FISH COMMUNITY STRUCTURE AND FOOD CHAIN DYNAMICS IN THE SURF-ZONE OF SANDY BEACHES: THE ROLE OF DETACHED MACROPHYTE DETRITUS

A. I. ROBERTSON

Division of Fisheries Research, CSIRO Marine Research Laboratories, P.O. Box 20, North Beach, W.A. 6020, Australia

and

R. C. J. LENANTON

Western Australian Marine Research Laboratories, P.O. Box 20, North Beach, W.A. 6020, Australia

Abstract: The surf-zones of sandy beaches near Perth, Western Australia often harbour huge accumulations of detached macrophyte detritus. During 2.5 yr sampling, 29 species of fishes were captured over two sandy beaches in this region and the fish community was dominated by juveniles. There was a highly significant positive relationship between the number of fishes and the quantity of detached macrophytes taken in each surf-zone netting. Comparisons of total fish abundance on beaches with and without surf-zone accumulations of detached plants, showed that fishes were two to 10 times more abundant on the beach with weed accumulations, depending on the time of day, and date of sampling. However, despite the overall lower abundance of fishes on the open sandy beach, there was a significant increase in the number of fishes captured over the sandy beach at night. There were also two to five times the number of species over the beach with weed during the day, as opposed to equal numbers of species at night. Seven fish species made up >95% of the total catch and these species fell into two groups with regard to diurnal distribution patterns; those that were equally abundant in weed dominated or open surf-zones, and those that were weed-associated. Analyses of the diets of these fishes and the daytime distribution of an important avian piscivore in the surf-zone suggested that the large quantities of weed in the surf-zone of sandy beaches in this region provide both a rich feeding site for fishes, as well as a refuge from diurnal predators. At night, when visual feeding predators are absent, some fish species move to open sandy areas to feed. Because the majority of fishes in this surf-zone community feed on weed-associated prey, and the input of macrophyte detritus is the major source of primary production in the surf-zone, we argue that the food chain dynamics in the surf-zone in this region are fundamentally different to those of sandy beaches that have been studied previously.

Key words: surf-zone; sandy beach; fish community; detached macrophytes; food chain

INTRODUCTION

The surf-zones of exposed sandy beaches are harsh, structurally homogeneous environments for nektonic organisms and previous work on the fish faunas of sandy beach surf-zones has shown that they are low diversity faunas, dominated by small planktivores and benthic feeding fishes and their larger but rarer fish predators (e.g.

Present address: Australian Institute of Marine Science, P.M.B. No. 3, Townsville, M.C., Qld. 4810, Australia.
A majority of surf-zone fish species are represented solely by immature individuals (McFarland, 1963; Modde, 1980) and year-to-year variations in abundance and species composition of these fish communities (e.g. Hillman et al., 1977; Modde & Ross, 1981) are probably tied to fluctuations in recruitment success.

The trophic spectrum observed within any surf-zone fish community appears to be controlled primarily by three factors, the form of primary production input to the surf-zone, the pattern of water movement and the geomorphology of the sandy beaches. For instance, phytoplankton blooms occur regularly on some beaches with broad, flat surf-zones and these beaches usually have rich infaunal and zooplankton assemblages available to fishes (e.g. Lewin, 1977; McLachlan, 1980b; McLachlan et al., 1981; Lasiak, 1983). By contrast, where surf-zones are narrow and beaches are subject to greater sand movement, or where input of macroalgal debris occurs in large quantities, there may be little in the way of infaunal prey available to fishes (McLachlan, 1980a).

In habitats other than sandy beaches, including coral reefs, seagrass meadows, kelp forests and the open sea, increased structural heterogeneity provided by corals, and attached or drifting macrophytes has a positive influence on the abundance and species richness of fish communities (Mitchell & Hunter, 1970; Luckhurst & Luckhurst, 1978; Orth & Heck, 1980; Stoner & Livingston, 1980; Kulczycki et al., 1981; Moreno & Jara, 1984; Schulman, 1984). The results of some studies suggest that detached plant debris, or algae growing on man-made structures may also influence the structure of sandy beach fish communities by providing shelter and/or food resources not otherwise available to fishes in this stark environment (e.g. Edwards, 1973b; Wheeler, 1980).

In temperate Western Australia, storms and associated wave-action remove macroalgae and seagrass material from the extensive limestone reefs and seagrass meadows which run parallel to the shore, and large quantities of detached vegetation accumulate in the surf-zone of many sandy beaches (Robertson & Hansen, 1982). During certain periods of the year up to 1200 m$^3$ of the surf-zone per kilometre of coast may be occupied by detached macrophyte detritus (Lenanton et al., 1982). Earlier work on the fishes of estuaries and embayments on the open coast of south-western Western Australia showed that these extensive deposits of macrophyte detritus harbour large numbers of fishes and may serve as important nursery grounds for several fish species which were previously thought to be estuarine dependent (Lenanton, 1982; Lenanton et al., 1982).

