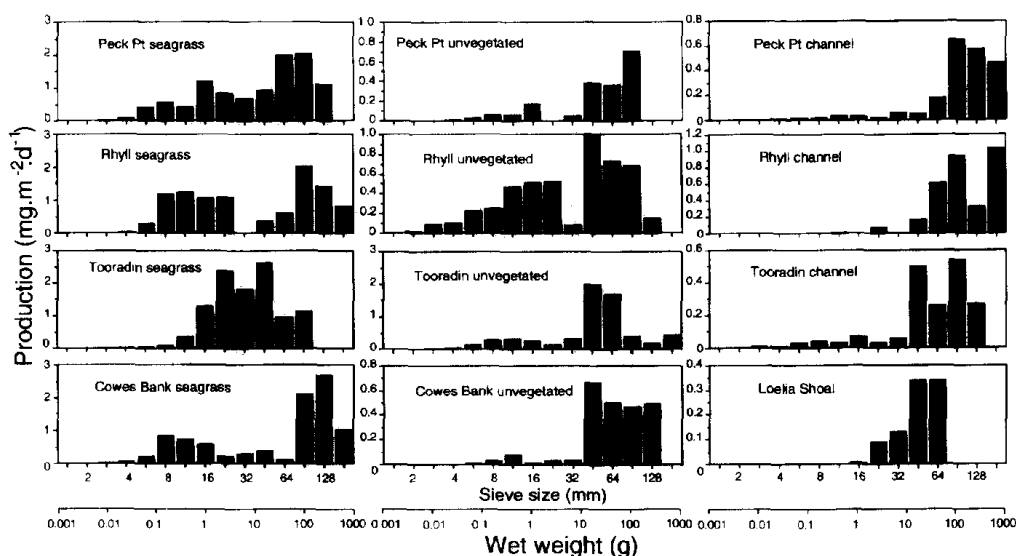


Fig. 4. Estimated daily production ($\text{mg AFDW} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) of different size-classes for small fish assemblages associated with seagrass, unvegetated and channel habitats in Western Port. In order to facilitate comparisons between fish, benthos and fish prey size-classes (Edgar et al., 1994; Edgar & Shaw, 1995), size is expressed using two different scales: wet weight of fish and sieve size-class. The latter represents the measured range in biomass of benthic animals retained by sieves of different mesh size (Edgar, 1990).

habitats using seine nets, no significant difference in number of fish 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: $\text{df} = 2/8$, $F = 1.62$, $p > 0.05$). However, approximately twice as many fishes were collected from Loelia Shoal as from the primary localities (Fig. 6), possibly because that site was

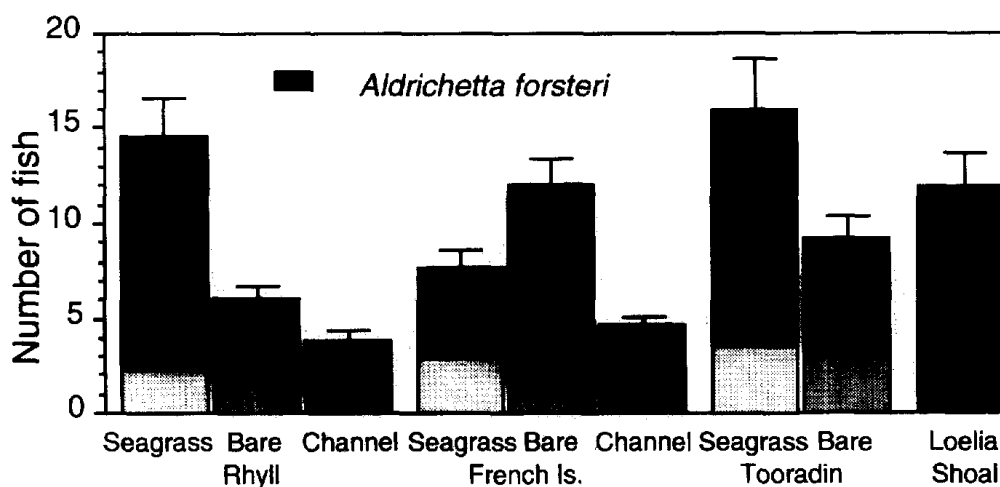


Fig. 5. Mean abundance ($\pm \text{SE}$) of fishes collected in 64-mm mesh gillnets from different sites.

