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Why do juvenile fish utilise mangrove habitats?

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Abstract

Three hypotheses to discern the strong positive association between juvenile fish and mangrove habitat were tested with field and laboratory experiments. Artificial mangrove structure in the field attracted slightly more juvenile fish than areas without structure. Artificial structure left to accumulate fouling algae attracted four-times the total number of juvenile fish than areas without structure or areas with clean structure. Community composition of fish attracted to structure with fouling algae was different when compared with areas with no structure or clean structure; five species were attracted by structure with fouling algae whilst two species were associated with structure regardless of fouling algae. Algae were linked to increased food availability and it is suggested that this is an important selection criteria for some species. Other species were apparently attracted to structure for different reasons, and provision of shelter appears to be important. Predation pressure influenced habitat choice in small juvenile fish in laboratory experiments. In the absence of predators, small juveniles of four out of five species avoided shelter but when predators were introduced all species actively sought shelter. Large fish were apparently less vulnerable to predators and did not seek shelter when predators were added to their tank. Feeding rate was increased in the mangrove habitat for small and medium-sized fish compared with seagrass beds and mudflats indicating increased food availability or foraging efficiency within this habitat. Larger fish fed more effectively on the mudflats with an increased feeding rate in this habitat compared with adjacent habitats. The most important aspect of the mangrove habitat for small juvenile fish is the complex structure that provides maximum food availability and minimises the incidence of predation. As fish grow a shift in habitat from mangroves to mudflat is a response to changes in diet, foraging efficiency and vulnerability to predators. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Mangroves; Juvenile fish; Nursery; Shelter; Predation; Feeding rates

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1. Introduction

Both tropical and subtropical mangrove habitats are recognised worldwide as important nursery habitats for juvenile fish (Weinstein and Brooks, 1983; Wright, 1986; Robertson and Duke, 1987; Little et al., 1988; Chong et al., 1990). Juveniles of many species, including several of commercial importance, are found exclusively in mangrove habitats compared with adjacent habitats such as mudflats and seagrass beds, so that assemblages of juvenile fish in mangrove habitats are unique (Thayer et al., 1987; Morton, 1990; Robertson and Duke, 1990; Laegdsgaard and Johnson, 1995). However, while the nursery role of mangroves is well established, it is not clear why mangroves are so attractive to juvenile fish, and the question has generated much speculation. Three main hypotheses emerge as possible, but not mutually exclusive, explanations of this phenomenon: (1) the structural heterogeneity hypothesis – juvenile fish are attracted to the structural heterogeneity of mangrove habitats per se, (2) the predation risk hypothesis – risk of predation is lower in mangroves than in other habitats due to increased structural complexity, and (3) the food availability hypothesis – availability of food for juvenile fish is greater in mangrove habitats than in other habitats.

It is well established that fish will reliably flock to structure of many forms, ranging from artificial reefs and other fish attraction devices to floating algae (Orth et al., 1984; Holbrook and Schmitt, 1984; Robertson and Lenanton, 1984; Walsh, 1985; Diamant et al., 1986; Jara and Cespedes, 1994; Basset, 1994; Brandon et al., 1994; West et al., 1994). Thus, it may be that the aerial roots, tree trunks and overhanging branches of mangrove forests actively attract fish independent of the secondary effects of structure such as reduced predation and increased food availability. Alternatively, fish may be more abundant in mangrove habitats in the presence of predators because the increased structural complexity affords greater shelter and therefore reduced risk of predation. Certainly there is a striking relationship between increased complexity and decreased incidence of predation on invertebrates and some fish in other vegetated aquatic habitats (Ware, 1972; Heck Jr. and Thoman, 1981; Stoner, 1982; Crowder and Cooper, 1982; Savino and Stein, 1982; Bickerstaff et al., 1984; Robertson, 1984; Orth et al., 1984; Leber, 1985). Observations that complex habitats are used only during daylight hours, when risk from predation by visual predators is greatest, is also supportive of the protective function of structural complexity and suggest that some prey actively seek shelter when they are vulnerable to predators (Walsh, 1985; Schlosser, 1988; James and Heck Jr., 1994).

A third explanation is that mangrove habitats, which are highly productive systems, have greater availability of food for juvenile fish than do other habitats, either directly as detritus or indirectly through the structural complexity attracting a greater number of prey items. Many vegetated areas are a rich source of invertebrates (Harrington and Harrington, 1961; Stoner, 1982; Heck Jr. and Thoman, 1984; Orth et al., 1984; Bell and Westoby, 1986; Lubbers et al., 1990) that are suitable prey for small planktivorous fish. However, if the vegetation is too dense, fish may be hampered in their capture of prey, so that intermediate levels of structure of some seagrass and marsh plants effects the most profitable food returns (Vince et al., 1976; Crowder and Cooper, 1982; Stoner, 1982). Mangrove pneumatophores offer structure of a medium density, and their epiphytes facilitate increased abundance of planktonic prey species.

The three hypotheses described were tested separately in this study using a combination of field- and laboratory-based manipulative experiments. The suite of experiments were necessary to overcome the inherent interdependencies associated with any single experiments, for example, increasing structural complexity may at the same time decrease predation risk in the field, thus confounding the effects of structural heterogeneity per se and predation. In an attempt to address these difficulties, the first two hypotheses examined the number of juvenile fish associated with artificial mangrove structure in the field, and the behaviour of juvenile fish in response to shelter in the laboratory conditions where predation risk can be set at either zero or very high. This enabled determination of whether it is shelter on its own attracting fish, or whether fish were responding to the availability of shelter in the presence of predators. The rate at which food is acquired in three habitats was assessed to determine the relative importance of mangrove habitats in terms of food availability and/or catchability. Particular size classes of juvenile fish were considered separately since the behaviour and responses of fish may depend on ontogenetic stage. Dietary shifts accompanied by shifts in habitat and reduced risk of predation are commonly associated with increased size (Keast, 1978; Werner and Hall, 1977; Mittelbach, 1981, 1984; Werner et al., 1983a,b; Jones, 1984)

The results of this study show that of the small juvenile fish examined most were not attracted to structure per se but will move into shelter in the presence of predators or if there is food associated with shelter. This demonstrates that the strong positive association between juvenile fish and mangroves can be attributed to preferences (active choice) despite the fact that there is also differential survival among habitats which may account for high densities of juvenile fish in some habitats and not others. It also becomes clear from the findings of this study that as fish grow and become less vulnerable to predators, their needs change and they move from a protective environment (mangroves) to one that provides more food (mudflats). Identifying these mechanisms provides further support for careful conservation of these habitats to ensure the increase of fish stocks and the continued health of the fishing industry.

2. Materials and methods

2.1. Site description

All field experiments were carried out at Deception Bay in Moreton Bay, South East Queensland, Australia (Fig. 1). The extensive mangrove area at this site is a fisheries habitat reserve and therefore subject to recreational fishing only. The site is a nursery area for many species of juvenile fish, including several commercial species (Laegdsgaard and Johnson, 1995), and thus provides a suitable area to investigate why juvenile fish differentially inhabit mangrove areas. The mangrove forests consist entirely of the grey mangrove *Avicennia marina* that has small (10–20 cm) aerial pneumatophores that form extensive mats. Expansive mudflats and large beds of the seagrass *Zostera capricorni* adjacent to the mangrove forest at Deception Bay allow for comparisons among habitats.

