Vol. 307: 233–246, 2006 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published January 24

Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches

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ABSTRACT: Detached macrophytes (seagrass and macroalgae) are transported from more offshore areas and accumulate in substantial volumes in surf zones, where they are commonly called wrack. Fishes were sampled using seine nets in 4 volume categories of detached macrophytes (bare sand, low, medium and high volumes) in the surf zone at 2 sandy beaches in southwestern Australia to determine how increasing volumes of surf-zone wrack influences fish community and size composition. Species composition and densities of fish, which were dominated by juveniles, differed between areas where wrack was present or absent, and also among volumes of wrack in the surf zone. Total fish abundance and biomass increased as the volume of wrack increased. *Cnidoglanis macrocephalus* and *Pelsartia humeralis* were the dominant species and were most abundant in medium and high wrack volumes. Fish gut contents were analysed for *C. macrocephalus* and *P. humeralis*, and verified that *Allorchestes compressa* is a major prey item for juveniles of these species. A series of habitat preference trials conducted in outdoor aquaria tested whether juvenile *C. macrocephalus* and *P. humeralis* showed a preference for different types of detached macrophytes as a habitat, i.e. seagrass, brown algae, or a mixture of both macrophyte types. Non-parametric goodness-of-fit binomial tests for differences in the number of fish between each habitat type showed no clear pattern in habitat preference for either species of fish. Field and laboratory results suggest that the amount, rather than type, of detached macrophytes is more important in providing a habitat for juvenile *C. macrocephalus* and *P. humeralis.*

KEY WORDS: Detached macrophytes · Fish communities · Surf zone · Sandy beaches · Habitat structure · Wrack

INTRODUCTION

The surf zones of sandy beaches have been described as physically dynamic environments that provide little habitat complexity and minimal shelter for fishes (McLachlan 1983, Robertson & Lenanton 1984, Lasiak 1986, Romer 1990, Ayvazian & Hyndes 1995). Compared to seagrass meadows and reefs, unvegetated areas are often considered a poor substitute in fish habitats due to their diminished structural complexity (Bell & Pollard 1989, Jenkins & Wheatley 1998). Nevertheless, unvegetated nearshore areas are able to support significant fish populations (Lasiak 1981, Lenanton 1982, Ayvazian & Hyndes 1995), with the fish fauna primarily comprising juveniles and dominated by a small number of numerically abundant species (Lasiak 1981, Modde & Ross 1981, Lenanton 1982, Lasiak 1984, Ayvazian & Hyndes 1995, Santos & Nash 1995). One factor contributing to these high abundances of fish is the presence of detached macro-

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phytes (seagrasses and macroalgae), which accumulate in surf zones, where they are commonly called wrack and provide a habitat for invertebrates (primarily amphipods) and fish (see Kirkman & Kendrick 1997, Colombini & Chelazzi 2003). Since the increased habitat complexity and heterogeneity provided by attached seagrass and algae can strongly influence fish assemblages (Wheeler 1980, Bell & Pollard 1989, Carr 1994, Jenkins & Sutherland 1997, Jenkins & Wheatley 1998, Jackson et al. 2001), it is likely that these detached macrophyte accumulations benefit surf-zone fauna by providing a greater food source (Robertson & Lenanton 1984) and increasing habitat complexity.

Accumulations of detached macrophytes in near-shore areas are derived from coastal seagrass beds and reefs (Kirkman & Kendrick 1997, Colombini & Chelazzi 2003). During storms and heavy swells, large quantities of macrophytes can detach and accumulate along the shore in the surf zone and on beaches (Kirkman & Kendrick 1997, Colombini & Chelazzi 2003). The amount and timing of accumulations is extremely variable and may differ geographically depending on climate and hydrodynamics, and the vicinity to rocky shores, reefs or seagrass meadows (Ochieng & Erftemeijer 1999, Colombini & Chelazzi 2003). In southwestern Australia, wrack accumulations show a high degree of temporal and spatial variability (Robertson & Lenanton 1984). The longshore distribution of detached macrophytes along the southwestern Australian coastline is likely to range from 100s to 1000s of metres, with the offshore distribution likely to extend from 10 to 100 m. Furthermore, biomass of wrack changes daily due to the exchange of material between the beach and the surf zone, and seasonally through the strong influence of storm events. Higher biomass of detached macrophytes is present in late autumn to early spring, which correlates with the time of year when frequent storms increase the intensity and frequency of seas and swell in the region (Lemm et al. 1999).

Previous studies have shown that some fish species rely either directly on detached macrophytes (as shelter from predators or as a means of dispersal), or indirectly by feeding on the associated invertebrate fauna (e.g. Stoner & Livingston 1980, Lenanton et al. 1982, Robertson & Lenanton 1984, Lenanton & Caputi 1989, Safran & Omori 1990, Kingsford 1992, Langtry & Jacoby 1996). Fish abundance has been positively correlated with the presence and volume of detached macrophytes (Lenanton et al. 1982, Robertson & Lenanton 1984, Lenanton & Caputi 1989, Vanderklift & Jacoby 2003). However, these studies have focused on particular species rather than the broader fish community and have not tested this relationship empirically. Furthermore, since wrack can consist of different types of macrophytes (e.g. seagrass and brown algae), which exhibit different plant structure, fish may show a preference for wrack with different habitat structure.

Detached macrophytes can form large accumulations in surf zones of southwestern Australia, where large numbers of fish, particularly the juveniles of *Cnidoglanis macrocephalus* (cobbler, Plotosidae) and *Pelsartia humeralis* (sea trumpeter, Teraponidae) occur (Lenanton et al. 1982, Robertson & Lucas 1983, Robertson & Lenanton 1984, Lenanton & Caputi 1989). Wrack in the surf zone of this region largely comprises seagrass and brown algae (particularly the kelp *Ecklonia radiata*), with smaller amounts of red and green algae (Hansen 1984, Kirkman & Kendrick 1997). The habitat structure of detached macrophytes, in terms of the volume and type of plant material, may therefore influence fish communities. We thus aimed to determine whether increasing volumes of surf-zone wrack is likely to influence fish community and size composition. We also aimed to determine whether juveniles of 2 dominant wrack-inhabiting species show a preference for different types of macrophyte as a habitat, and to examine the dietary composition of these 2 dominant species.

MATERIALS AND METHODS

Wrack volume sampling. Fish were sampled in the surf zone of 2 sandy beaches (Shoalwater Bay and Hillarys) on the southwestern coast of Australia (Fig. 1). These sites were chosen because, during autumn and winter, they regularly receive large amounts of wrack, consisting of a mixture of different types of detached macrophytes (i.e. both seagrass and macroalgae) rather than a homogeneous spread of either seagrass or macroalgae. In addition, the 2 sites provided different levels of exposure to wave and swell activity, with Shoalwater Bay being less exposed. The 2 sites were categorised according to the criteria provided by Valesini et al. (2003) as 'moderately exposed to wave activity, with dense seagrass beds located more than 50 m from the shoreline' (Habitat type 4) for Shoalwater Bay, and 'moderately to fully exposed to wave activity, with reefs present within 50 m of the shoreline and also further offshore; vegetation largely restricted to macroalgae associated with reefs' (Habitat type 5) for Hillarys. These 2 habitat types are representative of the surf-zone habitats within the broader study region. Sampling was carried out in autumn and winter at Shoalwater Bay (May and June 2003) and in winter at Hillarys (July and August 2003), when sufficient wrack was present in the surf zone.

