



Removal of seagrass canopy: effects on small fish and their prey

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Abstract

In an experiment in a southern Australian estuary, patches of seagrass canopy were removed to test the importance of the canopy to fish in areas where all other factors were known to be consistent with seagrass presence. The total number of fish was slightly lower in patches cleared of seagrass than in patches of undisturbed seagrass, but was not as low as in unvegetated patches. The benthic habitat was expected to be especially important to non-pelagic species, yet their numbers, and those of the most important commercial species, *Sillaginodes punctata*, were not lower in patches cleared of seagrass, despite being lower in unvegetated patches. The disturbance associated with removing seagrass was simulated and was not found to affect fish numbers. The diet of all fish caught consists mainly of invertebrates associated with the seagrass canopy and sediment surface (epifauna). Epifaunal abundance and production were highest in seagrass patches, lowest in unvegetated patches and intermediate in patches cleared of seagrass. Patterns of fish abundance did not provide evidence of the importance of seagrass canopy in attracting increased fish abundances compared with unvegetated areas but were consistent with a model stressing the importance of prey availability in the role seagrass plays as habitat for small fish.

Keywords: Epifauna; Habitat selection; Predation; Seagrass; Statistical power; *Zostera*

1. Introduction

Seagrass meadows in many parts of the world support large numbers of juvenile fish and provide a nursery habitat for many commercially important species (Pollard, 1984). The importance of seagrass is implied by reports of declining seagrass cover being

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matched by declining fish catches in, for example, King George whiting [*Sillaginodes punctata* (Cuvier & Valenciennes)] (Bell & Pollard, 1989). Unvegetated areas adjacent to seagrass meadows have also been shown to have different fish assemblages, usually with fewer fish and fewer species (Bell & Pollard, 1989). The difference between fish assemblages of seagrass and unvegetated areas is, however, only an association. Environmental factors (e.g. a water quality variable) concomitant with, or resulting in, seagrass absence may also be the cause of differing fish assemblages.

Attempts to demonstrate the importance of seagrass have mostly involved the construction of patches of artificial seagrass in unvegetated areas. The question posed is: what is the effect on fish of placing seagrass mimic in positions having all other factors consistent with absence of seagrass? An alternative is to remove seagrass from areas where it is naturally occurring. The question then becomes: what is the effect on fish of removing seagrass from positions having all other factors consistent with seagrass presence? This more closely matches the question: what is the effect of seagrass loss on fish? The disadvantages of seagrass removal are firstly that regrowth necessitates either a short-term experiment or repeated removal, and secondly that seagrass removal is irresponsible except when working with species that recover quickly.

The importance of seagrass probably lies either in the protection it offers from predators (larger fish), or in the greater abundance of associated food (mostly small invertebrates). Bell & Westoby (1986b) manipulated seagrass densities in field experiments and used predator exclusion cages to show that small fish were more common in denser seagrass regardless of predator presence/absence. They showed convincingly that low fish numbers in patches with less dense seagrass cover were not due to increased predation, and concluded that small fish select habitat. As Bell & Westoby (1986a) point out, their results may be explained in ways other than habitat selection by fish. Fish might, for example, be attracted to more abundant food in denser seagrass. Food abundance was not measured by Bell & Westoby (1986a,b). The lower abundance of fish in unvegetated areas is, according to the model of Bell & Westoby (1986a,b), the result of fish choosing to settle in seagrass beds in preference to adjacent unvegetated areas.

The aim of the present study was to determine the effects on small fish distribution of removing above-ground vegetation (seagrass canopy). If the seagrass canopy is important, for whatever reason, then patches from which the vegetation has been removed should support fewer fish and different fish assemblages than seagrass patches. Moreover, if the seagrass canopy is the important difference between seagrass and unvegetated habitat, then fish assemblages associated with patches from which the seagrass canopy has been removed should match assemblages from patches which were unvegetated prior to the experiment. If small fish are less abundant in unvegetated patches because they do not settle there then, as predicted above, the numbers of fish in patches cleared of seagrass should match the number from areas unvegetated prior to the experiment. If, on the other hand, small fish are attracted to seagrass directly to feed upon more abundant prey (as proposed, for example, by Edgar & Shaw, 1993), then the number of fish in patches cleared of seagrass should match prey abundance and production associated with the modified habitat and will not necessarily be the same as fish numbers from areas unvegetated prior to the experiment.