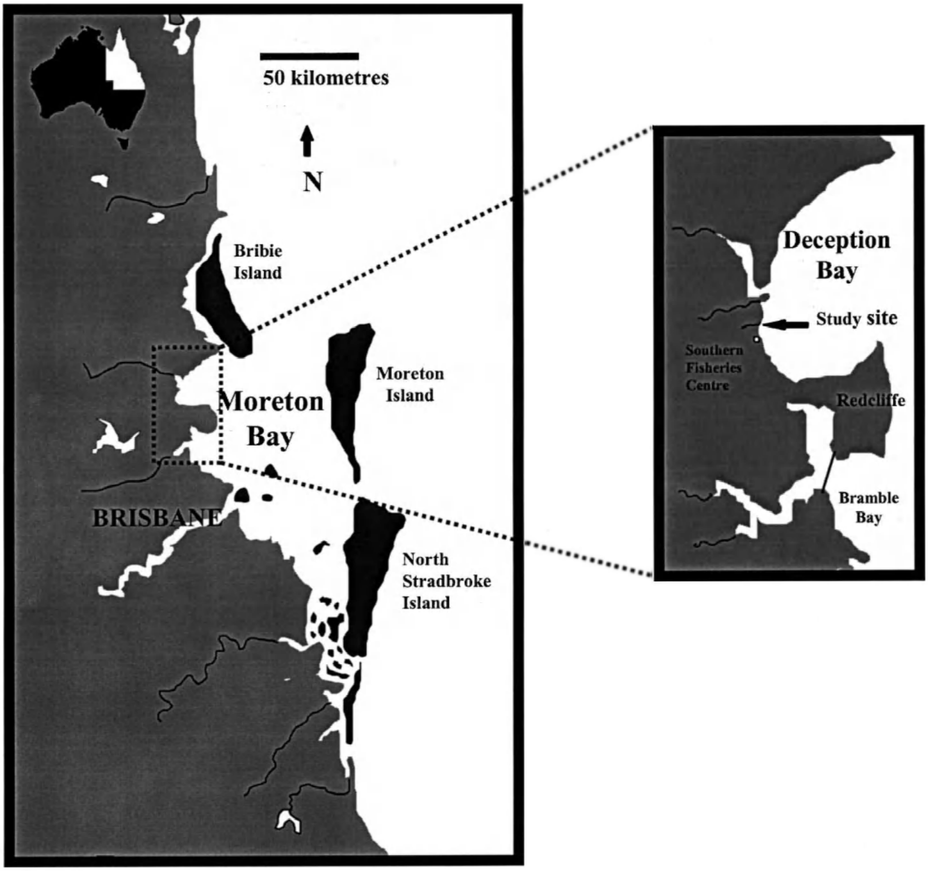

Fig. 1. Map of Moreton Bay with the site of field experiments at Deception Bay indicated.

2.2. Experimental methods

2.2.1. Selection of fish species

The majority of the manipulative laboratory and field experiments were conducted using three species of juvenile fish, viz. whiting (*Sillago* spp.), mullet (*Liza argentea*) and hardyheads (*Atherinomorus ogilbyi*).

These fish were chosen because of their high abundance as juveniles in subtropical estuarine habitats. In a study of habitat utilisation, Laegdsgaard (1996) showed that juveniles of *Liza argentea* utilise mangroves exclusively to a size of approximately 35 mm and do not appear to use other estuarine habitats (mudflats or seagrass) during their inhabitation of shallow estuarine areas. Additionally, juveniles of this species had a diet almost exclusively of mangrove forest insects (Laegdsgaard, 1996). *Sillago* spp. which is a commercially important species and is particularly abundant in estuarine habitats are found exclusively in mangroves at a small size (< 30 mm) while larger individuals

(30–50 mm) persist on the mudflats. Although *Atherinomorus ogilbyi* recruits to mangroves, this species is generally associated in greater abundances with the mudflat environment and shifts from mangroves to mudflats at a relatively small size (Laegdsgaard, 1996). This is a schooling species of fish that may be more adapted to life on the mudflats and was chosen to provide some contrast to the species more strongly affiliated with the mangroves.

2.2.2. Hypothesis 1: juvenile fish are attracted to habitats of high structural heterogeneity

2.2.2.1. Shelter use in the absence of predators. The behavioural response of the three species of juvenile fish to artificial structure per se (i.e., in the absence of predation risk) was tested in laboratory experiments. Whiting (*Sillago* spp.), mullet (*Liza argentea*) and hardyheads (*Atherinomorus ogilbyi*) were caught with a 6 m pocket seine net and transferred to holding tanks. *Sillago* spp. were divided into three size classes, small (10–20 mm), medium (21–30 mm) and large (31–40 mm) based on standard length (SL).

Twelve juvenile fish of any one species were introduced into a 1.5 × 2.5 m rectangular tank and allowed to acclimate over 2 h. After this time their behaviour was observed remotely by video for 60 min in the presence and absence of artificial pneumatophores (wooden stakes, standing 3–5 cm high, fixed to the bottom of the tank). The tanks were illuminated constantly and evenly with fluorescent lighting suspended above the tanks. Once the fish were placed in the tank there were no further disturbances in the experimental room for the duration of the acclimation and experimental periods.

Four replicate trials were made of each species subject to both of the two treatments. From the recordings, the proportion of juvenile fish in the half of the tank containing the artificial pneumatophores (or a randomly selected half in the case where artificial pneumatophores were absent) was determined at 10-min intervals (six observations).

Differences between replicates were tested and found to be not significant ($P > 0.25$) which allowed observations to be pooled (24 observations) to give a mean proportion of fish using the "experimental half" of the tank. This proportion was compared with t-tests to examine whether mean use differed significantly from 50%, which is the expected result if both sides of the tank were utilised equally.

2.2.2.2. Diel changes in shelter use. Thirty juvenile fish [five individuals of each of six species; whiting (*Sillago* spp.), mullet (*Liza argentea*), perchlet (*Ambassis marianus*), bream (*Acanthopagrus australis*), hardyheads (*Atherinomorus ogilbyi*) and silver biddy (*Gerresovatus*)] were placed in a circular tank 2 m in diameter. The additional fish species were used in this experiment to provide a greater potential for interaction among species to better simulate the conditions of a natural mangrove forest.

Half the area of the tank had previously been planted with artificial pneumatophores in the form of small stakes (protruding 2–5 cm above a sand base). The tank was set up in a blackened room with no natural light source. The experiment was conducted under constant red light illumination of the entire tank. The behaviour of the 30 juveniles was recorded over 24 h using time lapse photography (remote video). A similar experiment was carried out without the artificial pneumatophores as a control for tank bias. Four replicate trials were run on each of the two treatments.

For each trial, the position of individuals was determined every 10 min (144 observations) and the mean proportion of juveniles in the half of the tank containing the artificial pneumatophores (a randomly selected half of the tank was used when stakes were not present) during the day and at night was calculated. Differences between replicates were tested and found to be not significant ($P > 0.25$) which allowed observations to be pooled (288 night and 288 day observations) to give a mean proportion of fish using the ''experimental half'' of the tank.

The mean proportion of individuals occupying the ''experimental half'' of the tank during night hours was subtracted from the proportion present during daylight hours ($D_{\text{day-night}}$). Deviations of mean $D_{\text{day-night}}$ values from zero were assessed using t-tests. To test for the effect of artificial pneumatophores in the absence of predators, the proportion of fish within the ''experimental half'' of the tank was also analysed using t-tests to examine whether mean values differed significantly from 50% as would be expected if both halves of the tank were utilised equally.

2.2.2.3. Use of artificial structure in the field. Three experiments were undertaken in the field to test the hypothesis that the physical structure of mangrove roots and tree trunks attract juvenile fish. These experiments were conducted during summer months when recruitment of juvenile fish species is greatest in estuarine habitats (Laegdsgaard and Johnson, 1995). Although it has been demonstrated that distinct assemblages of fish occur within spatially separated estuaries, their role as nurseries is ubiquitous. Thus, a hierarchical spatial component was not included in this experiment as the question being investigated related to the use of structure per se regardless of particular fish species and the location of the estuary.

Experiment 1: Small-scale artificial mangrove forests were created adjacent to the edges of the pneumatophore fringe of the mangroves in water of maximum depth 1 m at high tide. Sixteen plots of 1.5 m × 2.5 m were allocated randomly among four treatments being all possible combinations of ±artificial pneumatophores and trunks and ±shade.