Through comparisons of the species composition, abundances, habitat preferences and feeding habits of the fish community on sandy beaches with and without drifting macrophytes, we show in this paper how the presence of detached macrophyte accumulations causes a major shift in the structure of the surf-zone fish fauna of south-western Western Australia. On the basis of data presented here and previous work on food chain dynamics in the surf-zone (e.g. Robertson & Hansen, 1982; Robertson & Lucas, 1983) we also argue that the structure of the food chain supporting the fish fauna differs significantly from that for other sandy beaches that have been intensively studied.
SITE AND FIELD METHODS

All sampling of fishes was done within the surf-zone of Mullaloo and Sorrento beaches near Perth, Western Australia (31°51' S: 115°45' E). The two beaches are 1 km apart and both are semiprotected behind a limestone reef which runs parallel to the shore, usually ≥ 2 km offshore. The beaches are bordered on their seaward side by extensive, multispecies seagrass meadows which are usually between 100 and 200 m from the surf-zone (see Kirkman, 1981 for a map of the site). Modal wave period on the beaches is 6.5 s and mean significant wave height just off the beach is 0.4 m while modal maximum height is 1.0–1.5 m (McLachlan & Hesp, in press a) as opposed to 1.4 m and 2.0–2.5 m respectively outside the reef (Steedman et al., 1977). The coast in this region has a small tidal range and meteorological effects can override tides (Hodgkin & di Lollo, 1958; Elliot et al., 1983). The intertidal faces of both beaches are fairly steep (6°) and the surf-zone is usually narrow (10–20 m). On a 20-point scale for rating the exposure of the intertidal zones of sandy beaches (McLachlan, 1980a) both beaches rate 11.5 (= exposed) (McLachlan & Hesp, in press a). The surf-zone of Sorrento beach is usually free of large accumulations of macrophyte detritus, while the surf-zone of Mullaloo beach often harbours significant quantities of detached plants.

A small seine net (15 m long, 1.6 m deep with a 3 m pocket and 1 cm mesh throughout) was used to sample fish. The net, which was set by hand in 1.0–1.5 m of water and dragged perpendicular to the beach, swept an area of ≈ 60 m².

During the period April 1981 to February 1982, 18 daytime (1500–1800) nettings were taken to provide specimens for gut analyses. These samples, and our previous work on the open coast in this region (Lenanton, 1982; Lenanton et al., 1982) suggested that the presence or absence of many species of fish in the surf-zone of sandy beaches was related to the quantities of macrophyte detritus in the water. Therefore, we designed a sampling regime to investigate the habitat preferences of the major species in the community. In 20 days between 30 March and 19 April 1982 we performed 11 replicate daytime nettings in each of three habitat types in the surf-zone, viz; within dense accumulations of detached macrophyte detritus (WEED habitat), at the edge of detached macrophyte patches (EDGE habitat) and over areas of beach clear of plant detritus (SAND habitat). WEED and EDGE samples were taken on Mullaloo beach while SAND samples were taken 0.5 and 1 km to the south on Sorrento beach. For all nettings the species composition and abundance were recorded in the field and subsamples of the most abundant species were retained for gut analyses. The total volume of plant material in each netting was also recorded using a 25-l plastic bucket as the measuring device.

To determine if the patterns of habitat preferences we observed in the above sampling program were maintained on a diel and seasonal time scale we also sampled the fish community in SAND and WEED habitats at day and night in June and October 1983. Fishes were identified and counted in the field, the volumes of weed recorded, and in June 1983 samples of the most abundant species were retained for examination of possible diel dietary shifts.
In using beaches with and without accumulations of detached macrophytes to investigate the influence of plant detritus on surf-zone fish community structure we faced the problem of most "natural experiments", the lack of a suitable control for other factors which may act on the fish fauna at each site. However we found a significant relationship between the volume of weed and the abundance of fishes at both test beaches (see p. 270). This occurred even though the range of weed volumes recorded from nettings at Sorrento beach was very small (0–12.5 l) compared to that at Mullaloo beach (6.3–575 l). These results suggest that except for the presence or absence of detached plants, the two beaches offer similar habitats for fishes.

The relationship between fish abundance and species richness and drift algal abundance may in part be related to the shelter from predators provided by drift algae (e.g. Kulczycki et al., 1981). In Western Australia one obvious and potentially important predator on surf-zone fishes is the pied cormorant, Phalacrocorax varius (Gmelin), which is known to feed on several of the major fish species recorded in nettings from the surf-zone, including cobbler Cnidoglanis macrocephalus and yellow-eyed mullet Aldrichetta forsteri (Serventy, 1938; Serventy & Whittell, 1976). To examine the relationship between cormorants and patches of detached plant material in the surf-zone, we counted the number of actively hunting cormorants engaged in predatory activity within 50 m of the shore along 19.7 km of sandy beaches north of Perth, Western Australia. We censused this area on three occasions between September 1981 and January 1982, on each occasion recording the length of the surf-zone filled with detached macrophyte material and the number and feeding site (open sand or detached plant accumulations) of cormorants.