2. Materials and methods

The Barker Inlet/Port River region (138° 30' E, 34° 45' S) is a sheltered, marine-dominated estuary comprising extensive intertidal areas with either eelgrass (*Zostera*, *Heterozostera*) cover or no vegetation. A comparison of assemblages of small fish from eelgrass and unvegetated areas has demonstrated the typical differences described above (Connolly, 1994a). The estuary is strongly tidal, typically with two tides per day, with a maximum tidal amplitude of 2 m, and fish occupying the lower intertidal zone must choose anew the habitat over which they swim on every incoming tide. The experiment was situated in an area dominated by *Zostera muelleri* Irmisch ex Aschers., a fast growing, colonising species. The experiment was done in September 1991, and was timed to coincide with the seasonal recruitment into the estuary of juveniles of the most important commercial fish species, *Sillaginodes punctata*, which accounts for nearly half the value of inshore scalefish landings in South Australia (Anon., 1992).

Fish were collected from the following four habitats (treatments) marked as 5.5 × 5.5 m squares:

- (1) eelgrass in natural state (control = C),
- (2) eelgrass removed by cutting with shears at the sediment surface whilst emergent on low tides (removed = R),
- (3) eelgrass uncut, but with equivalent time and effort spent at site mimicking cutting (procedural control = P), and
- (4) unvegetated mudflat (unvegetated = U).

Six eelgrass sites were assigned to each of the first three treatments in a randomised block design. That is, one replicate of each of the first three treatments was assigned at random to six randomly selected areas (blocks) along a 1 km stretch of shore. The unvegetated treatment could not be randomly assigned. Instead, the nearest unvegetated site to the block occurring at the same height in the intertidal was selected as the unvegetated patch. The blocked design guaranteed interspersion, which is important because of the potential patchiness of fish abundances.

Patches were prepared over several days, and fish were collected 14 days later. This was a short enough interval to avoid eelgrass regrowth. The order in which patches were prepared and therefore netted was chosen so that on any day only one patch within a block was netted, so as to avoid disturbance of nearby patches. During the experiment the netting schedule was disrupted by inclement weather and attempts to collect fish from one block were abandoned in a bid to return to schedule. Fish were collected only from a 5 × 5 m square in the centre of each patch, avoiding the edges of habitats. Fish were netted using a buoyant pop net released in water depths from 40–100 cm on an incoming daytime tide. The pop net was designed to collect fish neatly from experimental plots, a situation for which more conventional seine netting is too unwieldy (Connolly, 1994b). All fish were identified and counted. Species considered to be pelagic (*Atherinosoma microstoma* Günther – Atherinidae, *Arripis georgianus* Valenciennes – Arripidae and *Spratelloides robustus* Ogilby – Clupeidae) were excluded from some analyses.

The amount of food available to fish within each patch was estimated by sampling the small, motile invertebrates (epifauna) associated with the eelgrass canopy and sediment surface. Epifauna, especially crustaceans and polychaetes, are the predominant food of virtually all of the fish species, including juvenile stages of larger species, normally caught with small nets in the shallow waters of the Barker Inlet – Port River region (Connolly, unpubl. data). Three randomly placed collections were made within each patch on the day prior to fish collection. Invertebrates were collected using a 95 μm mesh net with a 25 \times 25 cm opening, following the method of Sergeev et al. (1988) in which the net is placed rapidly over the canopy onto the sediment before dragging shut the net opening along the sediment surface. Invertebrates were later separated into sieve size classes of 2 mm, 1 mm, 500, 250, 125 and 75 μm before being identified to major taxa and counted. Numbers of very abundant taxa were counted from random subsamples with the aim of counting between 50 and 200 individuals of each taxon per sieve size in any sample. Nematodes and foraminifera were excluded from this study because they are taken rarely or not at all by the fish species caught. Ash-free dry weights (AFDW) were calculated by converting abundances for each taxon for each sieve size using Edgar's (1990) equation, $\log B = a + b \cdot \log S$ [where B = AFDW (mg), S = sieve size (mm) and a and b vary depending on broad taxonomic category]. This permits estimation of epifaunal production using Edgar's (1990) equation, $P = 0.0049 \cdot B^{0.80} \cdot T^{0.89}$, relating production (P , $\mu\text{g}/\text{day}$) to sample AFDW (B , μg) and water temperature (T , $^{\circ}\text{C}$).