Artificial pneumatophores were in the form of small sticks pushed firmly into the mud at the same height (5–10 cm above the mud) and density (200 m^{-2}) as natural pneumatophores. Larger wooden stakes (10 cm wide × 5 cm deep × 1 m tall) were added to resemble trunks of saplings or small trees of *Avicennia marina*. Eight plots, four with stakes and four without, were covered with a roof of shade cloth (2 m above the plot). The 16 plots were left for 2 weeks then sampled over 2 consecutive days (two replicate plots from each treatment per day). The plots were encircled with a drop net of 1 mm mesh, 1 m above the substratum with a triggering device. The nets were triggered at high tide and a heavy chain at the bottom of the net ensured that it rested firmly on the substratum after release. The nets were emptied at low tide and all fish were preserved in 10% formalin in sea water. Fish were retrieved rapidly at low tide to avoid predation by crabs.

Community data were analysed initially using a three-way (±shade and ±stakes as fixed factors and ''day'' as a random factor) multivariate analysis of variance (MAN-

OVA), and a three-way analysis of variance (ANOVA) was conducted on total fish abundances in each treatment. The initial analyses indicated differences among days were not significant, so data were re-analysed as a two-way model I design with ±stakes and ±shade as fixed factors.

Experiment 2: Four plots with stakes were left in the field for a further 12 months to accumulate algal growth. These plots and four unstaked plots were then sampled on the same tide using drop nets as outlined above. A one-way model I ANOVA was used to analyse total abundances with ±stakes as a fixed factor. The significance of differences in community structure was determined in a one-way MANOVA. Data were $\sqrt{\sqrt{}}$ transformed to prevent abundant species from swamping the analysis.

Data from experiments 1 and 2 were then combined to test for differences in the numbers of fish caught in plots with clean stakes, stakes with algae and the control plots (with no stakes) from each year. A significant result in the overall one-way MANOVA on the four treatments was followed by a multiple comparison procedure consisting of four separate one-way MANOVAs as a limited number of a priori pair-wise tests (see Johnson and Field, 1993). As recommended by Johnson and Field (1993), Roy's greatest root and an adjusted α of 0.0125 was used in the pair-wise tests and a canonical discriminate analysis (CDA) was conducted to present a graphical representation of the MANOVA results. MANOVA was appropriate for these data since there were few zeros in the data matrix, and transformed data met assumptions of the models sufficiently well.

Experiment 3: Adjacent to the mangrove forest, two large plots (10 × 10 m) were established on intertidal mudflats approximately 20 m out from the pneumatophore fringe where water attained a depth of approximately 2 m at high tide. One plot was planted with both small stakes to resemble pneumatophores (5–10 cm above the mud at a density of 200 m^{-2}) and larger stakes (1 m above the mud at a density of 1 m^{-2}) mimicking the trunks of saplings. The other plot was left unadorned as a control. Replication of these plots was not possible because of the scale of the manipulation. These two plots were left for 2 weeks before netting once a day over 4 days. A buoyed net anchored to and restrained on the mud bottom at low tide was released at high tide to encircle the entire plot. All fish were collected and preserved in 10% formalin in seawater. The experiment was repeated after covering the plots with a roof of shade cloth (2 m above the plot).

Although the plots could not be replicated, all fish caught on any day were sacrificed, so that any dependence on plot site could not be ascribed to repeated measurement of the same community. This experiment was included to allow for comparison with the replicated but smaller plots described above.

2.2.3. Hypothesis 2: juvenile fish seek shelter to reduce the risk of predation

2.2.3.1. Predator avoidance. The behavioural response of three species of juvenile fish to the presence of predators was tested in laboratory experiments. Whiting (*Sillago* spp.), mullet (*Liza argentea*) and hardyheads (*Atherinomorus ogilbyi*) and a range of local predator species were caught with a 6 m pocket seine net and transferred to holding tanks for a period of 3–5 days before the experiments were conducted. Predators were fed live food made up of brine shrimp, small fish and mosquito larvae during the holding period. *Sillago* spp. were divided into three size classes of, small (10–20 mm), medium (21–30 mm) and large (31–40 mm) standard length and fed freeze dried brine shrimp during the holding period.

Twelve juvenile fish of any one species were introduced into a 1.5 × 2.5 m tank and allowed a 2 h acclimation before their behaviour was observed remotely by video for 60 min in the presence or absence of artificial pneumatophores (wooden stakes fixed to the bottom of the tank standing 3–5 cm high). After 1 h of observation post acclimation, two predators [one tailor (*Pomatomas saltatrix*) and one moses perch (*Lutjanus russellii*)] were added to each treatment and the behaviour of the juveniles filmed for a further 60 min.

Four replicate trials, each with a different group of fish, were made of each of the four treatments (all combinations of ±stakes and ±predators). From the recordings, the proportion of prey fish in the half of the tank containing the artificial pneumatophores (or a randomly selected half in the case where artificial pneumatophores were absent) was determined at 10-min intervals.

The mean percentage of fish occupying half of the tank before addition of predators ($= b$) was subtracted from the mean percentage after the addition of predators ($= a$) to yield a difference score (D_{b-a}). For *Liza argentea* and *Atherinomorus ogilbyi* the significance of differences in D_{b-a} values among treatments with and without stakes were examined by a one-way model I ANOVA. For *Sillago* spp. a two-way model I ANOVA was used to examine the significance of the effects of both shelter and fish size.

To establish whether a denoted "experimental half" of the tank (a randomly allocated half or the half with stakes) was used equally before and after the addition of predators, *t*-tests were used to examine the significance of deviations of D_{b-a} values from zero.

2.2.3.2. Refuge value of habitats. To compare the relative refuge value of the three habitats (mangrove, seagrass, mudflat) to whiting (*Sillago* spp.), which is a vagile fish species, it is necessary to restrain their movement by tethering. Tethering techniques have the shortcoming of potentially producing experimental artifacts that complicate meaningful ecological interpretation of results (Peterson and Black, 1994; Micheli, 1996; Curran and Able, 1998). Artefacts are generally related to interference of tethers with escape responses causing increased susceptibility to predators (Barbeau et al., 1994; Zimmer-Faust et al., 1994) or to tethers inducing behavioural changes in response to habitat which may make prey more or less susceptible to predators (Curran and Able, 1998). Peterson and Black (1994) also suggested that artifacts induced by tethering could be habitat dependent due to differences in predator assemblages. While we recognise the limitations of the technique, in this study we were not concerned with estimating habitat specific predation rates per se but obtaining a measure of relative refuge value of the different habitats. We considered that tethering was a useful means to examine the relative refuge value of different habitats provided that fish were tethered in a consistent manner among habitats and that the mobility of the fish was not so severely restricted by the tethers that they were hampered from seeking shelter from predators. Absolute predation rates within habitats were not estimated from the results of the tethering experiments as they are likely to be overestimates (Peterson and Black, 1994).

These experiments were one of several approaches we used to assess response of juvenile fish to habitat.

Fish captured with a 6 m pocket seine net were placed in flow-through holding tanks overnight before tethering with very fine nylon thread passed through muscle tissue above the caudal vertebrae. The nylon thread was 1 m in length, which allowed the fish sufficient mobility to seek shelter in each habitat.

Tethering stations were established at low tide and consisted of a cord tied between two poles approximately 2 m apart and 0.1 m off the substratum. At high tide, six tethered *Sillago* spp. were attached at equal distances along each cord where they remained until low tide when surviving fish were counted and released. Four replicate tethering stations were established in each of the seagrass, mudflat and mangrove habitats. Controls were established (four replicates) to determine whether fish could break free from their tethers. Controls comprised tethering stations set up as above but surrounded by a 1 mm mesh cage to exclude predators and contain any escapees. Results were analysed by a one-way ANOVA followed by Tukey's HSD multiple comparison procedure.

2.2.4. Hypothesis 3: habitat selectivity by juvenile fish reflects differential food availability

Field experiments were used to compare feeding rates of juvenile whiting (*Sillago* spp.) in seagrass, mudflat and mangrove forest habitats. Four replicate cages, each 1.5 m^2 with 1 mm-mesh sides and open at the top, were secured firmly to the substratum in each habitat to ensure no gaps remained at the bottom edge. In the mangrove habitat, pneumatophores were cut off level with the substratum in all cages to facilitate easy capture of fish. The pneumatophores were left loose within the cage as a potential food source. Cages were installed at low tide to ensure that they contained only those fish added during the experiment.