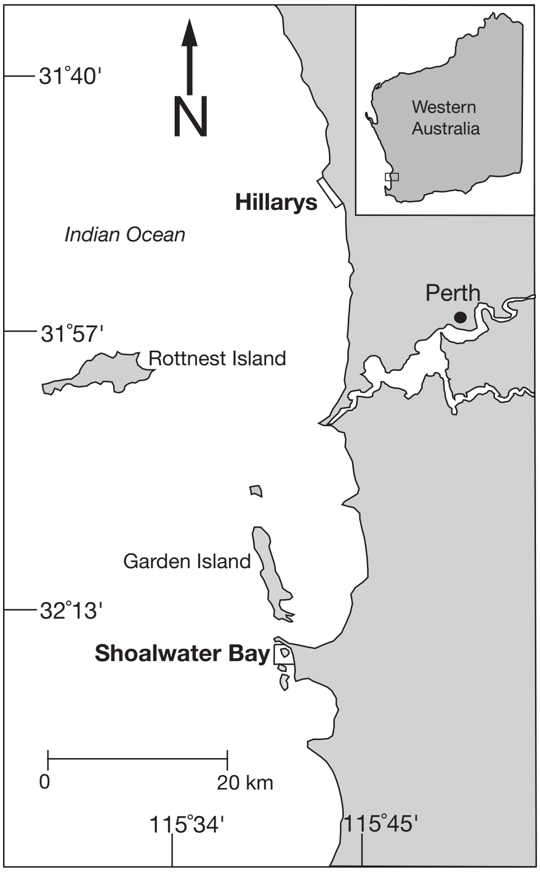

Fig. 1. Map of study area showing location of Shoalwater Bay and Hillarys beaches on the southwestern coast of Australia

At both sites, fish were sampled in surf-zone areas containing 1 of 4 volume categories (per 100 m^2) of detached macrophytes: bare sand (0 l), and low (50 to 150 l), mid (250 to 450 l) and high (750 to 1650 l) volumes. These categories of wrack volumes were selected because they reflected the natural amounts of wrack present in the surf zone. The mean and range of wrack volumes sampled for each site are summarised in Table 1. Since it was impossible to determine from the shore the actual volume of wrack in the water, samples were kept only when the volume of wrack fitted within the range of one of the above categories. Volumes of wrack greater than the high volume category were not sampled because they were too heavy for use of this method.

A 21.5 m long and 1.5 m high seine net comprising 10 m long wings (6 m of 9 mm mesh and 4 m of 6 mm mesh) and a 1.5 m bunt (6 mm mesh) was used to sample fish at Shoalwater Bay. However, this net tore repeatedly during sampling at the more exposed Hillarys site, due to the additional surge of water and greater pressure on the net, and therefore seining for fish at this site was carried out using a different net of same length and height but with a wing mesh size of 15 mm with a 1.5 m bunt (6 mm mesh). The seine nets were fully extended parallel to the beach at a depth of approximately 1 m, and dragged towards the beach, sweeping an area of approximately 116 m^2 to collect both detached macrophytes and fish.

Six replicate samples were collected from each of the 4 volume categories (i.e. bare sand and low, mid and high macrophyte volumes) over the 2 mo sampling period. Fish and wrack from each seine were sorted on the beach and the volume of wrack collected in each haul was measured using an 80 l plastic container and recorded. In the laboratory, the number of individuals and biomass (to the nearest 0.1 g wet weight) for each fish species and the total length (TL, to the nearest mm) of each individual were recorded.

A total of at least 10 individuals of juvenile *Cnidoglanis macrocephalus* (<180 mm) and *Pelsartia humeralis* (<100 mm) were collected in wrack at each site in winter 2003 and 2004 for gut content analysis. The stomach from each fish was removed and stored in 70% ethanol. The gut contents were examined under a dissecting microscope and each dietary item was identified to the lowest possible taxon. Since *C. macrocephalus* does not have a well-defined stomach (Nel et al. 1985), the content of their diet was based on the first two-thirds of the intestine. Since some dietary items were quite decomposed, making it difficult to determine accurately the number of individuals for each dietary item, the contribution of each dietary item was recorded as percentage contribution to the total volume of all dietary items present in each stomach for each individual (%V) (Hyslop 1980).

Multivariate analyses were used to investigate patterns in the species composition of fish in the different categories of wrack volume using Primer 5 (Clarke & Gorley 2001). The abundance and biomass data, derived from the 6 replicate samples in each wrack volume category, were square-root transformed and the Bray-Curtis similarity measure was used to construct the similarity matrix. Data were ordinated using nonmetric multi-dimensional scaling (nMDS) to examine

Table 1. Mean (±SE) and range of wrack volumes (l per 100 m^2) for bare sand, low, mid and high volume categories at Shoalwater Bay and Hillarys. Sample size is 6 for each wrack volume category at each site

Category	Shoalwater Bay		Hillarys	
	Mean	Range	Mean	Range
Bare sand	0 ± 0	0–0	0 ± 0	0–0
Low	93 ± 12	55–140	84 ± 14	55–140
Mid	330 ± 21	280–420	320 ± 23	275–430
High	944 ± 65	790–1205	1070 ± 119	785–1585

overall patterns in similarities of species composition and 1-way analysis of similarities (ANOSIM) was used to test for differences among volume categories. One replicate from the mid volume category from Shoalwater Bay was removed from the nMDS analysis since it contained no fish. Pairwise comparisons for each category were carried out to determine which categories differed significantly. Multivariate dispersion (MVDISP) was used to determine the variability in the species composition of samples within each category, while similarity of percentages (SIMPER) was used to determine which fish species were causing the dissimilarity between categories.

The number of each species at each site was expressed as densities, i.e. number of individuals per 100 m^2. Since different nets had to be used at each site, analysis of variance (ANOVA) was carried out separately for Shoalwater Bay and Hillarys. Thus, for each site, 1-way ANOVA was used to determine whether there were significant differences among wrack volume for the number of species, total density of individuals and total biomass, as well as for the density and biomass of *Cnidoglanis macrocephalus* (cobbler) and *Pelsartia humeralis* (sea trumpeter). Bare sand and low volume categories that did not contain any fish were excluded from the analyses for *C. macrocephalus*, as consistent zero values in these categories resulted in a high level of heterogeneity in the variance. Analyses were carried out using SPSS (Windows, Rel. 11.5.0. 2002 Chicago: SPSS). Wrack volume was considered a fixed factor. Prior to performing ANOVAs, the data were examined for normality and tested for homogeneity of variance using Levene's test and $\log_{10}(N + 1)$-transformed if necessary. Tukey's HSD test was used to test for significant differences in pairwise comparisons of wrack volume categories.

Wrack type experiment. A habitat-choice experiment for juvenile *Pelsartia humeralis* (between 80 and 120 mm TL) and *Cnidoglanis macrocephalus* (between 100 and 180 mm TL) was conducted using different macrophyte habitat types. A series of attempts was made to carry out this part of the study *in situ*. However, due to strong longshore currents and the water movement resulting from tides, it became impossible to retain the various wrack types in confined areas. Trials were therefore conducted in a series of outdoor aquaria during spring 2003. The aquaria were made of fibreglass (50 cm high, 160 cm long and 70 cm wide), and equipped with flow-through seawater and maintained at a water depth of approximately 45 cm, with the aquaria emptied and the water changed in between trials. The tanks were housed in an outdoor wire cage and were exposed to natural sunlight and weather conditions. The temperature of the flow-through seawater was approximately 18°C throughout the duration of the experiment.