The surface area of eelgrass leaves within all patches that supported eelgrass prior to the experiment was estimated before setting up the experiment and again on the day after fish collection. Leaf area was calculated for each patch from measurements of the number of leaves per 400 cm^2 quadrat, and the length and width of ten leaves, at five randomly selected sites. Prior to the experiment, leaf area did not differ between patches selected for the three treatments involving eelgrass (C: 1.54 m^2 leaf area/ m^2 sediment surface; P: 1.31; R: 1.39; ANOVA: $p = 0.651$). After removal, the leaf area within patches of treatment R was reduced almost to zero, whilst patches of P remained similar to patches of C (C: 1.55; P: 1.46; R: 0.02; ANOVA: $p < 0.001$; Tukey's HSD pairwise comparisons: C P R).

2.1. Data analysis

The number of fish (all species combined and key species separately) from the four habitats were compared using a randomised block analysis of variance (ANOVA); this is equivalent to a mixed model, two-way ANOVA without replication, in which "habitat" is the fixed factor and "block" the random factor. Results of the significance test for effects of block have been reported, but should be treated cautiously since they depend on the untested assumption that the interaction effect is small (Zar, 1984). Furthermore, the intention of allocating treatments to blocks was to guarantee interspersed of treatments rather than to search for differences in fish abundances along the coast. However, by removing the variance due to block, a more sensitive test for differences amongst habitats is made than would be the case with a simple one-way ANOVA. Significant ANOVA results were followed by Tukey's HSD pairwise comparisons

between habitat means. *Atherinosoma microstoma* is a species that schools strongly, unlike the other species analysed. This behaviour results in large fluctuations in number per net since catch rates are either zero or, if a school happens to be caught, in the order of 100 individuals. $\log_{10}(x + 1)$ transformation failed to render data normal, and *Atherinosoma microstoma* numbers were therefore analysed using Friedman's non-parametric equivalent to the ANOVA described above (Zar, 1984). Invertebrate abundance and production in the four habitats were analysed in the same way as fish abundances, after averaging the three values from each patch. For both fish and invertebrates, sample variances increased with increasing means, and analyses were performed on \log_{10} transformed data after checking that the transformation increased homoscedasticity. Pearson's r -test was used to detect association between fish abundances and epifaunal production by patch. Significance levels are 0.05 throughout.

Fish assemblages from the four habitats were compared using an analysis of similarities (ANOSIM), which is a non-parametric analogue to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. ANOSIM has an additional advantage over MANOVA in being able to detect differences between groups without any need for assumptions of constant spread within each group (Clarke, 1993). ANOSIM compares ranked similarities between and within groups selected a priori (here the four habitats) using a randomisation test for significance. Since habitat differences could have been obscured by any block effect, a two-way ANOSIM without replication, equivalent to the univariate ANOVA described above, was also used to test simultaneously for differences amongst habitats and blocks (Clarke & Warwick 1994). The ANOSIM tests involved 5000 simulations using the PRIMER package from Plymouth Marine Laboratory, UK.

The relationships amongst assemblages from each patch are graphically represented using non-metric multidimensional scaling (MDS), which is an ordination technique that uses the same matrix of ranked similarities as ANOSIM. MDS displays samples in low (usually two) dimensional space while retaining as nearly as possible the similarity rankings between samples.

For comparisons of fish assemblages among the four habitats, raw counts were transformed using $x^{0.25}$ to emphasise the distribution of less common species in the analysis. The transformation $x^{0.25}$ gives slightly more emphasis to less common species than $\log(x + 1)$ in cases such as this where counts are small (Clarke, 1993). The Bray-Curtis similarity coefficient was used, as a meaningful and robust measure (Clarke, 1993).

3. Results

3.1. Fish

A total of 2170 fish of 11 species were caught during the study, with 504 individuals of the three species categorised as pelagic. The mean number of individuals of each species and for all species together from each habitat is shown in Table 1.