Fish were captured using a 6 m pocket seine dragged through shallow water adjacent to the mangrove forests. Fish were sorted into three size classes, viz. small (10–20 mm SL), medium sized (21–30 mm SL) and large (31–40 mm SL), and separate experiments conducted for each size class. A total of 200 fish were starved for 24 h in flow-through holding tanks before 50 individuals were introduced into each cage at mid to high tide. At no time did the water rise to the top of the cages. Six individuals were selected randomly and removed from each cage with a dip net at 15 min intervals over 90 min and fixed immediately in 10% formalin in sea water.

Stomach contents were dissected from each preserved fish and dried separately from the body of the fish. Whole dried fish and stomach contents were weighed and an index of gut fullness calculated as follows:

$$\text{Gut fullness} = \frac{\text{Stomach content dry weight}}{\text{Total dry weight (including stomach contents)}} \times 100\%$$

Four independent replicate feeding rates (from four different cages) were obtained for each size class of *Sillago* in each habitat. Gut index values were $\sqrt{}$ transformed to obtain linear gut fullness/time relationships in estimating feeding rate. Feeding rates and gut fullness after 75 min, were compared among effects of habitat (fixed effect) and size (fixed effect) using two-way model I ANOVA followed by a Tukey's HSD multiple comparison test.

3. Results

3.1. Hypothesis 1: juvenile fish are attracted to habitats of high structural heterogeneity

3.1.1. Shelter use in the absence of predators

Examination of size-specific use of shelter in the absence of predators by *Sillago* spp. (Table 1) indicated that all size classes of *Sillago* avoid shelter and spent more time in unstaked areas of experimental tanks than expected from random movement (Table 1). Similar to the results for *Sillago*, *Atherinomorus ogilbyi* clearly avoided shelter whereas *Liza argentea* was highly associated with staked areas (Table 1).

3.1.2. Diel changes in shelter use

The pattern of shelter use in six species of juvenile fish did not show any diel shift, and the difference in shelter use during day and night did not differ significantly from zero (Table 2). There was no inherent bias in the use of the tank since, in the absence of both shelter and predators, each side of the tank was used similarly ($t=-2.12$, df$=7$, $P=0.06$).

3.1.3. Use of artificial structure in the field

3.1.3.1. Total abundance. Addition of both artificial pneumatophores and shade in small (1×2 m) plots significantly affected total abundances of fish relative to open mudflats (Table 3). There were more fish in areas with simulated pneumatophores than without regardless of shade. Fish were in greatest numbers in unshaded plots with

Table 1
Shelter use in three species of juvenile fish demonstrated either selective use of shelter (*Liza argentea*) or avoidance of shelter (*Sillago* spp. and *Atherinomorus ogilbyi*) in the absence of predators[a]

Species	Size	Tank with half area staked	Tank with no stakes
Sillago spp.	Small (10–20 mm)	25.0±4.4***	56.5±5.5
	Medium (21–30 mm)	31.3±4.6***	44.9±5.3
	Large (31–40 mm)	33.9±5.7***	44.9±5.3
Liza argentea	Small	84.6±5.3***	56.0±7.3
Atherinomorus ogilbyi	Small	33.9±4.3***	48.9±5.3

[a] Data are percentages (mean±1S.E.) of fish in the "experimental half" of a tank. In the tank where stakes are present the mean number on fish within the staked half are given, in the tank with no stakes the percentage of fish in a randomly selected half of the tank are given. Means that differ significantly from 50% are indicated (***$P<0.0001$).

Table 2

Total number of all species of fish in the staked half of the tank where artificial pneumatophores (stakes) are present or in the "experimental half" of the tank where stakes are absent during day or night[a]

	Day	Night	$D_{\text{day-night}}$
Tank with half area staked	34.5±3.0***	29.7±3.1***	2.2±1.2 ns
Tank with no stakes	51.8±1.8	52.0±1.7	−0.03±0.8 ns

[a] The pattern of usage of the tank did not differ between night and day as the differences in proportions ($D_{\text{day-night}}$) of fish were not significantly (ns) different from zero (tank with stakes, $t=1.88$, df=3, $P=0.16$; tank with no stakes, $t=-0.03$, df=3, $P=0.98$). There was significant avoidance of artificial pneumatophores as the proportion of fish within the stakes was significantly less than 50% regardless of the time of day (***$P=0.0001$).

simulated pneumatophores and least abundant beneath shade cloth but in the absence of other shelter (Table 3).

These results were also reflected in large-scale plots (10×10 m) in which total abundances of juvenile fish (all species) were ca. 1.7-times lower in unstaked plots than in staked plots irrespective of the presence of shade, and ca. 4.4-times lower in shaded than in unshaded plots regardless of the presence of stakes (Table 3).

After epiphytes were given time to establish on the artificial pneumatophores, the number of fish caught in these plots was significantly greater than those caught in unstructured plots at the same time (Table 3). The number of fish in unstructured plots did not differ in consecutive years (one-way ANOVA, $F_{1,1}=17.62$, $P<0.25$). This similarity between years in unstructured plots allows some validity in comparing fish densities in of plots with epiphytised stakes in 1 year with unfouled stakes in another. The number of fish caught in plots with epiphytised stakes was significantly greater than those in plots with unfouled stakes and in bare plots (one-way ANOVA, $F_{1,2}=211$, $P<0.005$) (Table 3).

Table 3

Summary of mean absolute abundances of fish (±1S.E.) in the three experiments in which artificial pneumatophores (stakes) were deployed on mudflats adjacent to mangrove forests[a]

Stakes	Shade	1×2 m Plots with algae (Experiment 1)	1×2 m Plots (Experiment 2)	10×10 m Plots (Experiment 3)
+	−	50.3±3.9	14.8±1.2	45.0±11.3
−	−	12.5±2.2	9.5±1.8	25.8±5.5
+	+	n.a	8.0±1.8	10.3±2.7
−	+	n.a	3.0±0.8	5.8±0.9

[a] Note that plots left to accumulate algae were never shaded (n.a, not applicable). Fish were ca. four-times more abundant in plots fouled by algal epiphytes than in unstructured plots (experiment 1), and this difference was highly significant (one-way model I ANOVA, no transformation, $F_{1,6}=75.8$, $P<0.0001$). In 1×2 m plots without algae (experiment 2) fish occurred in significantly greater abundances in the presence of simulated pneumatophores but in the absence of shade cloth (two-way model I ANOVA, no transformation, effect of stakes $F_{1,12}=5.0$, $P=0.04$). Where shade cloth only was present there were significantly less fish ($F_{1,2}=9.3$, $P<0.01$). Similar responses to simulated pneumatophores and shade cloth were evident in the larger scale experiment (experiment 3) using 10×10 m plots. Note that the means for the 10×10 m plots are from four consecutive nettings of the same plot.

3.1.3.2. Community response. At the community level, MANOVA indicated that adding stakes significantly changed community structure in the small plots (Pillai's trace; $F_{1,12}=6.3$, $P<0.02$) but the presence/absence of shade cloth had no effect on community composition. Of the seven species recorded, only three demonstrated individually significant responses to shade and/or presence of artificial pneumatophores (Table 4). There were significantly fewer *Sphyraena obtusata* in shaded areas regardless of the presence of simulated pneumatophores (Fig. 2A), significantly more *Liza argentea* in staked plots regardless of shade (Fig. 2B), and *Sillago* spp. were significantly more abundant in unshaded areas with stakes and least abundant in areas without shade or stakes (Fig. 2C).

Overall there were significant differences among communities in areas with unfouled stakes, fouled stakes and no stakes (Pillai's trace; $F_{18,24}=17.2$, $P<0.0001$) and a priori multiple range tests revealed that communities within areas of unfouled stakes were significantly different from communities within areas of fouled stakes (MANOVA, Roy's greatest root; $F_{6,1}=45\ 918.7$, $P<0.004$). The CDA highlights this result; the two areas without stakes show very similar community structure in consecutive years (Fig. 3). There is a clear separation in fish community structure between staked areas with and without fouling algae (Fig. 3).