FISH GUT ANALYSES

In the laboratory, fishes were measured and weighed wet and their stomachs (or the first third of the gut for species without true stomachs) were removed and the contents examined under a dissecting microscope. Prey were identified to as low a taxonomic level as possible. For each sample of a fish species we recorded the percent occurrence of prey \(O\) (i.e. the percentage of fish in a sample which contained each prey type) and the percentage of the total volume of food which was made up by each prey \(V\). Prey volume estimates followed the method described in Robertson (1977). A prey ranking index \(K = O \cdot V\) modified from Hobson (1974) was calculated for each prey item in the diet of a sample of fish (e.g. Harmelin-Vivien & Bouchon-Navaro, 1983). By combining measures of the frequency of occurrence and the bulk of each prey in the diet, the index gives a clearer indication of the most important prey to the "average" fish in a sample, than would either of the two measures used alone (Hobson, 1974).
Fishes

Where possible, we used analysis of variance (ANOVA) to compare the means for abundance and distribution data. For the data from the intensive diurnal sampling of SAND, WEED and EDGE habitats in March and April 1982 we used one-way ANOVA to test the null hypotheses that equal total numbers of fishes and species of fish were captured per netting in the three habitats. In all cases raw data were heteroscedastic ($F_{\text{max}}$, test), but transformed data [$\log_{10}(x + 1)$] satisfied the assumptions of ANOVA. For analyses of single species abundances from the above data set, transformed data for *Pelsartia humeralis* (Ogilby), *Sillago bassensis* Cuvier and *Crapatalus arenarius* McCulloch were also heteroscedastic ($F_{\text{max}}$ tests; $F_{2,10} = 5.05, 5.39$ and $4.52$ respectively; $0.05 > P > 0.01$) but ANOVA was used because the analysis is robust for such small deviations from homoscedaticity, especially when sample sizes are equal (Box, 1953). For *Sillago bassensis* and *Crapatalus arenarius* there was no problem in making a Type-I error (Sokal & Rohlf, 1969) in interpreting the ANOVAs, because the analyses showed that the null hypotheses of equal mean catches should be accepted. However, for *Pelsartia humeralis* ANOVA gave a highly significant result (see p. 272). So as to decrease the probability of rejecting the null hypothesis when it may have been true, we reanalysed the *P. humeralis* data using a modified ANOVA in which the means were weighted according to the reciprocal of the variance of the sample (Sokal & Rohlf, 1969).

For two fishes, *Cnidoglanis macrocephalus* (Valenciennes) and *Haletta semifasciata* (Valenciennes), 11 daytime nettings from the SAND habitat in March and April 1982 yielded only 1 and 0 specimens respectively, indicating that this was not an important habitat for either species. Comparisons of mean catches of these species were therefore confined to EDGE and WEED habitats using t-tests on $\log_{10}(x + 1)$-transformed data. For *H. semifasciata* an approximate t-test, with reduced degrees of freedom (Sokal & Rohlf, 1969, p. 374) was used for the analysis because transformed data were still heteroscedastic.

We used a three-way ANOVA for unequal sample sizes, with date, time of day and habitat as factors, to analyse data on total catch per netting from the diel sampling program in June and October 1983. Each of the habitat-time-date replicate samples was expressed as a proportion of the total catch taken during the two dates ($\Sigma N = 1423$ fishes) and the analysis was performed on arcsin $\sqrt{P}$-transformed data ($F_{\text{max}}$ test $P > 0.05$), since the raw data were heteroscedastic. Raw data for the number of species per netting from the June and October sampling periods were homoscedastic, and were analysed using a three-way ANOVA for unequal sample sizes.
Birds

Because the sample size of actively feeding cormorants was small on each of the three sampling dates ($N \leq 25$) we used the binomial distribution to calculate the exact probabilities of finding birds feeding over sandy beaches or near patches of detached macrophytes (Sokal & Rohlf, 1969, p. 82). The expected probabilities of birds feeding in either of the two habitats were calculated by using the relative proportions of the total length of beaches that were taken up by either habitat.

Results

Fish Community Composition

A total of 29 species from 26 families were recorded during the study and seven species made up > 95% of the total number of fishes captured (Table I). Amongst these major seven species, *Pelsartia humeralis* (Teraponidae), *Sillago bassensis* (Sillaginidae), *Cnidoglanis macrocephalus* (Plotosidae) and *Crapatalus arenarius* (Leptoscopidae) were captured in > 50% of all nettings, while *Aldrichetta forsteri* (Mugilidae), *Haletta semifasciata* (Odacidae) and *Torquigener pleurogramma* (Tetraodontidae) were taken in fewer nettings (Table I). In numerical terms, the community was dominated by juvenile fishes, with five of the top seven species being represented almost entirely by immature individuals (Table I).