Total fish abundance in habitat P was greater than in habitat U. Fish abundances in habitats C and R were not different from each other and were intermediate between

Table 1
Fish abundance by habitat

	Control	Procedural control	Removed	Unvegetated	Total abundance	% of all fish
<i>F. lateralis</i>	37.2 (61,23)	56.8 (93,35)	49.6 (81,30)	26.4 (43,16)	850	39
<i>Sillaginodes punctata</i>	45.0 (74,27)	40.6 (66,24)	51.8 (85,31)	14.2 (23,8)	758	35
<i>Atherinosoma microstoma</i>	62.2	29.8	0.4	5.0	487	22
<i>Kaupus costatus</i>	1.2	1.6	0.8	0.2	19	1
<i>Tetractenos glaber</i>	1.2	0.8	0.6	0.8	17	1
<i>Spratelloides robustus</i>	0.4	2.8	0	0	16	1
<i>Gymnapistes marmoratus</i>	0.6	1.4	0.2	0.4	13	1
<i>Heteroclinus perspicillatus</i>	0.8	0.2	0	0	5	<1
<i>Rhombosolea tapirina</i>	0	0	0.2	0.4	3	<1
<i>Arripis georgianus</i>	0	0	0	0.2	1	<1
<i>Hyporhamphus melanochir</i>	0.2	0	0	0	1	<1
All species combined	148.8 (239,96)	134.0 (207,87)	103.6 (160,67)	47.6 (74,31)	2170	

Numbers for each habitat are means, with 95% confidence limits in parentheses (confidence limits are anti-log values of confidence limits calculated using \log_{10} transformed data and residual variance from ANOVA, and are therefore shown only for taxa analysed using ANOVA) ($n = 5$). Total abundance is number of individuals.

the other two habitats (ANOVA: Habitat – $p = 0.034$, Block – $p = 0.654$; Tukey's: P C R U).

Excluding pelagic species, more fish were caught in habitats C, P, and R than in U. Differences between catches in the first three habitats were not significant (ANOVA: Habitat – $p = 0.003$, Block – $p = 0.232$; Tukey's: R P C U).

Abundances of *Sillaginodes punctata* were higher in habitat R than in U. Abundances in habitats P and C were not different from each other and were intermediate between the other two habitats (ANOVA: Habitat – $p = 0.022$, Block – $p = 0.051$; Tukey's: R P C U).

Comparisons for *Favonigobius lateralis* (Maclay) and *Atherinosoma microstoma* detected no significant differences in abundance amongst habitats (*F. lateralis* – ANOVA: Habitat – $p = 0.498$, Block – 0.182; *Atherinosoma microstoma* – Friedman's: Habitat – $p = 0.316$, no test for block). These non-significant results are more meaningful if the statistical power of the tests is examined. Power is the complement of β , which is the probability of making a Type II statistical error (i.e. when a test fails to reject a false

null hypothesis). Power is related to α , the probability of making a Type I statistical error (i.e. when a test rejects a true null hypothesis), sample size and effect size. Effect size is defined as the minimum departure from the null situation able to be detected with the power specified. This is usually set as the minimum departure of biological interest. In the case of the fixed factor in a randomised block ANOVA, effect size can be specified as the difference between the two most extreme means (Zar, 1984). For the test amongst means of *F. lateralis* abundance, I consider it important to detect a departure from the null in which one treatment has a mean 50% lower than other treatments. An example of this effect size for *F. lateralis* would be the following means (units are fish/net): C = P = R = 50, U = 25. On \log_{10} data this translates to: C = P = R = 1.7, U = 1.4. The chance of detecting a difference amongst habitats in mean abundance of *F. lateralis* with the effect size specified above was 0.22 ($\beta = 0.78$) (Equ. 13.33; Zar, 1984). No formal power calculations are possible on the Friedman's non-parametric test of *Atherinosoma microstoma* abundances, but it is possible to apply the known power efficiency of Friedman's test compared with the equivalent ANOVA (0.76 for four treatment means; Zar, 1984) to an estimate of what power would have been if an ANOVA had been applied to the data. The effect size for *Atherinosoma microstoma* would be similar to that for *F. lateralis* and degrees of freedom are identical, but variance is larger and therefore power would be something less than the figure of 0.22 for *F. lateralis*. This figure would be reduced further upon application of the power efficiency factor (multiply estimated power of ANOVA by 0.76), and the best estimate of power to detect a difference amongst median abundances of *Atherinosoma microstoma* is therefore considerably less than 0.2. The low power in tests of *F. lateralis* and *Atherinosoma microstoma* abundances suggests that, although no differences were detected, it should not be concluded that there are no biologically important differences amongst abundances of these species. Rather, the test results demonstrate a need for increased numbers of patches.