Three different habitat types were examined: (1) seagrass only (*Posidonia* and *Amphibolis* species); (2) brown algae only (*Ecklonia* and *Sargassum* species); and (3) a mixture of seagrasses and brown algae in equal proportions. These types of macrophytes were chosen on the basis that, in terms of volume, they were the most prevalent types of macrophyte in the wrack in the surf zone, and therefore provided the most likely suite of habitats available for fish to occupy. Wrack at a range of locations along the coastline of the study region comprised 26% brown algae, 46% seagrass and 19% red algae in terms of biomass (K. Crawley unpubl. data). Pairwise comparisons between each habitat type were used in each treatment, giving a total of 3 treatments. The experiments were conducted over a period of 4 wk, with 3 tanks available on each occasion. Six replicates were conducted for each of the 3 treatments, with 1 replicate for each treatment carried out on each occasion. The replicates for each treatment were randomly assigned to the tanks for each trial. The wrack used in the experiment was collected fresh from local beaches and sorted by type of wrack. Epiphytes remained on the macrophytes to keep the wrack as close to its natural state as possible. The wrack was defaunated by bubbling CO_2 through it to remove the influence of food in the habitat choice made by the fish. The wrack was pre-prepared for the trials and then stored in a –20°C freezer until it was defrosted for use in the trials.

Pelsartia humeralis and *Cnidoglanis macrocephalus* were chosen for the trials since they were the most abundant species in the wrack during the field component of the study. Individuals of both species were caught using a seine net from surf zones containing wrack accumulations in the Hillarys region. Juvenile sea trumpeter and cobbler were transported in containers with aerated seawater and then transferred to holding tanks containing small amounts of wrack. The fish were kept in the holding tanks for at least 24 h to allow them to acclimatise to being in captivity before being used in experimental trials. The fish were fed either amphipods or brine shrimp and their condition was monitored daily.

Two distinct habitat types were created in each tank by placing 5 l of the appropriate macrophytes at either end of each experimental tank. This volume of wrack material equated to the high wrack volumes described above and was chosen based on the results that this volume contained the greatest abundance of cobbler and sea trumpeter. A corridor of approximately 70 cm of no wrack was established in the middle of the tank between the 2 habitat types to prevent mixing of wrack types.

Since both species appear to occupy wrack during both the day and night, and feed on similar prey during both periods (Robertson & Lenanton 1984), observations were restricted to the diurnal period. Ten randomly selected individuals of each species were added to the centre of each tank at dusk between 17:00 and 18:00 h. The fish were then left overnight for approximately 18 h to select a habitat. The trials were terminated at midday by placing a divider down the middle of the tank, thereby containing the fish in their 'chosen' habitat type. Fish were removed from each half of the tank and the number of fish in each habitat type was recorded. Macrophyte material and individuals of fish were never used more than once during the experiment.

A non-parametric goodness-of-fit binomial test for nominal data was used to test whether the overall proportion of fish in either habitat across the 6 replicates showed a significant deviation away from a probability of 0.5 for equal distribution between habitat types. Bonferroni post hoc comparisons of treatment means were used to determine which treatments differed from one another. Analyses were carried out using SPSS (Windows, Rel. 11.5.0. 2002 Chicago: SPSS).

RESULTS

Wrack volume sampling

Total catches and species contributions

Seine hauls from both sites yielded 25 species of fishes from 16 families, with 23 species from 15 families at Shoalwater Bay and 10 species from 9 families at Hillarys (Table 2). At both sites, the high wrack volume category contained more fish than the other categories (Table 2). *Pelsartia humeralis* was the only species found in all 4 volume categories at both sites, and its abundance increased as wrack volume increased. In comparison, *Cnidoglanis macrocephalus* was absent from bare sand at both sites, and like *P. humeralis*, its abundance increased in the higher wrack volumes (Table 2).

At Shoalwater Bay, *Pelsartia humeralis* and *Cnidoglanis macrocephalus* were far more abundant in the highest volume of wrack, while *Atherinosoma elongata*, *Leptatherina presbyteroides* and *Atherinomorus ogilbyi* were also more abundant in this category. In

Table 2. Total abundance and average total lengths (TL, mm) (and range) of the species contributing to the catches in bare sand (BS), low, mid and high volumes of wrack at Shoalwater Bay and Hillarys. Sample size is 6 for each wrack volume category at each site

Family	Species	Shoalwater					Hillarys				
		Abundance				Length (mm)	Abundance				Length (mm)
		BS	Low	Mid	High	Average (range)	BS	Low	Mid	High	Average (range)
Atherinidae	*Atherinosoma elongata*	4	0	9	85	47 (33–57)	0	0	0	0	0
Atherinidae	*Leptatherina presbyteroides*	4	22	60	78	51 (34–64)	0	0	0	0	0
Atherinidae	*Atherinomorus ogilbyi*	6	40	2	90	69 (59–79)	0	0	0	20	95 (82–112)
Clinidae	*Cristiceps australis*	0	0	0	1	145 (145–145)	0	0	0	1	121 (121–121)
Clupeidae	*Spratelloides robustus*	27	5	0	0	27 (22–30)	0	0	0	0	0
Clupeidae	*Hyperlophus vittatus*	83	1	0	1	26 (20–114)	2	0	1	17	61 (52–90)
Enoplosidae	*Enoplosus armatus*	0	0	0	3	53 (46–63)	0	0	0	0	0
Leptoscopidae	*Lesueurina platycephala*	2	3	0	0	58 (49–68)	0	0	1	1	54 (38–71)
Monacanthidae	*Scobinichthys granulatus*	0	0	1	0	46 (46–46)	0	0	0	0	0
Mugilidae	*Aldrichetta forsteri*	1	0	2	4	188 (332–107)	3	0	0	3	286 (110–342)
Mugilidae	*Mugil cephalus*	0	0	0	0	0	1	2	1	12	27 (22–29)
Odacidae	*Haletta semifasciata*	0	0	0	16	102 (80–137)	0	0	0	0	0
Platycephalidae	*Platycephalus speculator*	2	2	2	0	107 (45–182)	0	0	0	0	0
Pleuronectidae	*Ammotretis elongatus*	1	0	0	0	115 (115–115)	0	0	0	0	0
Plotosidae	*Cnidoglanis macrocephalus*	0	0	10	199	108 (50–454)	0	16	39	80	169 (98–435)
Scorpididae	*Scorpis georgianus*	0	0	0	0	0	0	23	2	2	31 (24–38)
Sillaginidae	*Sillago bassensis*	3	4	2	1	94 (68–124)	0	0	0	0	0
Sillaginidae	*Sillago vittata*	2	0	1	0	90 (83–96)	0	0	0	0	0
Sillaginidae	*Sillago schomburgkii*	0	1	1	0	156 (101–210)	0	0	0	0	0
Syngnathidae	*Stigmatopora argus*	1	0	0	0	53 (53–53)	0	0	0	0	0
Syngnathidae	*Mitotichthys meraculus*	0	1	0	0	77 (77–77)	0	0	0	0	0
Teraponidae	*Pelsartia humeralis*	3	15	93	203	59 (24–103)	3	40	63	112	82 (22–140)
Teraponidae	*Pelates sexlineatus*	0	12	0	2	69 (38–98)	0	0	0	0	0
Tetraodontidae	*Torquigener pleurogramma*	0	0	2	1	62 (51–82)	9	91	380	8	58 (45–73)
Tetraodontidae	*Contusus richei*	7	0	0	0	29 (24–38)	0	0	0	0	0
Total catch		146	106	185	684		18	172	487	256	
No. of species		14	11	12	13		5	5	7	10	

contrast, *Hyperlophus vittatus* and *Spratelloides robustus* were the most abundant species in bare sand, with the former species being found almost exclusively in this habitat type (Table 2). At Hillarys, *P. humeralis* and *C. macrocephalus* were also more abundant in the highest volume of wrack, while *Scorpis georgianus* tended to be more abundant in low volumes of wrack and *Torquigener pleurogramma* was present in far greater numbers in medium volumes of wrack (Table 2).