Detached Plants and Fish Distribution

For all nettings ($\Sigma N = 63$) for which the volume of detached plants was recorded, i.e. after February 1982, there was a highly significant, positive correlation between the total number of fishes and the volume of weed captured in each netting ($r_s = 0.76$, $P < 0.01$; Fig. 1). The ranges of weed volumes and total fish abundance were 0–575 l and 0–376 l, respectively. When day and night samples were considered separately they also exhibited significant correlations between weed volume and fish abundance (day $r_s = 0.74$, $P < 0.01$; night $r_s = 0.81$, $P < 0.01$). Although the surf-zone of Sorrento beach was nearly always clear of plant detritus, weed volumes and fish catches were significantly correlated at both Sorrento ($r_s = 0.55$, $P < 0.02$) and Mullaloo ($r_s = 0.34$, $P < 0.05$) beaches.

To determine whether the abundances of all species reacted in a similar fashion to the presence of detached macrophytes in the surf-zone, we compared the mean day-time abundances of fishes captured over open sandy areas (SAND) and at the edge of (EDGE) and within accumulations of detached macrophytes (WEED). There were significantly fewer fishes and less species per netting in the SAND habitat than either the EDGE or WEED areas (Table II). Much of the variance associated with the mean catch per netting in the EDGE samples was due to the presence or absence of schools of *Aldrichetta forsteri*. If the data for *A. forsteri* were omitted from the analysis, then the abundance of fishes
in each habitat increased in the order \textit{SAND EDGE WEED}. Comparisons of the mean abundances of individual species in each of the three areas showed that, for the five species for which sufficient data were available, there existed two groups of fishes which could be separated on the basis of their diurnal distribution patterns (Table II). \textit{Sillago bassensis} and \textit{Crapatalus arenarius} exhibited no significant difference in mean densities across habitats, while \textit{Pelsartia humeralis}, \textit{Cnidoglanis macrocephalus} and \textit{Haletta semifasciata} were all most abundant in \textit{WEED} areas (Table II).

\textit{Aldrichetta forsteri} form large schools which present an obvious problem for com-
Fig. 1. The relationship between the ranked volume of detached macrophytes in each netting and the ranked abundance of fish per netting: data are for the 47 daytime (●) and 16 night-time (○) nettings in which the volumes of detached plants were recorded (see p. 267); $r_s$, Spearman rank correlation coefficient for pooled data; **, significant at $P = 0.01$.

**TABLE II**

Comparison of variables for day-time nettings in the SAND, EDGE and WEED habitats: all nettings ($n = 11$ for each habitat) performed between 30 March and 19 April 1982; the mean total number of fish and species per netting, as well as five single species comparisons are compared using one-way ANOVA on log$_{10} (x + 1)$-transformed data; for two species only one individual was captured in the SAND, habitat and $t$-tests were used to compare means for EDGE and WEED habitats (see p. 269); all means shown are for untransformed data and underlined means are not significantly different at $P = 0.05$ (SNK test); ***, significant at $P = 0.001$; NS, not significant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>SAND</th>
<th>EDGE</th>
<th>WEED</th>
<th>$F$ or $t$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>COMMUNITY</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total fish/netting (all species)</td>
<td>17.9</td>
<td>103.8</td>
<td>121.1</td>
<td>$F_{2,30} = 16.12^{***}$</td>
</tr>
<tr>
<td>Total fish/netting (minus data for Aldrichetta forsteri)</td>
<td>17.9</td>
<td>38.0</td>
<td>120.8</td>
<td>$F_{2,30} = 18.52^{***}$</td>
</tr>
<tr>
<td>Total species/netting</td>
<td>2.5</td>
<td>4.9</td>
<td>5.6</td>
<td>$F_{2,30} = 13.45^{***}$</td>
</tr>
<tr>
<td><strong>SINGLE SPECIES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sillago bassensis</td>
<td>14.8</td>
<td>22.9</td>
<td>22.2</td>
<td>$F_{2,30} = 1.72$ NS</td>
</tr>
<tr>
<td>Crenilabrus arenarius</td>
<td>1.9</td>
<td>6.8</td>
<td>2.0</td>
<td>$F_{2,30} = 2.67$ NS</td>
</tr>
<tr>
<td>Pelsartia humeralis</td>
<td>0.5</td>
<td>3.5</td>
<td>55.1</td>
<td>$F_{2,30} = 45.63^{***}$</td>
</tr>
<tr>
<td>Cnidoglanis macrocephalus</td>
<td>0.1</td>
<td>2.1</td>
<td>35.0</td>
<td>$t_{20} = 11.98^{***}$</td>
</tr>
<tr>
<td>Neodax semifasciata</td>
<td>0</td>
<td>0.4</td>
<td>4.5</td>
<td>$t_{10} = 8.02^{***}$</td>
</tr>
</tbody>
</table>
parison of mean abundances between habitats using ANOVA. For *A. forsteri* the 33 nettings during the March–April sampling yielded 735 individuals, 732 of which were taken in two nettings in the EDGE habitat.