A total of 11 species were caught in the experimental plots with fouled stakes, while seven were caught in plots with stakes before algal growth occurred. Of the seven species caught in both experiments, three species *Ambassis marianus*, *Sillago* spp. and *Platycephalus fuscus* were significantly more abundant when stakes supported algae than in any other treatment (Fig. 4A–C). *Liza argentea* and members of the family Gobiidae were significantly more abundant in areas with stakes regardless of algal growth (Fig. 4D and E).

3.2. Hypothesis 2: juvenile fish seek shelter to reduce the risk of predation

3.2.1. Predator avoidance

Comparison of the number of *Sillago* spp. of different sizes in a randomly allocated "experimental half" of a rectangular tank before and after the addition of predators

Table 4
Results of ANOVAs of individual species caught in 1×2 m artificial mangrove plots[a]

Species	Shade (1,12 df)	Stakes (1,12 df)	Shade×stakes (1,12df)
Ambassis marianus	1.20 ns	0.00 ns	1.20 ns
Platycephalus fuscus	1.20 ns	0.00 ns	1.20 ns
Tetractenos hamiltoni	2.7 ns	0.12 ns	0.12 ns
Family Gobiidae	1.52 ns	1.52 ns	0.10 ns
Sphyraena obtusata	8.54*	0.14 ns	0.52 ns
Liza argentea	0.22 ns	27.31***	0.21 ns
Sillago spp.	6.40*	4.88*	0.00 ns

[a] Four treatments are represented as combinations of ±artificial pneumatophores and ±shade. F-values are given along with significance $P>0.05$ (ns), $0.01<P\leq0.05$ (*), $0.001<P\leq0.01$ (**) and $P\leq0.001$ (***).

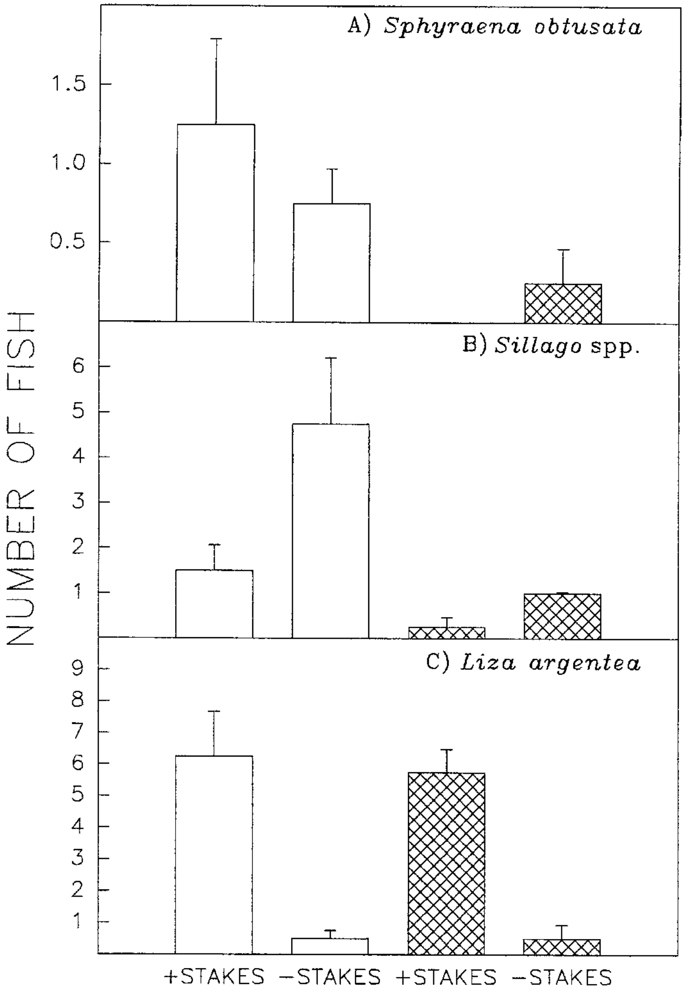

Fig. 2. The effect of shade and/or simulated pneumatophores (without algae) on abundances of three species of fish, in 1×2 m experimental plots. These species showed significant responses to the treatments (see Table 4). Bars represent means of four replicates of each treatment ±1S.E. Cross-hatched bars indicate shaded plots.

indicated a significant size×shelter interaction (two-way ANOVA, $F_{2,18}=5.6$, $P<0.01$). The presence of predators did not affect use of the experimental half of the tank for small, medium sized or large *Sillago* in tanks where shelter was not available (D_{b-a} values were not significantly different from zero in all cases, t-test $P>0.05$). In contrast, small and medium sized *Sillago* showed significantly increased use of shelter in the presence of predators (small, $t=10.7$, df=3, $P<0.001$; medium, $t=16.9$, df=3, $P<0.0005$) (Fig. 5A and B). Large *Sillago* also increased their use of shelter in the presence of predators, but the trend was not significant (Fig. 5C).

Responses of *Liza argentea* and *Atherinomorus ogilbyi* measured similarly (Fig. 5D

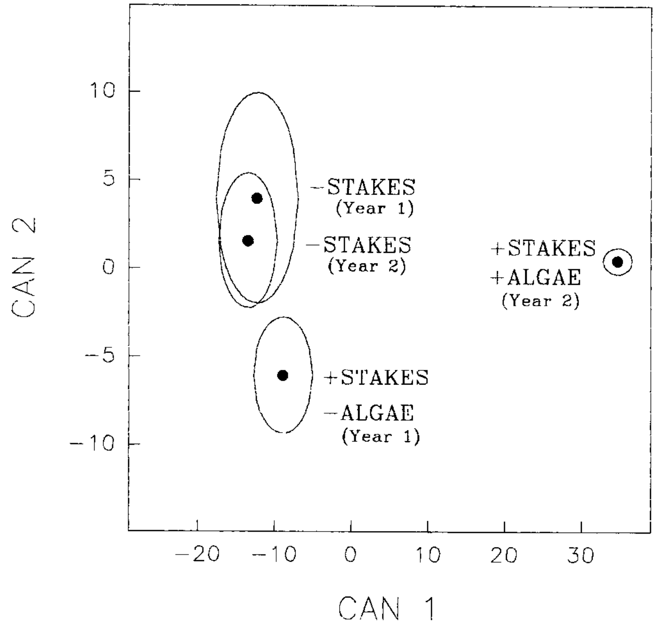

Fig. 3. Results of canonical discriminate analysis (CDA) comparing juvenile fish community structure among plots with ±artificial pneumatophores and artificial pneumatophores with ±algal growth. Points are group centroids with 95% confidence ellipsoids.

and E) indicated that *Liza argentea* also used shelter more after the addition of predators (one-way ANOVA, $F_{1,22}=34.9$, $P<0.0001$) (Fig. 5D). *Atherinomorus ogilbyi* showed the same trend, but the difference was not significant (Fig. 5E).

In the presence of predators small and medium-sized *Sillago* spp. actively sought shelter, with the proportion of fish in the sheltered portion of the tank being significantly greater than 50% (small, $t=-9.5$ $P<0.0001$; medium, $t=-10.1$, $P<0.0001$). These same fish avoided shelter when predators were absent (Fig. 6A and B). In contrast, large *Sillago* showed no evidence of seeking shelter and spent on average, similar time in and out of shelter (the proportion of large fish using shelter did not differ significantly from 50%; +predators $t=1.78$, $P>0.08$, −predators $t=1.86$, $P>0.08$) (Fig. 6C). *Liza argentea* individuals spent 100% of their time in shelter when predators were present (Fig. 6D) and *Atherinomorus ogilbyi* also showed significant increase in shelter use after the addition of predators ($t=-3.8$, $P<0.0008$) (Fig. 6E).

3.2.2. Refuge value of habitats

In the tethering experiment the control cages contained all the tethered individuals and none had broken free from their tethers.

In the uncaged areas, significantly fewer tethered *Sillago* spp. were recovered on the mudflats than in seagrass and mangrove habitats (Table 5).