Number of species, abundance and biomass

ANOVA demonstrated that the number of species did not differ significantly among volume categories at Shoalwater Bay (Table 3, Fig. 2), with mean number of species ranging from 3.0 to 4.8. In contrast, the number of species differed significantly among categories at Hillarys. Tukey's test showed that the high volume category contained more species than bare sand, with the mean number of species in the 4 categories ranging from 1.7 to 3.8 (Table 3, Fig. 2).

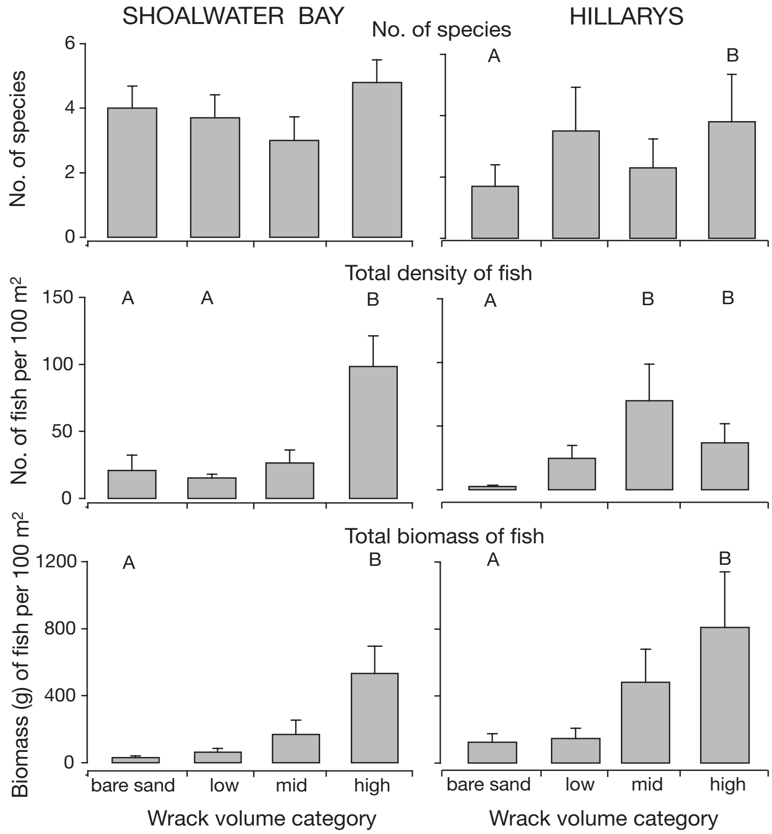

Fig. 2. Mean (+SE) number of fish species and density and biomass of fish found in bare sand, low, mid and high wrack volumes at Shoalwater Bay and Hillarys. Different letters denote volume categories that are significantly different ($p < 0.05$)

Table 3. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Shoalwater Bay and Hillarys: Results of 1-way ANOVA for the number of species, total density and total biomass of all fish, and density and biomass for *C. macrocephalus* and *P. humeralis* in 4 treatments: bare sand, low, mid and high wrack volumes. df: degrees of freedom; **bold** type indicates terms for which $p < 0.05$

Variable	Transformation	df	MS residual	*F*-ratio	p-value
Shoalwater Bay					
Number of species	Untransformed	3	3.008	1.159	0.350
Density	log(*x* + 1)	3	0.21	3.934	**0.023**
Biomass	log(*x* + 1)	3	0.387	4.086	**0.020**
Cnidoglanis macrocephalus					
Density	log(*x* + 1)	1[a]	0.265	9.671	**0.011**
Biomass	log(*x* + 1)	1[a]	0.674	9.149	**0.013**
Pelsartia humeralis					
Density	4th root	3	0.588	6.431	**0.003**
Biomass	Untransformed	3[b]	3673.304	3.974	0.023
Hillarys					
Number of species	Untransformed	3	1.750	3.492	**0.035**
Density	log(*x* + 1)	3	0.213	5.367	**0.007**
Biomass	log(*x* + 1)	3	0.444	3.364	**0.039**
Cnidoglanis macrocephalus					
Density	Untransformed	2[a]	73.928	1.761	0.206
Biomass	log(*x* + 1)	2[a]	0.658	7.644	**0.005**
Pelsartia humeralis					
Density	Untransformed	3[b]	85.897	3.000	0.055
Biomass	Untransformed	3[b]	8850.863	2.308	0.107