Significantly more fishes were also captured in diurnal nettings in WEED areas in June and October 1983, but the proportion of the total catch taken in each habitat at day or night changed significantly on both dates (Fig. 2 and Table III). At night there were

### Table III

Three-way ANOVA of the proportion of the total catch of fish captured at day and night in the two habitat types at two dates: $F_{\text{max}}$-test showed no significant heterogeneity of variance for arcsin $\sqrt{P}$-transformed data at $P = 0.05$; d.f., degrees of freedom; MS, mean square; *, significant at $P = 0.025$; ***, significant at $P = 0.005$; NS, not significant.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>MS</th>
<th>$F$ ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Time of day</td>
<td>1</td>
<td>0.179</td>
<td>0.02 NS</td>
</tr>
<tr>
<td>B. Habitat</td>
<td>1</td>
<td>488.806</td>
<td>46.55***</td>
</tr>
<tr>
<td>C. Date</td>
<td>1</td>
<td>75.746</td>
<td>7.21*</td>
</tr>
<tr>
<td>A x B</td>
<td>1</td>
<td>122.572</td>
<td>11.67***</td>
</tr>
<tr>
<td>A x C</td>
<td>1</td>
<td>11.685</td>
<td>1.11 NS</td>
</tr>
<tr>
<td>B x C</td>
<td>1</td>
<td>2.266</td>
<td>0.22 NS</td>
</tr>
<tr>
<td>A x B x C</td>
<td>1</td>
<td>13.486</td>
<td>1.28 NS</td>
</tr>
<tr>
<td>Within cell</td>
<td>22</td>
<td>10.501</td>
<td></td>
</tr>
</tbody>
</table>

![Fig. 2](image-url) The mean ($\pm 1$ SE) proportions of the total catch of surf-zone fish ($N = 1423$) taken in SAND and WEED habitats at day and night on two sampling dates in 1983: the number of nettings in each time–site–date combination is shown in parentheses; also shown are the relative proportions of the major fish species captured in each time–habitat–date sampling; P, *Pelsartia humeralis*; C, *Cnidoglanis macrocephalus*; S, *Sillago bassensis*; O, all other species.
fewer fishes captured in **WEED** habitats than during the day, while there were increased catches in the **SAND** habitat at night (Fig. 2 and Table III). Although there was no seasonal difference in the pattern of diel habitat use by the total fish community on each date (Table III, three-way interaction term, $P > 0.5$), overall, significantly more fishes were captured in the June sampling period (Table III and Fig. 2).

The diel samplings also revealed that the patterns of habitat choice exhibited by individual fish species changed with the time of day (Fig. 2). *Pelsartia humeralis* was less abundant in night-time **WEED** samples than in the equivalent daytime nettings in both June and October (Fig. 2), while in June *P. humeralis* was also abundant in night-**SAND** samples. Individuals of *Cnidoglanis macrocephalus* increased in abundance after dark in the **WEED** areas on both sampling dates, and like *Pelsartia humeralis* this fish was also more abundant in night **SAND** samples (Fig. 2). On both dates individuals of *Sillago bassensis* were absent from daytime **WEED** samples, but were present in night **WEED** nettings (Fig. 2). In June *S. bassensis* was equally abundant in day and night samples in the sand habitat, but occurred only in night-**SAND** samples in October (Fig. 2).

Analyses of the mean number of fish species per netting from the sampling in June and October showed that the main factors, time of day, habitat and date had a significant independent influence on the variance in the number of species (Table IV). Overall, less species were taken per netting in October, and there were more species per netting in **WEED** habitats during the daytime on both dates (Fig. 3 and Table IV). However, significantly more species were captured in the **SAND** habitat at night than during the day (Table IV and Fig. 3), and there was no difference in the number of species captured per netting in the **WEED** and **SAND** habitats at night. There was also virtually no difference in the number of species caught in the weed habitats between day and night (Fig. 3).

![Fig. 3. The mean (± 1 SE) number of fish species captured per netting in **SAND** and **WEED** habitats at day and night on two sampling dates in 1983: the number of nettings in each time–habitat–date combination is shown in parentheses.](image-url)
Three-way ANOVA of the number of fish species per netting: $F_{max}$-test on raw data showed no significant heterogeneity of variance at $P = 0.05$; d.f., degrees of freedom; MS, mean square; ***, significant at $P = 0.005$; NS, not significant.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>MS</th>
<th>$F$ ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Time of day</td>
<td>1</td>
<td>23.198</td>
<td>14.28***</td>
</tr>
<tr>
<td>B. Habitat</td>
<td>1</td>
<td>17.202</td>
<td>10.59***</td>
</tr>
<tr>
<td>C. Date</td>
<td>1</td>
<td>24.505</td>
<td>15.08***</td>
</tr>
<tr>
<td>A x B</td>
<td>1</td>
<td>5.445</td>
<td>3.35 NS</td>
</tr>
<tr>
<td>A x C</td>
<td>1</td>
<td>0.045</td>
<td>0.03 NS</td>
</tr>
<tr>
<td>B x C</td>
<td>1</td>
<td>0.080</td>
<td>0.05 NS</td>
</tr>
<tr>
<td>A x B x C</td>
<td>1</td>
<td>0.180</td>
<td>0.11 NS</td>
</tr>
<tr>
<td>Within cell</td>
<td>22</td>
<td>1.625</td>
<td></td>
</tr>
</tbody>
</table>