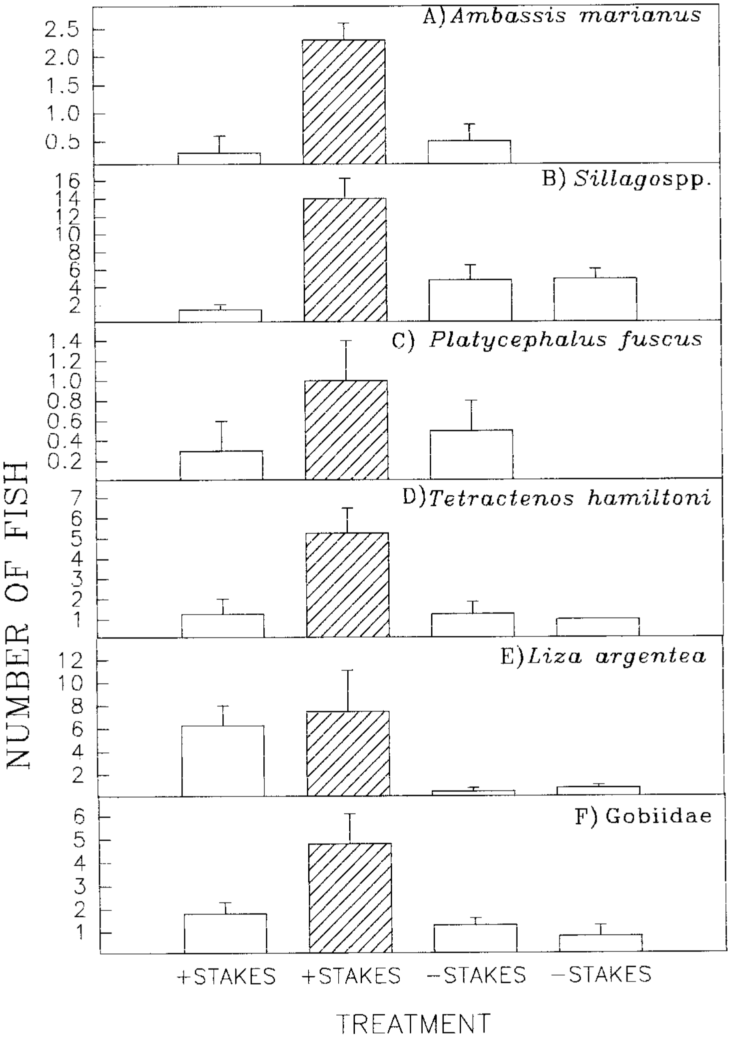

Fig. 4. Abundances of species used in the comparison of community structure in 1×2 m treatment plots of artificial pneumatophores with and without epiphytic algae and plots without stakes. Bars represent means from four replicates ±1S.E. Bars with diagonal lines indicate plots with algae.

3.3. Hypothesis 3: habitat selectivity by juvenile fish reflects differential food availability

3.3.1. Gut fullness

Examination of gut fullness after 75 min of feeding by starved fish indicated that gut fullness depends both on size of fish and the nature of the habitat in which they were feeding (two-way ANOVA, habitat×size interaction $F_{4,207}=9.8$, $P<0.0001$). At the end

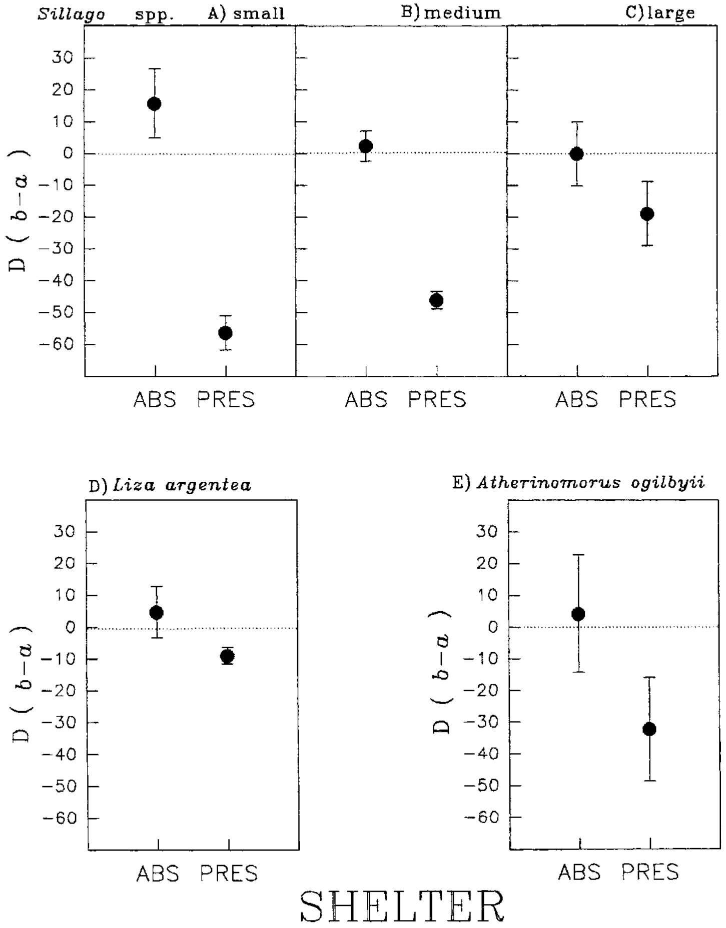

Fig. 5. Results of experiment examining shelter use by (A) small (10–20 mm), (B) medium (21–30 mm) and (C) large (31–40 mm) *Sillago* spp., (D) *Liza argentea* and (E) *Atherinomorus ogilbyi* in the presence (pres) and absence (abs) of predators. D_{b-a} represents the number of fish present in a randomly allocated "experimental half" of a tank before the addition of predators minus the number in this area after addition of predators. No species sought shelter in the absence of predators, but small and medium-sized *Sillago* spp. and *Liza argentea* significantly increased their use of shelter in the presence of predators. Points represent means of four replicates ±1S.E., after pooling of six observations per trial.

of the experimental period, small and medium *Sillago* spp. had the fullest guts in the mangrove habitat, whereas on the mudflats it was the large *Sillago* spp. that fed most effectively (Fig. 7). Large *Sillago* did not feed at all in the seagrass habitat. After feeding on mudflats, small and medium sized *Sillago* had similar amounts of food in their stomachs, but stomachs of large *Sillago* contained significantly more food (approximately twice as much) in their stomachs corrected for body size (Fig. 7).