No clear differences between habitats are discernible in the ordination plots showing relationships amongst fish assemblages from each patch for all fish species (Fig. 1a) and non-pelagic species only (Fig. 2a). Ignoring any block effects, statistical comparisons of fish assemblages found no significant differences amongst habitats whether or not pelagic species were included (One-way ANOSIM: All fish – $p = 0.526$; Pelagic species excluded – $p = 0.663$). Ordination plots including (Fig. 1b) and excluding (Fig. 2b) pelagic species show some signs of grouping according to block. Block effects are not significant, however, and nor are differences amongst habitats after removing effects of block (Two-way ANOSIM: All fish, Factor Habitat – $p = 0.098$, Factor Block – $p = 0.592$; Pelagic species excluded, Habitat – $p = 0.328$, Block – $p = 0.115$). No formal power calculations are currently possible with the ANOSIM method, but the small number of replicate patches serves as a reminder that a Type II error is possible.

3.2. Epifauna

A total of 40082 invertebrates were caught and placed into 19 taxa, 12 crustacean and seven other categories. Invertebrate abundance was higher in habitats C, P and R

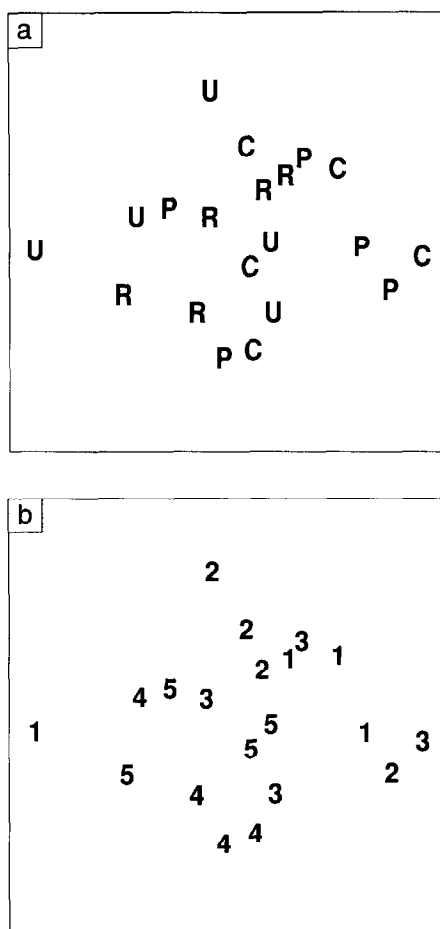


Fig. 1. Two-dimensional MDS ordination plot of fish assemblages, all species included: (a) by habitat, C = Control, P = Procedural control, R = Removed, U = Unvegetated, and (b) by block. Stress value (Kruskal's formula 1) = 0.162.

than in U. No difference was found between habitats C and P, but R had lower abundance than C (Table 2). (ANOVA: Habitat - $p < 0.001$, Block - $p = 0.759$; Tukey's: C P R U).

Table 2
Epifaunal abundance and production by habitat

	Control	Procedural control	Removed	Unvegetated
Abundance	903 (1263,646)	794 (1110,568)	381 (533,273)	48 (67,34)
Production	170 (258,112)	126 (191,83)	86 (131,57)	50 (76,33)

Numbers are means with confidence limits, calculated as described in Table 1, in parentheses ($n = 6$).

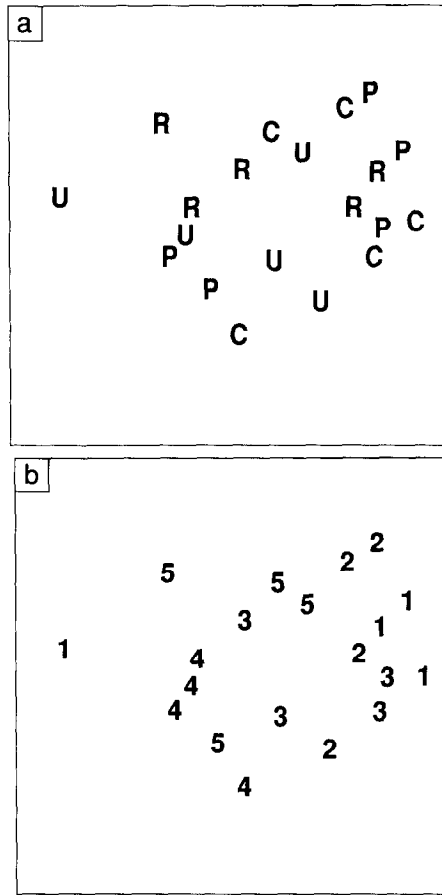


Fig. 2. Two-dimensional MDS ordination plot of fish assemblages, pelagic species excluded: (a) by habitat, lettering as for Fig. 1, and (b) by block. Stress value (Kruskal's formula 1) = 0.136.