[a]Bare sand and/or low categories excluded; [b]accept at 0.01

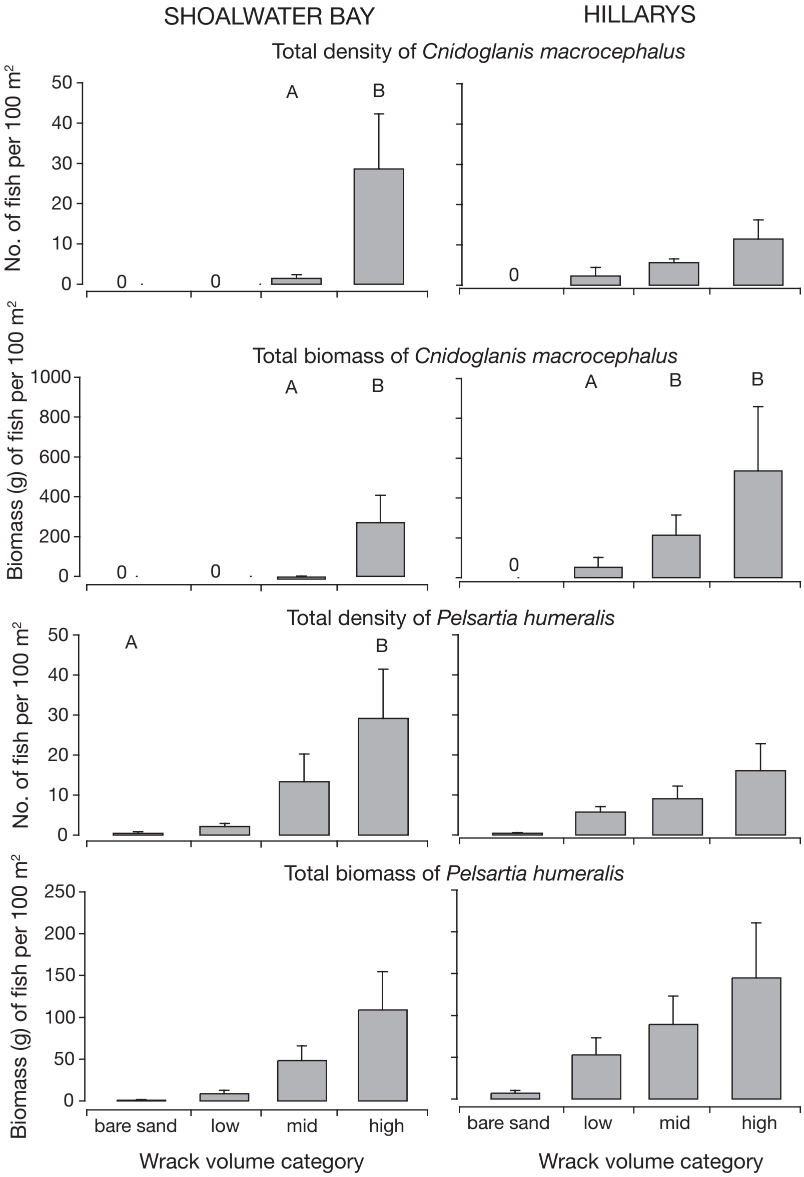

Fig. 3. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Mean (+SE) density and biomass in bare sand, low, mid and high wrack volumes at Shoalwater Bay and Hillarys. Different letters denote volume categories that are significantly different ($p < 0.05$)

ANOVAs revealed that both density and biomass of fish differed significantly among categories at both Shoalwater Bay and Hillarys (Table 3). At Shoalwater Bay, Tukey's test showed that high wrack volumes contained greater densities of fish than bare sand and low wrack volumes, with a trend for fish density to increase with wrack volume from low to high categories (Fig. 2). At Hillarys, Tukey's test showed that both the mid and high wrack categories had greater numbers of fish than bare sand ($p < 0.05$). However, more fish were found in mid wrack volumes than in the high category, due to 1 sample containing a large school of *Torquigener pleurogramma* (Table 2, Fig. 2). The mean density of fish per 100 m^2 in bare sand, low, mid and high volume categories was 20.9, 15.3, 26.6 and 98.3, respectively, at Shoalwater Bay, compared to 2.6, 24.7, 70 and 36.8, respectively, at Hillarys (Fig. 2). In terms of biomass, there was an increase as the volume of wrack increased at both sites (Fig. 2). At both Shoalwater Bay and Hillarys, Tukey's tests showed that the biomass of fish was greater in high wrack volumes than in bare sand ($p < 0.05$).

Cnidoglanis macrocephalus was absent from bare sand areas at both sites, and from the low volume category at Shoalwater Bay (Fig. 3). ANOVA of the remaining 2 categories at Shoalwater Bay revealed significantly greater densities and biomass of *C. macrocephalus* in the high category. While there was no difference in density of *C. macrocephalus* among categories at Hillarys, there was a significant difference in the biomass of this species. Tukey's test revealed that the biomass of *C. macrocephalus* was significantly greater in both high and mid categories compared to low volumes ($p < 0.05$). For both sites, there was a consistent increase in the mean density and biomass of *Pelsartia humeralis* as the volume of wrack increased. However, there was no significant difference among volume categories due to the high degree of variability in the higher volumes of wrack, except for the density of *P. humeralis* at Shoalwater Bay (Table 3, Fig. 3). Tukey's test revealed that the density of *P. humeralis* was significantly greater in high wrack volumes than bare sand at Shoalwater Bay ($p < 0.05$).

Size distribution of fish

At both Shoalwater Bay and Hillarys, 95% of all species were less than 150 mm TL, with only *Cnidoglanis macrocephalus*, *Aldrichetta forsteri*, *Platycephalus speculator* and *Sillago schomburgkii* having individuals greater than 150 mm TL (Table 2). Length distributions of *Sillago vittata*, *Sillago schomburgkii*, *Sillago bassensis*, *Spratelloides robustus* and *Hyperlophus vittatus* were largely represented by 0+ fish (Gaughan et al. 1996, Hyndes et al. 1996, Rogers et al. 2003).

At both Shoalwater Bay and Hillarys, *Cnidoglanis macrocephalus* was caught in 2 distinct cohorts. The majority of the individuals were <180 mm TL, which corresponds to the 0+ cohort (Nel et al. 1985). However, a number of individuals were greater than 180 mm TL at Hillarys, where they were mostly caught in mid or high wrack volumes (Fig. 4). The vast majority of *Pelsartia humeralis* caught at both sites were <130 mm TL (Fig. 4). There was a shift in the size distribution of fish for both *C. Macrocephalus* and *P. humeralis*, with larger-sized individuals caught at Hillarys compared with Shoalwater Bay. This is likely to be due to the later sampling period at Hillarys (May and June) compared with Shoalwater Bay (July and August), reflecting the rapid growth of juvenile fish during this early phase of their life cycles.

Species-composition

nMDS ordination analysis using abundance and biomass data for Shoalwater Bay yielded some distinct patterns showing clear separation of samples based on wrack categories (Fig. 5). Samples from high and mid categories were grouped together to the left of the ordination plot, while those from bare sand and low categories were more dispersed to the right of the plot (Fig. 5). One-way ANOSIM of replicate data for each category revealed that the species composition differed among categories (Table 4). Pairwise comparisons showed that the species composition of fish in high wrack volumes differed from that in both low volumes and bare sand (Table 4). Samples from high wrack volumes displayed dispersion values of 0.64, which was lower than those values for mid (1.02), low (1.05) and bare sand (1.30). The results of ordination and ANOSIM of biomass data for Shoalwater were nearly identical to those using abundance data (Table 4, Fig. 5). Using Shoalwater Bay abundance data, SIMPER showed that *Cnidoglanis macrocephalus* distinguished the fish fauna of high wrack volumes from both the bare sand and low categories (Table 5). *Pelsartia humeralis* distinguished the fish fauna of mid categories from low and bare sand categories, and also distinguished high categories from bare sand, low and mid categories. This species therefore accounted for more of the dissimilarity between categories when abundance data were used (Table 5). Using biomass data, SIMPER showed nearly identical results to abundance data, with *C. macrocephalus* also distinguishing the fish fauna of high wrack volumes from mid categories (Table 5).