Table 8
Total numbers of fishes collected from different sites using gillnets with 64-mm (Net 1) and 108-mm (Net 2) mesh panels

Site:	PH		PU		PC		RH		RU		RC		TH		TU		LS		Total
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
Net:																			
Species																			
<i>Heterodontus portusjacksoni</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Parascyllium ferrugineum</i>	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	5
<i>#Juncus vincenti</i>	0	0	0	0	4	0	0	0	0	0	0	0	3	0	0	0	0	0	7
** <i>Mustelus antarcticus</i>	5	32	16	9	7	25	0	1	0	0	0	1	2	5	2	2	0	2	109
** <i>Galeorhinus australis</i>	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	9
<i>Trygonorhina guanerus</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	4
<i>Raja lemprieri</i>	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	3
<i>Urolophus cruciatus</i>	0	0	2	0	0	1	0	0	1	0	3	1	0	0	0	0	0	0	8
<i>Urolophus paucimaculatus</i>	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	4
<i>Myliobatis australis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
* <i>Callorhynchus milii</i>	0	1	5	10	6	5	1	1	1	2	5	1	0	0	0	0	156	50	244
** <i>Pseudophycis bachus</i>	1	0	9	0	6	0	15	0	6	0	20	0	0	0	0	0	6	0	63
** <i>Genypterus tigerinus</i>	1	0	0	0	0	0	0	0	3	0	1	1	0	0	1	0	0	0	7
* <i>Hyporhamphus melanochir</i>	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Gymnapistes marmoratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
* <i>Platycephalus bassensis</i>	0	1	13	2	16	0	2	0	13	2	7	0	0	0	0	0	10	3	69
* <i>Platycephalus speculator</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
** <i>Platycephalus laevis</i>	35	7	1	0	9	0	22	2	6	0	14	0	8	1	2	0	0	0	107
* <i>Chelidonichthys kumu</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
* <i>Sillaginodes punctatus</i>	3	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	8
** <i>Pomatomus saltator</i>	3	0	4	0	1	0	1	0	0	0	1	0	6	0	7	0	10	0	33

<i>*Pseudocaranx dentex</i>	1	1	35	0	4	1	3	1	4	0	6	6	21	11	28	13	16	2	153
<i>*#Trachurus declivis</i>	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	4
<i>*#Aripis trutta</i>	0	0	355	12	31	0	1	0	1	0	1	0	0	0	1	0	0	0	402
<i>*#Aripis truttacea</i>	12	0	102	0	0	0	4	1	2	0	1	0	8	0	5	0	0	0	135
<i>*Petaceroopsis recurvirostris</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Dactylophora nigricans</i>	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>*Aldrichetta forsteri</i>	198	0	149	0	16	0	483	1	119	0	13	0	212	0	105	4	0	0	1300
<i>#Sphyræna novaehollandiae</i>	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	5
<i>*Haletta semifasciata</i>	6	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	9
<i>*#Thyrssites atum</i>	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	6
<i>*Seriotelella brama</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>*Ammotretis rostratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	3
<i>*Rhombosolea tapirina</i>	1	5	0	1	0	1	1	5	1	3	1	0	1	7	1	3	1	0	32
<i>*Meuschenia freycineti</i>	16	4	0	0	0	2	4	0	0	0	3	0	2	0	1	0	0	0	32
<i>Contusus brevicaudus</i>	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	3
<i>Tetractenos glaber</i>	5	0	2	0	0	0	2	0	7	0	1	0	1	0	1	0	0	0	19
<i>Diodon nichemerus</i>	20	5	3	3	2	2	5	5	1	2	1	7	8	3	0	3	0	0	71
Total	317	57	705	37	112	38	547	20	170	10	89	19	275	27	157	29	203	59	2871

Sites are abbreviated as follows: Peck Point seagrass (PH), Peck Point unvegetated (PU), Peck Point channel (PC), Rhyll seagrass (TH), Rhyll unvegetated (RU), Rhyll channel (RC), Tooradin seagrass (TI), Tooradin unvegetated (TU), Loelia Shoal (LS).

* Commercially-important species, # piscivorous species (see Edgar & Shaw, 1995).