FISH DIETS

The four fish species which were most abundant in the daytime EDGE OF WEED nettings fed mainly on the weed-associated amphipods *Allorchestes compressa* Dana and *Atylus* sp. (Lenanton et al., 1982) (Fig. 4). Weed-associated sphaeromimid isopods were also important in the diet of *Haletta semifasciata*, while both *Cnidoglanis macrocephalus* and *Aldrichetta forsteri* exhibited ontogenetic dietary differences. Bivalves and infaunal polychaetes formed a large portion of the diet of the larger size group of *Cnidoglanis macrocephalus*, while larger *Aldrichetta forsteri* individuals fed almost entirely on green algae, mainly *Ulva* sp. and *Enteromolpha* sp. as has been observed elsewhere (Robertson, 1984). *Torquigener pleurogamma* also fed predominantly on the two weed-associated amphipod species (Fig. 4).

*Sillago bassensis* and *Crapatalus arenarius*, which were equally abundant in SAND and WEED habitats during the day (Table II), had markedly different diets to all diurnally WEED-associated fish species (Fig. 5). The stomachs of individuals of *Sillago bassensis* that were captured in the WEED habitat in the surf-zone contained mainly infaunal and weed-associated polychaete species, as well as significant quantities of amphipods. Individuals of *S. bassensis* that were captured in the SAND habitat contained mainly bivalve siphons and some polychaetes. Infaunal polychaetes and sand were the major constituents of the gut contents of sandfish *Crapatalus arenarius* in both the WEED and SAND habitats (Fig. 5).

Analysis of the diets of the three most common fishes captured during diel sampling in June 1983, showed that there were often dietary shifts with both habitat and time of day (Fig. 6). For *Pelsartia humeralis*, day- and night-time diets were similar in the WEED habitat, with the weed-associated amphipods *Allorchestes compressa* and *Atylus* sp. and detritus being the main food items. The stomachs of fishes captured at day and night in the SAND habitat also contained large quantities of *Allorchestes compressa* (indicating that these fishes had only recently left the WEED habitat) as well as polychaetes, detritus and fishes (Fig. 6).
Cnidoglanis macrocephalus also fed on weed-associated amphipods in the weed habitat at day and night, but shifted their diet to mainly bivalves when feeding in the sand habitat at night (Fig. 6). Sillago bassensis, fed mainly on infaunal prey, including polychaetes and bivalve siphons, during the day in the sand habitat. At night, bivalve siphons and mysids were the major prey of *S. bassensis* in the sand habitat, while in the weed habitat at this time fish contained a variety of foods including weed associated amphipods as well as polychaetes, detritus, holothurians, fishes and bivalve siphons (Fig. 6).

**Distribution of Feeding Cormorants**

On all three dates when birds were counted, there was a highly significant association of actively-feeding cormorants *Phalacrocorax varius*, with patches of detached plants in the surf-zone (Table V).
Fig. 5. The diets of the two fish species that were captured in equal numbers in day-time nettings in WEED and SAND habitats: all fish were captured during the day between April 1981 and April 1982; pie diagrams and symbols as for Fig. 4., with the following additions; Bs, bivalve siphons; Fo, foraminifers; N, natantians; S, sand.

**TABLE V**

The distribution of actively-feeding cormorants, _Phalacrocorax varius_, in the surf-zone of sandy beaches: the data are the number of birds observed feeding over open sandy beaches (SAND) or in and near accumulations of detached plants (WEED); figures in parentheses give the expected number of birds if feeding occurred randomly along the shore (see p. 270); ***, significant at _P_ = 0.001.

<table>
<thead>
<tr>
<th>Date</th>
<th>SAND</th>
<th>WEED</th>
</tr>
</thead>
<tbody>
<tr>
<td>September 1981</td>
<td>2 (14.4)</td>
<td>13 (0.6)***</td>
</tr>
<tr>
<td>October 1981</td>
<td>10 (21.1)</td>
<td>15 (3.9)***</td>
</tr>
<tr>
<td>January 1982</td>
<td>5 (14.6)</td>
<td>10 (0.4)***</td>
</tr>
</tbody>
</table>
Fig. 6. Dietary changes with time of day and habitat (weed or sand) for the three major fish species captured in June 1983; Pie diagrams and symbols as for Fig. 4., with the following additions; F, fish; H, holothurians; M, mysids; T, Tethygeneia sp.; NA, no specimens available for analysis.