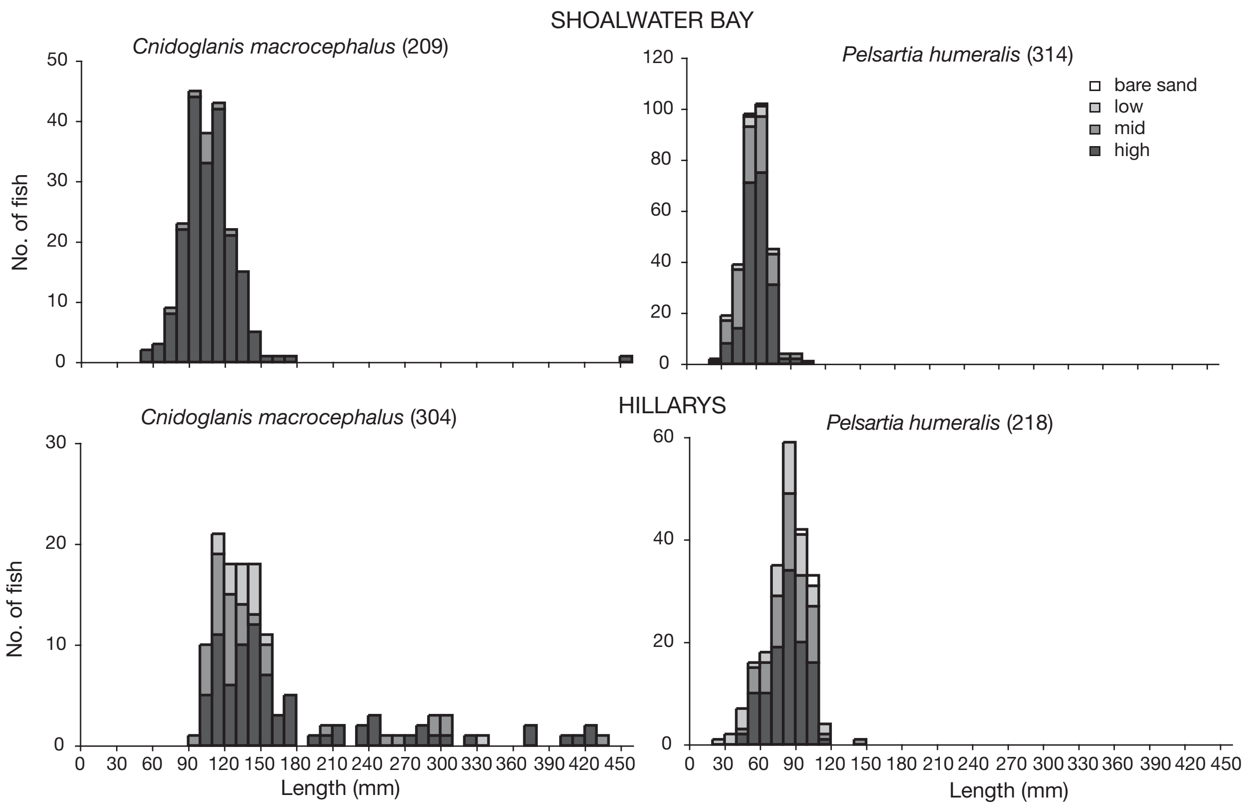

Fig. 4. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Length frequency histograms of fish in bare sand, low, mid and high wrack volumes at Shoalwater Bay and Hillarys. Total number of fish measured for each species is 209 and 304 for *C. macrocephalus* and 314 and 218 for *P. humeralis* at Shoalwater Bay and Hillarys, respectively

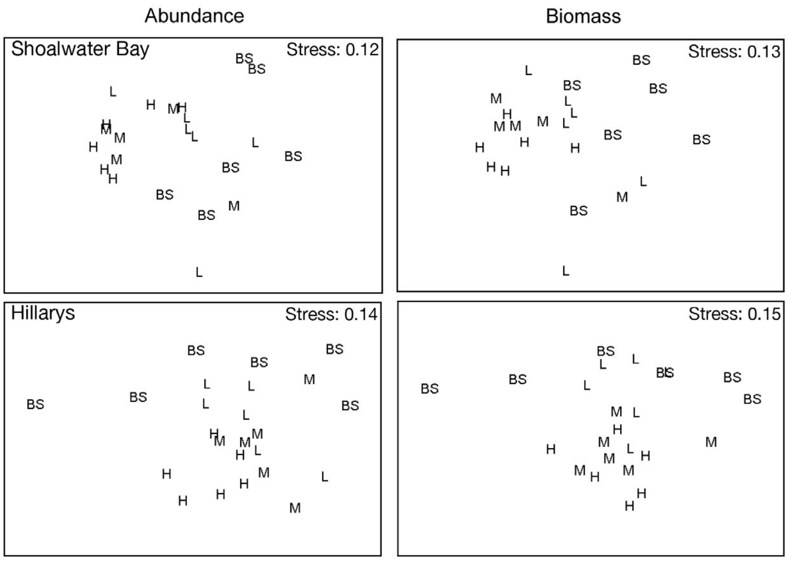

Fig. 5. Two-dimensional MDS ordination of the mean densities and biomass of each species in bare sand (BS), low (L), mid (M) and high (H) wrack volume categories at Shoalwater Bay and Hillarys

Results of ordination and ANOSIM using abundance and biomass data from Hillarys yielded clearer patterns than for Shoalwater Bay (Fig. 5). Using abundance data from Hillarys, samples from high categories formed a discrete group to the bottom centre of the ordination plot, with mid and low samples to the right of those from high, and bare sand samples highly dispersed towards the top of the plot (Fig. 5). One-way ANOSIM of replicate data for each category revealed that the species-composition differed among categories (Table 4). Pairwise comparisons showed that the species-composition of fish in bare sand differed from all other categories, as did those from low and high categories (Table 4). Samples from low, mid and high wrack volumes had dispersion values (0.81, 0.95 and 0.89, respectively) that were lower than bare sand (1.35)

Table 4. R-statistic and significance values from 1-way ANOSIM and pairwise comparisons in species composition using abundance and biomass data for treatment and pairwise comparisons in bare sand (BS), low, mid and high treatments. Number of permutations = 462. **Bold** type indicates terms for which p < 0.05

	Shoalwater Bay		Hillarys	
	Abundance	Biomass	Abundance	Biomass
Treatment	0.212 (**p < 0.050**)	0.219 (**p < 0.010**)	0.275 (**p = 0.001**)	0.311 (**p = 0.001**)
Treatment comparisons				
BS vs. Low	0.020 (p = 0.429)	0.015 (p = 0.448)	0.269 (**p < 0.050**)	0.219 (**p < 0.050**)
BS vs. Mid	0.171 (p = 0.130)	0.160 (p = 0.121)	0.369 (**p < 0.005**)	0.431 (**p < 0.005**)
BS vs. High	0.506 (**p < 0.005**)	0.503 (**p < 0.005**)	0.528 (**p < 0.005**)	0.500 (**p < 0.005**)
Low vs. Mid	0.051 (p = 0.275)	0.128 (p = 0.117)	0.067 (p = 0.223)	0.174 (p = 0.069)
Low vs. High	0.381 (**p < 0.050**)	0.408 (**p < 0.010**)	0.331 (**p < 0.050**)	0.461 (**p < 0.010**)
Mid vs. High	0.053 (p = 0.299)	0.104 (p = 0.149)	0.006 (p = 0.422)	−0.024 (p = 0.552)

Table 5. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Diagnostic species determined by SIMPER using abundance and biomass data from samples of fish collected in bare sand, low, mid and high wrack volumes at Shoalwater Bay and Hillarys. The category for which the species is diagnostic is shown in brackets. Species with ratio values ≥ 1.0 are presented

Category	Species	Shoalwater Bay		Hillarys	
		Abundance	Biomass	Abundance	Biomass
Bare sand and low	*Pelsartia humeralis*			1.5 (low)	1.0 (low)
Bare sand and mid	*Cnidoglanis macrocephalus*				1.2 (mid)
	Pelsartia humeralis	1.1 (mid)	1.6 (mid)		1.1 (mid)
Bare sand and high	*Cnidoglanis macrocephalus*	1.1 (high)	1.4 (high)	2.7 (high)	1.9 (high)
	Pelsartia humeralis	1.3 (high)	1.4 (high)	1.2 (high)	
Low and mid	*Cnidoglanis macrocephalus*				1.2 (mid)
	Pelsartia humeralis	1.3 (mid)	1.4 (mid)		
Low and high	*Cnidoglanis macrocephalus*	1.1 (high)	1.3 (high)	1.7 (high)	2.0 (high)
	Pelsartia humeralis	1.2 (high)	1.3 (high)	1.3 (high)	1.0 (high)
Mid and high	*Cnidoglanis macrocephalus*		1.1 (high)	1.1 (high)	1.5 (high)
	Pelsartia humeralis	1.2 (high)	1.3 (high)	1.2 (high)	