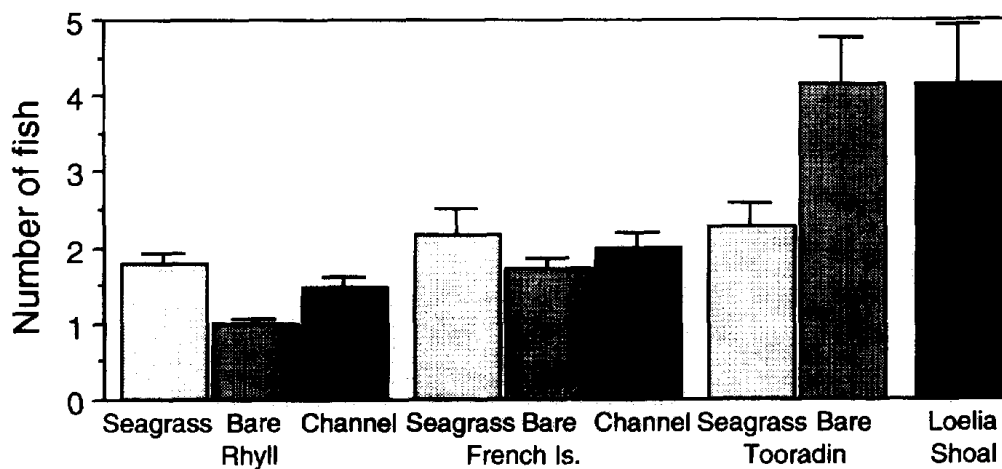


Fig. 6. Mean abundance (\pm SE) of fishes collected in 108-mm mesh gillnets from different sites.

near the entrance to the bay and was on a migratory route for coastal fishes entering the area (see Table 8).

4. Discussion

4.1. Seagrasses as nursery habitats

The study provided no indication that seagrass beds were more important nursery sites than other habitats in Western Port. Two species of minor commercial importance, the six-spined leatherjacket *Meuschenia freycineti* and blue rock whiting *Haletta semifasciata*, were found to associate strongly with seagrass beds; however, these two species were found in seagrass beds 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 (Edgar & Shaw, unpubl. data). Other fishery species (e.g. the flounders *Rhombosolea tapirina* and *Ammotretis rostratus* and the flathead *Platycephalus bassensis*) were associated with unvegetated habitats throughout their post-settlement lives, while the majority of the larger, commercial species (e.g. *Sillaginodes punctatus*, *Aldrichetta forsteri*, *Mustelus antarcticus* and *Arripis* spp.) were collected from both seagrass and unvegetated habitat types.

Robertson (1977) considered that King George whiting (*Sillaginodes punctatus*) utilized seagrass beds as nursery habitat, and this association between juvenile whiting and seagrasses has since been used to explain a decline in whiting catch rates in Western Port following seagrass dieback (Shepherd et al., 1989). Our data indicate 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

(Connolly, 1994), and observations while diving (by G. Edgar) indicated 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 (<10 g weight) was greater in seagrass habitat than in either shallow unvegetated or channel habitats (see Fig. 4). 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, pipefishes and weedfishes which also mature at a small size. In other areas, this small fish component may include a much greater proportion of commercially-valuable species.

4.2. Reliability of density and production estimates

The present study is only the second to provide estimates of densities and production of fish communities at a variety of sites (following Möller et al., 1985). The cost of investigating numerous sites rather than concentrating effort at a single location is a reduction in the accuracy of production estimates due to increased sampling error and the use of analytical approximations. The major source of error in density estimates probably resulted from the difficulty in calibrating fish numbers per net haul with absolute fish densities. The drop trap densities used to calibrate seine numbers were presumably themselves subject to error, although for small, relatively immobile species this error should not be great (Kushlan, 1981; Pihl & Rosenberg, 1982; Sogard et al., 1987). Of more concern is bias introduced if large or pelagic species were captured with substantially-different efficiency using seines than small demersal species. Such bias may well occur given the measured level of variation in capture efficiency for different species (Table 5). Pierce et al. (1990) found that open-water fishes were captured with an overall $\approx 20\%$ greater efficiency than demersal fishes in trials conducted in freshwater habitats. However, even if such bias does occur, the small open-water species contributed relatively little of the total production in most habitats in our study, with *Hyperlophus vittatus* the only open-water species that was common.