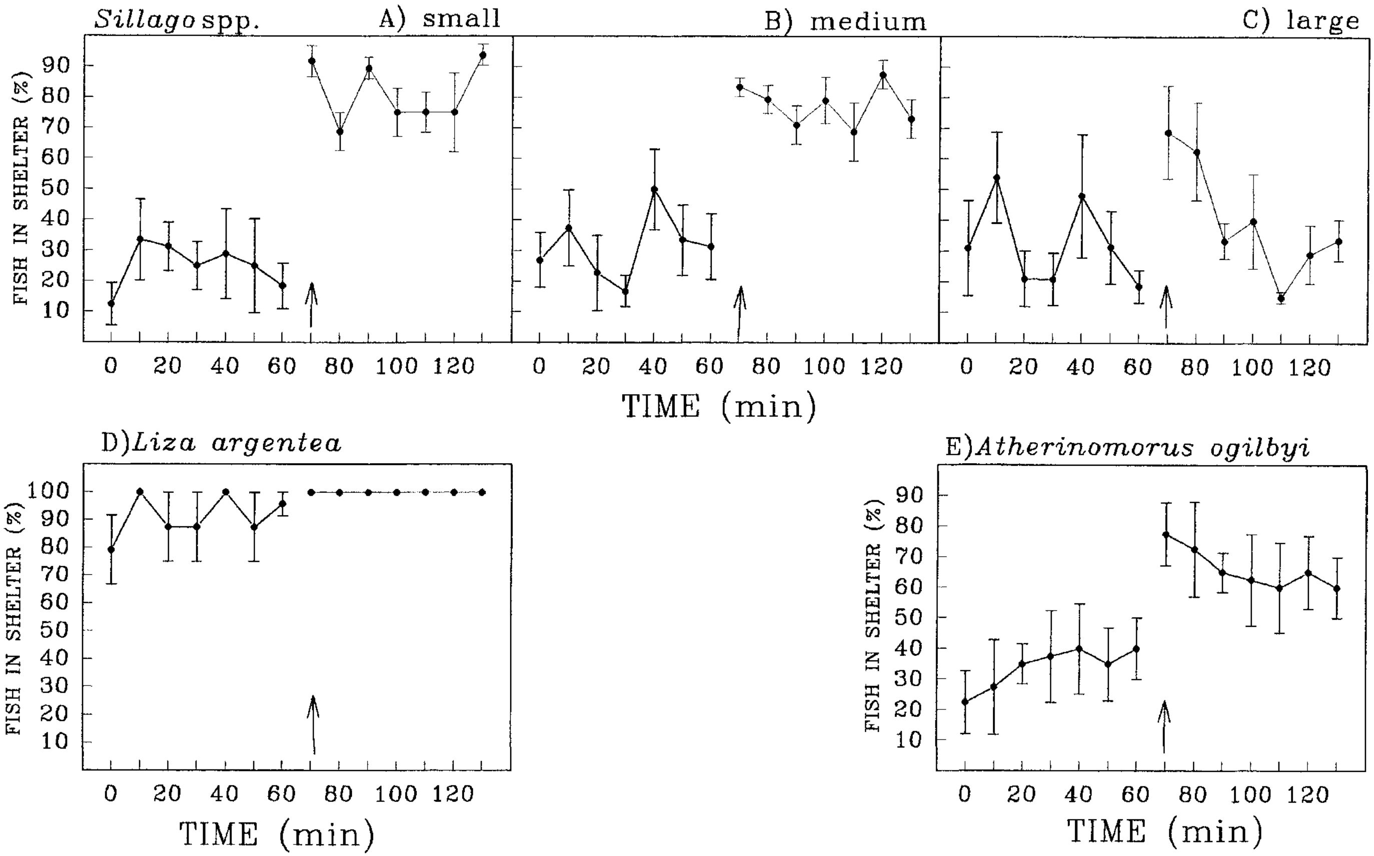

Fig. 6. Shelter use by (A) small (10–20 mm), (B) medium (21–30 mm) and (C) large (31–40 mm) *Sillago* spp., (D) *Liza argentea* and (E) *Atherinomorus ogilbyi* in tanks with shelter covering half the floor area in the presence and absence of predators. An arrow marks the point at which predators were added to the tank. Points represent means from four replicates ±1S.E.

Table 5
Survival of tethered *Sillago* spp. in each habitat (means±1S.E.); MF, mudflat, M, mangrove and SG, seagrass[a]

Habitat	% Survival
MF	37.5±7.9
M	91.5±4.9
SG	91.5±4.9

[a] A one-way ANOVA showed that losses to predators were significantly greater on mudflats than in mangrove and seagrass habitats ($F_{2,9}=26.7$, $P<0.0002$).

3.3.2. Feeding rate

Feeding rates of the three size classes of *Sillago* spp. derived from the slopes of increase in gut fullness over time (Fig. 7) indicated that small and medium sized *Sillago* fed at highest rates in the mangrove habitat, whereas large *Sillago* filled their stomachs more quickly on the mudflats than in any other habitat, resulting in a significant habitat×size interaction (two-way ANOVA, $F_{4,27}=9.3$, $P<0.0001$) (Fig. 7). Differences in feeding rates between small and medium-sized *Sillago* on the mudflats were not significant. Feeding rate of *Sillago* in seagrass was greatest in small fish.

4. Discussion

Mangrove habitats are utilised worldwide as nurseries by many species of fish, and much speculation has surrounded the question of why these habitats are so attractive. Preferential utilisation of, or increased survival in, mangrove forests by juvenile fish has commonly been related to three hypotheses, viz. (1) increased structure, (2) decreased predation or (3) increased food availability (Russell and Garrett, 1983; Rozas and Hackney, 1984; Chong et al., 1990). Rarely have these hypotheses been tested critically, and they have never been examined simultaneously in a single system. These hypotheses are not mutually exclusive and habitat choice by juvenile fish is likely to be influenced by a combination of factors.

4.1. Importance of structure

Structural complexity per se may not be greatly attractive to juvenile fish independently of the added benefits that structure can provide such as shelter or increased surface area for accumulation of food. The results in this study indicate that increased structural heterogeneity alone is insufficient to account for the strong association of large numbers of juvenile fish with mangrove forests. Although adding artificial mangrove structure to areas in the field significantly increased the total number of fish caught compared to unstructured areas, the increase was relatively slight. In contrast, artificial structure with accumulated algae attracted ca. four-times the number of juvenile fish when compared with either unfouled stakes or no structure. Many forms of vegetation allow for accumulation of small invertebrates (Stoner, 1982; Robertson, 1984; Lubbers et al., 1990; Schneider and Mann, 1991) that are an important food of many juvenile fish species. The epiphytic algae on mangrove pneumatophores accumulate an assemblage of

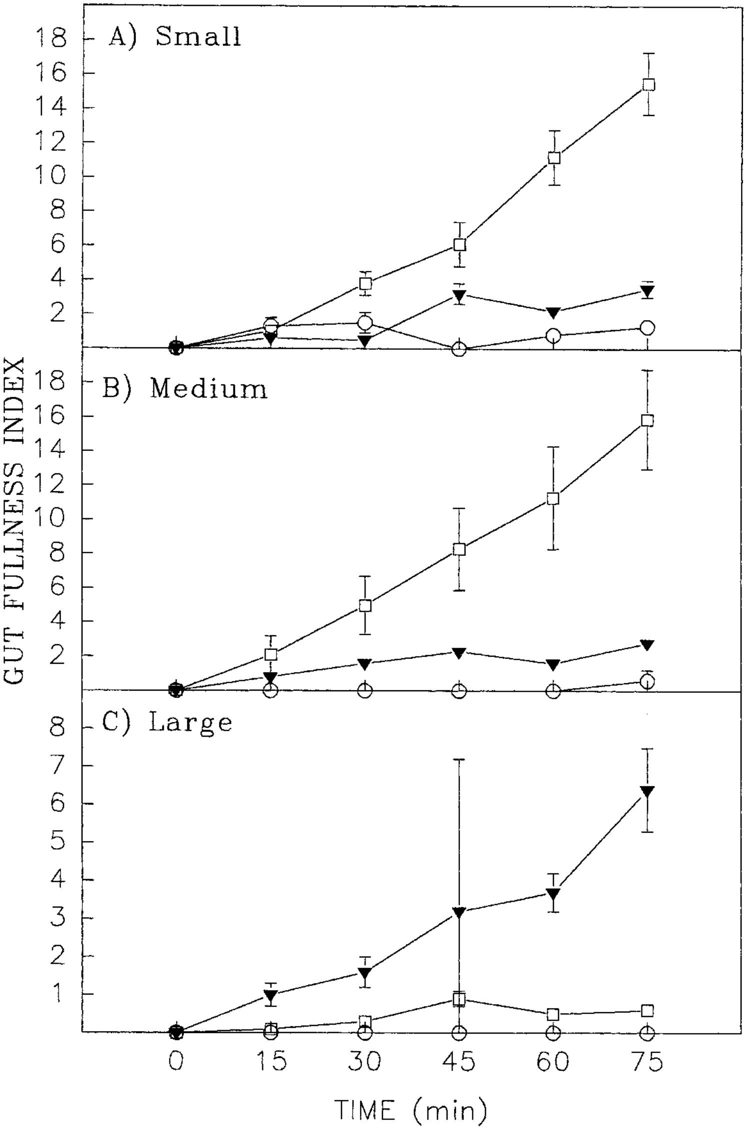

Fig. 7. Change in gut fullness with time (slopes were used to determine feeding rates) of three size classes (small; 10–20 mm, medium; 21–30 mm and large; 31–40 mm) of *Sillago* spp. in seagrass (○), mudflat (▼) and mangrove () habitats. Points are means from four replicates ±1S.E., after pooling data of six fish per replicate.

invertebrate species that is distinct from and richer than that of mangrove sediments, and the gut contents of juvenile fish species match the invertebrates associated with the algae that proliferate on pneumatophores (Laegdsgaard, 1996). It is therefore tempting to suggest increased food concentration about the fouled stakes as an explanation of these results. If food was relatively scarce around unfouled stakes, juveniles may have opted for nearby natural pneumatophores that supported epiphytes. However, the difference in physical heterogeneity between epiphytised and unfouled stakes, independent of differences in associated food, is an alternative explanation (that was not examined).