Table 6. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Results of non-parametric binomial goodness-of-fit data (number observed and associated significance values) testing the proportion of individuals in seagrass (S), brown algae (B) or mixed (M) wrack habitats. Bonferroni correction accept at $p < 0.017$

Comparison	*Cnidoglanis macrocephalus* No. observed	p-value	*Pelsartia humeralis* No. observed	p-value
Seagrass vs.	33		40	
brown algae	27	0.519	20	0.013
Seagrass vs.	25		31	
mixed wrack	35	0.245	29	0.897
Brown algae vs.	20		22	
mixed wrack	40	0.013	38	0.052
Summary	S = B, S = M, B < M		S = M > B	

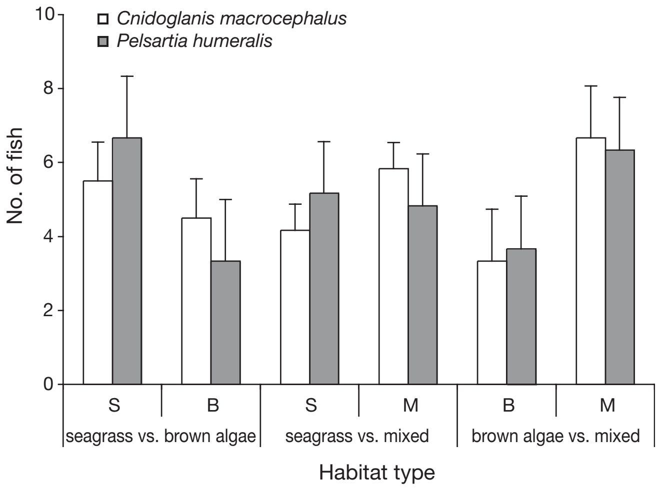

Fig. 6. *Cnidoglanis macrocephalus* and *Pelsartia humeralis.* Mean (+SE) number of individuals found in seagrass (S), brown algae (B) or mixed (M) wrack habitats

values. The results of ordination and ANOSIM of biomass data for Hillarys were virtually identical to those using abundance data (Table 4, Fig. 5). SIMPER showed that *Cnidoglanis macrocephalus* distinguished the fish fauna of high wrack volumes from bare sand, low and mid categories (Table 5). *Pelsartia humeralis* distinguished the fish fauna of high categories from bare sand, low and mid categories, as well as mid and low categories from bare sand, indicating that this species accounted for more of the dissimilarity between categories when abundance data were used (Table 5). Using biomass data, SIMPER showed that *P. humeralis* distinguished high wrack volumes from low categories and low from bare sand (Table 5). *C. macrocephalus* distinguished the fish fauna of high wrack volumes from bare sand, low and mid categories, as well as mid categories from bare sand and low categories, indicating that this species accounted for more of the dissimilarity between categories when biomass data were used (Table 5).

Wrack type experiment

A binomial goodness-of-fit test revealed that *Cnidoglanis macrocephalus* displayed a preference for mixed wrack rather than brown algae habitat types, but did not show a preference between other habitat choices (Table 6, Fig. 6). *Pelsartia humeralis* showed a preference for seagrass compared to brown algae, but there was no significant difference between other habitat choices (Table 6, Fig. 6).

Dietary analysis

Gut contents of juvenile *Cnidoglanis macrocephalus* and *Pelsartia humeralis* collected within detached macrophytes at the study sites primarily comprised the amphipod *Allorchestes compressa*, which contributed 70 to 96% of their dietary volume (Table 7). Isopods were the next most dominant and consistent prey item, making up to 3 to 10% of the diet. *C. macrocephalus* also consumed relatively large volumes of crabs (15%) at Shoalwater Bay and small volumes of bivalves at both sites (Table 7).

DISCUSSION

The fish collected in this study primarily comprised juveniles, regardless of whether or not wrack was present. In addition, those fish assemblages were dominated by a small number of numerically abundant species, which is consistent with fish assemblages in surf zones reported previously (Modde & Ross 1981, Lasiak 1983, Ross et al. 1987, Romer 1990, Ayvazian & Hyndes 1995, Vanderklift & Jacoby 2003). Since the composition of the fish fauna caught in detached macrophytes at both sites in this study was similar to each other and to the species caught in wrack at different locations in the broader region (cf. Lenanton et al. 1982, Robertson & Lenanton 1984), results from the current study are likely to be applicable to the relatively exposed surf zones that contain wrack accumulations along the lower west coast of Australia. Such accumulations are a conspicuous feature of many sandy beaches along the coastline (Lenanton et al. 1982), and appear to provide an important, but transient, habitat for a range of species.

The present study provides clear evidence that the volume of wrack strongly influences abundance, biomass and species composition of fish in surf-zone regions of the lower west coast of Australia. Greater

Table 7. *Cnidoglanis macrocephalus* and *Pelsartia humeralis*. Percentage composition by volume of different dietary categories found in fish collected at Shoalwater Bay and Hillarys. Sample sizes are shown in brackets

Dietary item	*Cnidoglanis macrocephalus*		*Pelsartia humeralis*	
	Shoalwater (12)	Hillarys (12)	Shoalwater (10)	Hillarys (11)
Allorchestes compressa	70.8	93.2	95.5	95.9
Isopods	10.0	4.6	3.5	2.9
Other amphipods	0.0	0.2	0.5	0.9
Crabs	15.4	0.0	0.0	0.0
Plant material	0.0	0.4	0.5	0.3
Bivalves	3.2	0.4	0.0	0.0
Tanaids	0.0	1.2	0.0	0.0
Gastropods	0.6	0.0	0.0	0.0

abundances and biomass of fish were caught in high wrack volumes than in bare sand areas at both sites, with both variables generally increasing from low to high volumes of detached macrophytes. Differences in species composition were largely due to *Pelsartia humeralis* and *Cnidoglanis macrocephalus* being more abundant in higher volumes of wrack. This was the case at both sites, despite sampling at different levels of exposure and times, and using different seine nets.

The change in species composition in higher volumes of wrack almost certainly reflects the addition of structural complexity that is provided by increasing amounts of detached macrophyte material. Increasing structure through the presence of wrack, therefore, has a similar influence on fish assemblages to that provided by attached macrophytes. The abundance, species- and size-composition of fish have been shown to be influenced by the presence of seagrass (e.g. Bell & Westoby 1986, Hindell et al. 2001, Jackson et al. 2001, Hyndes et al. 2003). In general, the greater structural complexity of seagrass relative to bare sand is considered a key factor in influencing fish assemblages, irrespective of seagrass species (Bell & Pollard 1989, Edgar & Shaw 1993, Connolly 1997, Jenkins & Wheatley 1998). Furthermore, differing densities of seagrass can influence fish assemblages in seagrass meadows (Edgar & Robertson 1992, Worthington et al. 1992, Hyndes et al. 2003). Within the broader study region, species richness and abundance of benthic fishes can be at least 3 times greater in seagrass beds than unvegetated sandy habitats (Edgar & Shaw 1993, Hyndes et al. 2003). Similarly, the structure provided by macroalgae on temperate reefs can be critical in influencing the dynamics of temperate fish populations (Choat & Ayling 1987, Anderson 1994, Levin 1994, Levin & Hay 1996), particularly at large spatial scales (Levin 1994). The structure of algal-dominated reefs had an important influence on the species- and size-composition of reef-associated fish assemblages in New Zealand (Choat & Ayling 1987). Thus, similar to attached macrophytes, the presence of detached macrophytes can strongly influence surf-zone fish assemblages. Fish abundance and biomass clearly increase with increasing wrack volume, but fish may respond differently to volumes greater than those that could be sampled in the present study due to sampling limitations. Fish abundance and biomass could level off in higher wrack volumes, or decrease beyond a threshold level if the wrack becomes too dense for fish to inhabit.