A systematic error would also have been introduced into calculations if the capture efficiency of seine nets differed substantially between habitats. The difference detected in overall net efficiency between seagrass (28%) and unvegetated (20%) habitats was ignored because it was relatively small and these efficiency values were based on a limited sampling program carried out at a single pair of sites over a short time period. Further work is needed to adequately determine whether the use of a single mean efficiency value for different habitats is justified, or whether the capture efficiency in vegetated habitats systematically differs from that in bare habitats. High macrophyte biomass was found by Pierce et al. (1990) to increase seine capture efficiency in freshwater habitats.

Other potential sources of error in density estimates were disturbance to the fish community during the setting and hauling of the seine net, and the lack of

information on the densities of fishes at night. These errors were probably minor because of the period allowed to elapse after setting the net before it was pulled (>2 min), and because no species clearly switched between habitats on a diel basis (see Table 2). The results of the ANOVA (Table 4) indicate that the total number of animals collected during the day at the Peck Point sites examined did not differ significantly from the number collected at night (see Sogard et al., 1987), and that little of the total variance in abundance estimates was contributed by the time of day factor.

Most of the error in estimates of production at different sites was probably caused by error in the calculation of fish densities, rather than in the conversion of density data to production data. At the primary seagrass and unvegetated sites most of the fish production was calculated directly using modal frequency analysis. The modes used in this analysis were generally clear (see Fig. 2) so annual estimates should be reliable. Seasonal estimates would be considerably less accurate than annual estimates because few size-classes were used for many species (Fig. 2). Although underestimated production may occur in one season by reading a mode at the lower rather than upper end of a size-class, these errors should be compensated by a corresponding overestimate in the following season.

The errors that may arise when estimating annual production using regression equations that relate production to biomass and water temperature have been discussed previously in relation to invertebrate data (Edgar, 1990). Such errors would be most substantial in channel habitats where only a relatively small proportion of fish production was calculated directly using size-frequency analyses.

Although the novel method used here to calculate small fish production incorporates a number of errors and approximations as described above, it produces estimates of annual production at Western Port that are comparable with the few published estimates for temperate and subtropical fish communities elsewhere. Production in Western Port seagrass beds ($\approx 3.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) was slightly lower than the estimate of Adams (1976) for fish production in an eelgrass bed in North Carolina ($\approx 4.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), slightly higher than the production of the four dominant fish in the Laguna Madre of Texas ($\approx 3.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Hellier, 1962), and approximately the same as the production of the six dominant fish species in Chesapeake Bay ($4.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Lubbers et al., 1990). Production at unvegetated Western Port sites (0.7 to $2.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) were within the range of estimates for sites along the Swedish coast (0.2 to $5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Möller et al., 1985) and marginally lower than in Chesapeake Bay ($2.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Lubbers et al., 1990).

The usefulness of the production approach used here will ultimately depend on whether a strong biological signal remains at the end of calculations, or whether the noise generated by accumulating errors swamps the information content contained in the original data set. Examination of Tables VI and VII indicates that production calculations yield a much more stable signal than density calculations. Despite an order of magnitude fluctuation in fish densities in different seasons and at different sites, the estimated production of fish communities varied over only a

twofold range between seasons at the unvegetated and channel sites, and over a similar range at different primary sites within a habitat type. The estimated production of fish assemblages associated with seagrass habitat seasonally varied over a fivefold range; however, this fluctuation corresponded with changes in seagrass biomass, and levels of production were similar in unvegetated habitat and seagrass habitat during the season of low plant biomass. We consider that these results, and the concurrence of community production estimates here with those produced using different methods overseas, indicate that production estimates provide better insight into the biological properties of communities than estimates of density; densities can differ greatly between sites due to considerable variation in the abundances of small animals that have little ecological importance. Furthermore, production estimates are not only of interest in their own right but are proportional to several other important properties of communities, most notably total consumption and respiration (see Edgar, 1993).