DISCUSSION

FISH COMMUNITY STRUCTURE

Large accumulations of macrophyte detritus which remain in the surf-zones of sandy beaches after storms in south-western Western Australia (Robertson & Hansen, 1982; Lenanton et al. 1982; J. A. Hansen, unpubl. data) have a significant influence on the abundance and species composition of the surf-zone fish community in this region.

Our data show that there was a significant relationship between the quantity of macrophyte detritus and the abundance of fishes for all nettings taken on the two study beaches. The relationship between these two variables is striking when it is considered that the data are pooled for day and night samples and for different sampling times during the year, including the periods of recruitment of several of the fish species (Lenanton et al., 1982). The fish community also includes several mobile, schooling species such as Aldrichetta forsteri, which a priori would be expected to obscure such a relationship. A further source of variance in the relationship between fishes and weed abundance is the macrophyte species composition and its influence on the fishes' prey densities. All detached macrophyte detritus is not of equal value to amphipods as food or shelter (Robertson & Lucas, 1983), and variation in the plant species composition of macrophyte patches leads to variation in the abundance of amphipods (A. Robertson,
unpubl. data). This may in turn influence the abundance of fishes associated with weed patches.

The comparisons of the abundance of fishes and the number of species in the surf-zone of beaches with and without detached plants showed that the number of fishes in the surf-zone of the beach with weed accumulations was two to 10 times that on the open sandy beach, depending on the time of day and date of sampling. Although plant accumulations harboured the greatest densities of fishes during both day and night the number of fishes over the sand beach increased significantly at night. The analyses also showed that during the day there were two to five times more species captured per netting over the beach with plant accumulations, but that at night there were equal numbers of species per netting over both the weed and sand beaches. These increases in the density and number of species of fish in the sand habitat at night probably result from movements of fishes out of adjacent accumulations of detached plants in the surf-zone as well as from nearby seagrass meadows which are known to have species in common with the surf-zone fish community (Dybdahl, 1979; pers. obs.).

Analyses of the distribution and abundance of individual fish species revealed that the numerically dominant species belonged to one of two groups. One group of species, which included *Pelsartia humeralis* and *Cnidoglanis macrocephalus* on all sampling dates as well as *Haletta semifasciata* on some occasions, were significantly more abundant in weed patches during the day. The two major food items for all of these fishes were the weed-associated amphipods *Allorchestes compressa* and *Atylus* sp. Previous work has shown that both amphipods are only found associated with detached plants in the surf-zone (Lenanton *et al.*, 1982; Robertson & Hansen, 1982; A. Robertson, unpubl. data). At night *Pelsartia humeralis* and *Cnidoglanis macrocephalus* were still more abundant in the WEED area, but some individuals of both species were found over sand areas. Individuals of *Pelsartia humeralis* captured at night over both weed and sand areas contained mainly weed-associated amphipods and plant detritus, indicating that these fish had not fed in the sand habitat. *Cnidoglanis macrocephalus* captured in the WEED habitat at night had a similar diet to daytime, WEED-inhabiting individuals, but at night in the sand area *C. macrocephalus* switched its diet to infaunal bivalves.

Because some individuals of both *Pelsartia humeralis* and *Cnidoglanis macrocephalus* leave patches of weed and move over adjacent sandy areas at night, it appears that in addition to the high availability of food in weed patches (Lenanton *et al.*, 1982) other factors may be responsible for the day-time distribution pattern of *Pelsartia humeralis* and *Cnidoglanis macrocephalus*. Both species are eaten by pied cormorants (Serventy, 1938; Serventy & Whittell, 1976) and during the day cormorants feed in close association with patches of detached plants in the surf-zone (Table V). Other known piscivores such as *Pomatomus saltator* (Pomatomidae) also feed along sandy beaches in Western Australia (Thompson, 1958), and it is probable, therefore, that patches of weed act as daytime refuges from predators as well as being important feeding sites for individuals of *Pelsartia humeralis* and *Cnidoglanis macrocephalus*.

In contrast, the distribution and feeding habits of two other major species in this fish
community did not appear to be tied to patches of plant detritus. Although the diel distribution pattern for *Sillago bassensis* changed seasonally, at no date was the abundance of *S. bassensis* greater in WEED than in the SAND habitat. And on the date when sufficient numbers of *Crapatalus arenarius* were available for proper analysis, the mean density of this species did not differ across habitats. Both species fed mainly on infaunal polychaetes and bivalve siphons, and were not dependent on the patches of weed for food. However, some weed-associated amphipods were present in the guts of *Sillago bassensis*. While the distribution of both species within the surf-zone does not appear to be influenced by diurnal predation, their behaviour may be modified by predator activity, as is evidenced by the ability of *Crapatalus arenarius* to bury in the sand during the day (Scott et al., 1974).