Community structure, as distinct from total abundances, was significantly different between unfouled stakes and adjacent unstaked areas, suggesting that some species may be attracted to structure alone. However, there was also a difference in community structure between stakes with and without fouling algae, while the fish assemblages captured in the two samplings without stakes were similar in structure. This suggests there may be differences in selection criteria among fish species; five species (*Ambassis marianus*, *Platycephalus fuscus*, *Tylosurus* sp., *Tetractenos hamiltoni* and *Sillago* spp.) were significantly more abundant in artificial structure that supported fouling algae, and for these species food may be the most important factor. Other species (*Liza argentea* and members of family Gobiidae) were attracted to stakes regardless of the presence of fouling algae and for these species the protective value of shelter may be more important. In some fish species both factors may play a role, for example, in surf perch selection of patches is influenced both by food quality and structural complexity. In this species, food quality is the primary selection criterion, and as predation risk increases then structural complexity becomes increasingly important (Schmitt and Holbrook, 1985).

4.2. Predation pressure and use of shelter

Predation can have a strong influence on habitat choice, and it is more often the risk of predation, rather than the number of predation events, that drives habitat selection. In the field the risk of predation is always present even if actual predation rates are low, so that to examine use of shelter independently of predation, the risk of predation must be removed. In the laboratory, shelter was actively avoided by six species of juvenile fish (*Gerres ovatus*, *Atherinomorus ogilbyi*, *Ambassis marianus*, *Acanthopagrus australis*, *Sillago* spp. and *Liza argentea*) during both night and day in 24-h trials in the absence of predators.

In shorter-term experiments, *Atherinomorus ogilbyi* and *Sillago* spp. also avoided structure. *Liza argentea* showed a higher affinity for structure although still ventured away from structure in the absence of predators. When predators were added to the tanks, shelter was sought actively by all three species and the incidence of sorties into the open became fewer. These results differ to those for several other species in which the introduction of shelter had little or no effect on spatial distribution in the absence of predators (Werner et al., 1983a; Utne et al., 1993). However, there are many examples showing that in the presence of predators, aquatic fauna shift to areas offering improved shelter from predation (Stein, 1977; Stein and Magnuson, 1976; Sih, 1982; Vuorinen et al., 1983; Power et al., 1985; Utne et al., 1993). Thus, in terms of the hypothesis of predation risk, decreased risk of predation appears to be an important factor underpinning the preferred use of mangrove habitats by juvenile fish. The tethering experiments indicated that relative risk of predation was similar in mangrove forests and seagrass beds, and significantly reduced in these habitats compared with mudflats.

The nature of shelter may also play a vital role in habitat selection. In the field, despite that relative refuge value was approximately equivalent in both seagrass beds and mangrove forests, species richness and abundance of juvenile fish is much greater in mangrove habitats than in seagrass (Thayer et al., 1987; Laegdsgaard and Johnson, 1995). A partial explanation is that invertebrates on which juvenile fish feed are afforded better protection from predators in seagrass and are not so easily captured in this habitat (Ware, 1972; Heck Jr. and Thoman, 1981, 1984; Crowder and Cooper, 1982; Stoner, 1982; Summerson and Peterson, 1984). The success of small fish in prey capture is greatest at an intermediate density of structure (Heck Jr. and Thoman, 1981; Crowder and Cooper, 1982), of which areas of mangrove pneumatophores are a prime example, and this increases the effective availability of food to small fish.

4.3. Importance of food

Feeding rates of small and medium-sized fish were significantly greater in the mangroves compared with mudflat and seagrass habitats. Small fish were capable of feeding in the seagrass beds whereas medium sized fish were not, although neither size class were ever observed naturally in the seagrass beds (Laegdsgaard and Johnson, 1995).

While these results support the third hypothesis that the effective availability of food for small fish is greater within the mangrove habitat than in adjacent areas, it must be recognised that foraging gains are often balanced against the risk of predation. For example, small bluegills suffer a reduction in energy gain by feeding in vegetation where they are better protected from predators (Mittelbach, 1984), while sticklebacks decrease their foraging effort in the open to allow for surveillance for predators (Milinski and Heller, 1978). Results from this study show clearly that small juvenile fish in mangrove habitats have the benefit of both increased acquisition rates of food and increased protection. The large amounts of algae covering the pneumatophores provide shelter and food for many invertebrates that are food for juvenile fish. Food intake in the seagrass habitat is greatly reduced although the protective value is equivalent to that of mangroves, indicating an overall net benefit in selecting the mangrove habitat.

4.4. Size-specific selection of habitats

Patterns of shelter use in the presence of predators, feeding rates and the identity of habitats in which food acquisition rates were greatest, all depended on the size of the fish. Unlike small fish, larger animals did not flee to shelter in the presence of predators. Small and large sunfish and several other species (Stein and Magnuson, 1976; Sih, 1982; Werner et al., 1983a) show a similar behaviour, and in general, there is a paucity of large piscivorous predators in shallow water habitats (Blaber, 1980; Ansell and Gibson, 1990). With growth, increased size affords either a refuge in size or greater mobility and ease of escape from predators, which allows successful migration towards the deep-water habitat of adult populations via more open estuarine habitats.

Feeding rates of small fish were greater in mangrove than in other habitats, whereas ingestion rates of large fish were greatest on the mudflat habitat, which is the preferred habitat of this size class (Laegdsgaard, 1996). In most fish species, like those in this study, there appears to be a strong association between small individuals and vegetated habitats with larger size classes moving to less vegetated habitats (Werner et al., 1983a; Mittelbach, 1984; Thayer et al., 1987; Lubbers et al., 1990; Laegdsgaard, 1996) with concomitant shifts in diet (Keast, 1978; Stoner, 1982; Lubbers et al., 1990; Laegdsgaard, 1996). For many fish species, increase in size confers an ability to feed on larger food items and a decreased vulnerability to predators (Vince et al., 1976; Mittelbach, 1981, 1986; Werner et al., 1983a,b; Jones, 1984; Power, 1984; Ebeling and Laur, 1985; Archambault and Feller, 1991). This increases the ability of larger fish to exploit new habitats where dietary components are more abundant or easier to attain, however it is unknown whether differential food availability drives, or simply tracks, shifts in habitat. The structure of mangrove habitats, which provide both protection and ample food for small juvenile fish, may hamper effective prey capture by larger fish in the same way that large killifish are unable to feed in marsh where structural complexity is high (Vince et al., 1976). Similarly, in high densities of seagrass (*Syringodium*), pursuit and capture of invertebrates by pinfish is inhibited in larger size classes due to restriction of movement of the pectoral fin, while the same habitat is apparently no barrier to locomotion in small pinfish (Stoner, 1982). Habitat shifts are likely to be a mechanism to reduce intraspecific competition between size classes, and have been demonstrated for sunfish (Werner et al., 1983b), grey snapper (Thayer et al., 1987) and several other species of fish (Butner and Brattstrom, 1960; Laegdsgaard, 1996).

5. Conclusions

For small fish arriving at the estuary as post larvae, the most important pressures governing habitat selection and/or differential survival among habitats are the risk of predation and the availability of food, both of which relate to the nature of physical structure. Mangrove forests provide structure at an intermediate scale in which capture of invertebrate food prey by juvenile fish species appears optimal and risk from piscivorous predators is reduced. In other habitats within the estuary, such as seagrass beds, there is equal protection from predators but foraging success is reduced and therefore seagrass beds are less suitable for post-larval fish. With increased size, juvenile fish switch to mudflat habitats as their foraging success in mangroves is reduced (presumably because the complex structure of the mangrove forests becomes restrictive of foraging) and the fish become less vulnerable to predators and are able to forage in relative safety on the more open mudflats.

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