The overall patterns in species composition of fish in wrack were largely driven by 2 species, *Pelsartia humeralis* and *Cnidoglanis macrocephalus*, which were also highly abundant in wrack in previous studies in southwestern Australia (Lenanton et al. 1982, Robertson & Lenanton 1984). At both Shoalwater Bay and Hillarys, *C. macrocephalus* and *P. humeralis* showed a clear preference for wrack over bare sand areas. *C. macrocephalus* was caught only when wrack was present, and even then, only in moderate to high volumes of wrack. In comparison, the abundances of *P. humeralis* increased with increasing wrack volume. These results suggest that juvenile *C. macrocephalus* and *P. humeralis* prefer to inhabit higher wrack volumes with greater habitat complexity than lower wrack volumes or bare sand. Similarly, their adult counterparts have been shown to prefer seagrass meadows with greater structural complexity and density over sparse seagrass or unvegetated areas (Hyndes et al. 2003).

From tank trials, *Cnidoglanis macrocephalus* and *Pelsartia humeralis* showed no clear preference for any particular type of macrophyte that dominates the wrack in terms of volume or biomass, i.e. brown algae or seagrass. Indeed, the greater proportion of *C. macrocephalus* in a mixture of brown algae and seagrass possibly suggests that this species prefers a mixture of different types of macrophytes. In the case of *P. humeralis*, it is difficult to explain why the tank trials showed a preference for seagrass over brown algae, particularly when no other pairwise comparison exhibited a significant result. Thus, the type of macrophyte that can dominate wrack, at least in terms of brown algae and seagrass, does not appear to influence the habitat choice of either of these species, despite the fact that different types of macrophytes differ in morphology. The brown alga *Ecklonia* has a large, flattened leaf surface area, while *Sargassum* has numerous, dense branches. *Posidonia* seagrasses have simple, long strap-like leaves, while the leaves in *Amphibolis* seagrasses are shorter and attached at the tips of long wiry stems (Huisman

2000, Hyndes et al. 2003). The apparent lack of preference for a particular structure therefore contrasts with fish assemblages in seagrass and algal reefs, where fish can respond to changes in plant structure (Bell & Westoby 1986, Anderson 1994, Levin & Hay 1996, Jenkins & Sutherland 1997, Connolly et al. 1999, Hyndes et al. 2003). In the case of seagrass, changes in the structure of seagrass leaves have been shown to influence predation rates of fauna, such as prawns (Kenyon et al. 1995). The lack of any influence of different wrack types with different structures on the habitat choice for *C. macrocephalus* and *P. humeralis* may differ under field conditions due to the influence of food, predation and water motion, though this was impossible to test in the region of study. Previous research has suggested that not all types of detached macrophytes are of equal value to the amphipod *Allorchestes compressa* (one of the main prey items of these fish) as food or shelter (Robertson & Lucas 1983, Robertson & Lenanton 1984). This being the case, changes in the composition of macrophytes in wrack may also influence the abundance of fishes associated with different types of wrack in the field.

The overall structure provided by accumulations of detached macrophytes is likely to provide shelter from predators, as well as a source of food, as has been shown in seagrass meadows (Heck & Orth 1980, Orth et al. 1984, Jackson et al. 2001). Accumulations of wrack in southwestern Australia can contain high densities of potential prey, such as the amphipods *Allorchestes compressa* and *Atylus* sp. (Robertson & Lucas 1983, Crawley unpubl. data). In this study, *A. compressa* dominated the diets of juvenile *Cnidoglanis macrocephalus* and *Pelsartia humeralis* caught within wrack, which supports the results of previous studies (Lenanton et al. 1982, Robertson & Lenanton 1984). Robertson & Lenanton (1984) showed that both fish species were more abundant in wrack than in nearby bare sand and their diets were dominated by wrack-associated macro-invertebrates during both the day and night. The high invertebrate abundance in wrack is considered to be a major factor responsible for the significant fish-wrack association (Robertson & Lenanton 1984, Lenanton & Caputi 1989). In terms of protection from predation, detached macrophytes are thought to provide diurnal refuge for juvenile fish from larger fish and avian predators, such as cormorants, which would feed less effectively in dense wrack accumulations in the shallow waters of the surf zone (Lenanton et al. 1982, Robertson & Lenanton 1984).

In this study, we have shown that different species and numbers of fish inhabit different densities of surf-zone wrack. The results from this study suggest that the density of wrack is more important than the type of wrack in providing a habitat, particularly for juvenile *Pelsartia humeralis* and *Cnidoglanis macrocephalus*, the latter being a recreationally and commercially important fish species. The initial arrival of these juvenile fish on the open coast may be opportunistically timed to coincide with the period of greatest accumulations of surf-zone wrack in the study region during winter months, particularly after storms (Lenanton et al. 1982, Lenanton & Caputi 1989). Since adult-sized *C. macrocephalus* occur in more offshore seagrass meadows (Hyndes et al. 2003) and spawn during spring (Nel et al. 1985, Laurenson et al. 1993), the juveniles that are released from parental care (Laurenson et al. 1993) may rely on the movement of macrophytes from those more offshore regions to transport them into the surf-zone region. Subsequently, the winter accumulations of detached macrophytes in the surf zone are likely to provide an important habitat for juvenile *C. macrocephalus* during their first year of life. However, since the volume of detached macrophytes strongly influences the abundance and composition of fish, the spatial and temporal variability of wrack accumulations in surf zones of beaches in southwestern Australia will result in the fish abundance and community structure in surf zones being highly variable. It is therefore difficult to establish how critical these dynamic habitats are to the juveniles of species such as *C. macrocephalus* and *P. humeralis*. However, wrack is a prominent feature of the surf zone in the region during late autumn to early spring. Our results suggest that some fish species, such as *P. humeralis* and *C. macrocephalus*, could be adversely affected by a reduction in the volume of detached macrophytes, either through a reduced supply of macrophytes (e.g. Vanderklift & Jacoby 2003), or through the removal of wrack resulting from beach-cleaning practices.

Acknowledgements. We thank the many people who assisted with the collection of fish, particularly R. Ince, G. Coupland, J. How and M. Burt. We thank B. Knott from the University of Western Australia for the use of their outdoor aquaria and facilities for the tank trials, and the Department of Fisheries, Western Australia, for providing a seine net for sampling at Hillarys. We also thank J. King from the Department of Fisheries, Western Australia, for providing brine shrimp for fish food in the tank trials. We acknowledge financial support from Edith Cowan University and the CSIRO SRFME (Strategic Research Fund for the Marine Environment) project to K.R.C. for her PhD.

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Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA

Submitted: April 4, 2005; Accepted: July 29, 2005
Proofs received from author(s): December 20, 2005