Because previous work on other sections of the coast in south-western Western Australia has also shown that increased catches of fishes in the nearshore marine environment occur in the presence of detached plant material (Lenanton, 1982), we feel that the conclusions regarding the influence of macrophyte detritus on the abundance and species richness of the surf-zone fish fauna in this study can cautiously be applied to the whole temperate west coast region of Western Australia.

The accumulation of detached macrophytes in the surf-zones of beaches in Western Australia is patchy in space and time, and we expect this to be a major influence on the structure of the fish community at any particular surf-zone site. Some beaches harbour deposits of macrophyte debris year-round, others accumulate detritus only after storms (which occur mainly in winter), and some beaches remain relatively clean year-round (J. Hansen, unpubl. data). Because the abundance and species composition of the fish fauna is so dependent on the presence or absence of detached plants, descriptions of the structure of the surf-zone fish community will be highly dependent on the scale of observation. Our previous work in the surf-zone has shown that when summed over 50 km of coast, the quantity of plant detritus in the surf-zone shows a definite seasonal fluctuation with most detritus present in the winter months, June to October (Lenanton et al., 1982; Robertson & Hansen, 1982), indicating that even on such a large scale there are likely to be seasonal changes in the abundance and composition of the surf-zone fish fauna.

**SURF-ZONE FOOD CHAINS**

Like other surf-zone fish faunas (e.g. McFarland, 1963; Modde, 1980; Lasiak, 1983), the present fish community is dominated by juvenile fishes. However, a striking feature of the fish fauna in the present study is the dominance of benthic feeding fishes and the relative scarcity of planktivores, which form a major trophic group within other surf-zone fish communities (e.g. see Table V in Modde & Ross, 1981; McLachlan et al., 1981; Lasiak, 1983; McDermott, 1983). Large schools of two planktivorous clupeids *Spratelloides robustus* Ogilby and *Hyperlophus vittatus* have been captured in other surf-zone sampling in Western Australia (Lenanton, 1982; McLachlan & Hesp, in
press a), but these were either absent (e.g. *Spratelloides robustus*) or rare in the present study. The reason(s) for the absence of planktivores in the surf-zones of Sorrento and Mullaloo beaches is not known, but the large numbers of benthic feeding fishes is obviously linked to the presence of extensive patches of macrophytes in the surf, which appear to provide both food and protection from predation for fishes. In Venezuela, Edwards (1973a, b) also observed that relative to an open sandy beach, there was a higher proportion of benthic feeders on a beach which had large quantities of detached *Enteromorpha* spp., and Wheeler (1980) has observed that algae attached to man-made structures on open sandy beaches in England caused a similar shift in the trophic habits of the fish community.

The structure of the food chain supporting surf-zone fishes at the study sites, therefore, appears to be fundamentally different to that in the surf-zones of sandy beaches elsewhere in the world. In those sandy beach systems that have been extensively studied to date, it appears that phytoplankton blooms occur regularly in the surf-zone, providing the major energy and nutrient input to rich zooplankton and infaunal assemblages (Lewin, 1977; McLachlan, *et al.*, 1981) which are in turn consumed by planktivorous and benthic feeding fishes (McLachlan *et al.*, 1981; Lasiak, 1983). Nutrients excreted by the dense infaunal populations appear to be sufficient to sustain the phytoplankton blooms, and the food chain is almost self-contained within the surf-zone (Lewin, 1977; Lewin *et al.*, 1979; McLachlan, 1980b; McLachlan *et al.*, 1981). By contrast the major input of primary production to beaches in south-western Western Australia is macrophyte detritus which is swept into the surf-zones by storms (Robertson & Hansen, 1982). Estimates of the turnover time of this material in the surf-zone and on beaches near Perth, Western Australia reveal that \( \approx 20 \) percent of the nearshore benthic primary production, or 240 tonnes dry wt \( \cdot \text{km}^{-1} \cdot \text{yr}^{-1} \), of detached plants are processed through the sandy beach system (Hansen, 1983 & her unpubl. data).

Phytoplankton production is low in the inshore waters near Perth (D. Smith, pers. comm.) and phytoplankton blooms are rarely seen in the surf-zone along the lower west coast of Western Australia, although they have been observed on the southern coast (McLachlan & Hesp, in press b).

As the macrophyte material decomposes in the surf-zone in Western Australia, it is fed upon by large populations of the amphipod *Allorchestes compressa*, which has a major influence on detrital turnover in this system (Robertson & Lucas, 1983). Since *A. compressa* is the major constituent of the diets of the majority of fish species occupying the surf-zone, the macrophyte detritus–amphipod–fish pathway appears to be the major route of energy flow in this system.
ACKNOWLEDGEMENTS

R. E. Johannes, C. J. Crossland and D. A. Hancock read and commented on earlier drafts of the manuscript. During the project A. I. Robertson was supported by a CSIRO Postdoctoral Fellowship and an MST Research Fellowship.

REFERENCES