4.3. Effect of seagrass loss on fish production

Small fish assemblages at the primary seagrass sites were over twice as productive as at unvegetated sites ($3.82 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in seagrass cf. $1.58 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in unvegetated habitat). 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 (Edgar et al., 1994), the difference in small fish production between habitats ($2.24 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) translates to a total reduction of small-fish production throughout Western Port of ≈ 630 tonnes AFDW $\cdot \text{yr}^{-1}$ since 1970. This estimate should, however, be treated with caution as it assumes that fish communities present on seagrass habitat prior to seagrass dieback were similar to those found in the present study. The dominant species in our study differed from those collected by Robertson (1980) at Crib Point on the western shore of Western Port in 1974/1975, with three of the 10 common species listed by Robertson (1980) being rare in our seine samples. (A further species *Arenigobius bifrenatus* was also disproportionately abundant in 1974 but was presumably misidentified *Arenigobius frenatus*, a species that had not been recognized from Victorian waters in 1980.) This difference between studies was, however, probably related to differences in sampling techniques rather than long term changes in the fauna. The species disproportionately abundant in Robertson's study (*Atherinosoma presbyteroides*, *Atherinosoma microstoma* and juvenile *Aldrichetta forsteri*) tend to remain in shallow water following the tide and are therefore concentrated near the waters edge (Edgar & Shaw, unpubl. obs.). Robertson's technique of pulling the net into shore would therefore result in disproportionately high numbers of these species being collected relative to numbers obtained by pulling the seine into a boat.

A study by Howard & Koehn (1985) nevertheless provides clear evidence that the pipefish fauna has changed during the past 15 yr. Howard & Koehn (1985) sampled Rhyll seagrass beds for pipefish by beam trawl in 1978 and collected only two specimens of *Stigmatopora nigra* and no *Stigmatopora argus*, whereas other

syngnathid species were abundant. *Stigmatopora nigra* was by far the most common fish collected from this site during our study, with *Stigmatopora argus* also common.

Direct estimates of the effect of seagrass loss on larger fishes cannot be made from this study because gillnets are highly selective samplers; however, the elevated small fish production in seagrass habitats does not seem to flow substantially up the food chain to the larger carnivorous fishes. Only the presence of yellow-eyed mullet elevates total catches of fish 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 fish collected with the 108-mm mesh gillnet were found between seagrass and unvegetated habitat types.

One reason for the differences in small fish production between seagrass and unvegetated habitats not translating into major differences in the production of larger fishes may be that many of the larger species fed on pelagic resources that are distributed independently of benthic habitat type. The fishery species *Arripis trutta*, *Arripis truttacea*, *Trachurus declivis*, *Thyrsites atun* and *Pomatomus saltator* were all commonly collected in our gillnets and fed primarily on clupeoid fishes (see Edgar & Shaw, 1995) which in turn fed on planktonic copepods. The presence of much greater numbers of these fishes compared with demersal species in gillnet catches may have obscured habitat differences.

Because the number of yellow-eye mullet collected by small mesh gillnet differed between habitats with $\approx 70\%$ more collected from seagrass than unvegetated habitat, the loss of seagrass habitat from the Bay may have resulted in a overall decline in the population size of this species. This prediction is not, however, supported by fishery catch statistics from Western Port, which show that the total catch of mullet increased following the period of seagrass dieback (Shepherd et al., 1989). As expected, fishery catch data indicate that populations of the two major species directly associated with seagrass beds, *Haletta semifasciata* and *Meuschenia freycineti*, declined rapidly following the loss of seagrass cover (Shepherd et al., 1989).

Catch statistics for the two other commercially-important demersal species commonly collected in our study, gummy shark (*Mustelus antarcticus*) and elephant shark (*Callorhynchus milii*), are not available for Western Port. However, catches of these species would not be expected to have declined significantly following the loss of large areas of seagrass because neither species was positively associated with seagrass habitat, with only three elephant shark collected from this habitat type.

While our study indicated that seagrass habitat in Western Port did not support substantially higher densities of large fishes than unvegetated habitat, nor did it provide a major habitat for juveniles of economically-important fish species, we cannot fully assess the value of seagrass habitat to the local commercial fishery because the large scale environmental effects of seagrass beds remain unknown. Relationships between seagrass production and fish production were only investigated on the scale of hundreds of metres, whereas most seagrass production is not utilised *in situ* but is exported from seagrass beds (see Whitfield, 1988). The

long-term effects of the loss of seagrass beds on a bay-wide scale should therefore include greatly reduced production of detritus, much of which is bound into the sediment. Turbidity within the bay has also increased during the past two decades (Shepherd et al., 1989), probably largely because seagrass beds formerly present in shallow water precipitated and trapped suspended particulate material. These changes are likely to affect fish production in unvegetated as well as vegetated habitats throughout the bay.

Acknowledgements

The project was funded by a grant from the Fishing Industry Research and Development Corporation. Comments on the manuscript provided by G.F. Watson and G.P. Jenkins were much appreciated, as was access to unpublished data of A.I. Robertson.

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