Total epifaunal production was greater in habitat C than in U, and in P and R was intermediate between and not significantly different from C and U (Table 2). (ANOVA: Habitat – $p = 0.014$, Block – $p = 0.646$; Tukey's: C P R U).

Neither total fish abundance nor total non-pelagic fish abundance were correlated with epifaunal production of patches (All species: Pearson's $r = 0.249$, $p = 0.291$; Pelagic species excluded: $r = 0.279$, $p = 0.233$). For a specified effect size of $r = 0.5$, the power of Pearson's correlation test was 0.64 ($\beta = 0.36$) (Cohen, 1988).

The relationship between mean fish abundance and mean epifaunal production by habitat is perhaps of greater importance than the search for a correlation between fish abundance and epifaunal production by patch. The relationship between mean fish abundance and mean epifaunal production by habitat is contrasted in Fig. 3 with the relationship between mean fish abundance and mean seagrass cover (leaf area) in the four habitats. Total abundance of all fish species matches epifaunal production rather

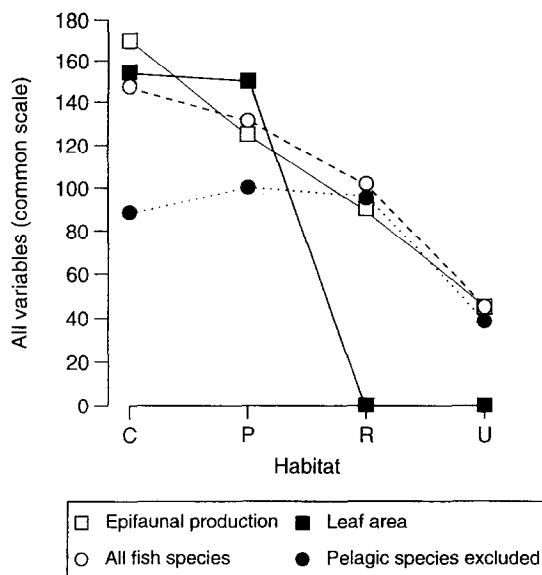


Fig. 3. Relationship of total number of fish and total number of non-pelagic fish (fish/net) to epifaunal production ($\mu\text{g}/\text{day}$) and seagrass cover (m^2 leaf area/ m^2 sediment area) by habitat. All symbols represent means, with common scale. Lines are included to make patterns clear and do not imply that measurements are possible between habitats.

than seagrass cover, and this is true also when pelagic species are excluded, although fish abundances then match epifaunal production less closely.

4. Discussion

The differences in fish catches from patches of the four habitats were not in assemblage composition but in overall fish abundance and abundance of *Sillaginodes punctata*. The main difference was between habitat U and the other three habitats. Independent surveys of eelgrass and unvegetated patches in the region also show lower total fish abundances and fewer *Sillaginodes punctata* over unvegetated habitat (Connolly, 1994a). Surveys also show unequivocal differences between assemblages of the two habitats at all times of year, yet these were not evident in this study. The patch sizes of unvegetated habitat in the present study were slightly smaller than the smallest patches netted during survey work, and this difference in scale may explain why assemblage differences between undisturbed eelgrass and unvegetated patches were not apparent in the current study. Ferrell & Bell (1991) have shown that the distance of unvegetated sites from eelgrass affects how different the fish assemblages are from those of adjacent *Zostera* beds. The total area netted in this experiment was only about one third of the area netted with seine nets during each survey period. Less common species were therefore less likely to be caught during this experiment, and so species typical of a habitat without being abundant there, such as the syngnathid *Stigmatopora nigra* Kaup and the odacid *Haletta semifasciata* (Valenciennes) from eelgrass habitat, were not caught. The num-

ber of *F. lateralis* was similar at all habitats. This species was also found in similar numbers over eelgrass and unvegetated habitat during survey work. *F. lateralis* individuals are intimately associated with the seabed and even in eelgrass areas tend to occur in bare patches between clumps of eelgrass. The fish are well camouflaged when they are over sediment.

Total fish numbers tended to be lower over habitat U than over the other habitats, and these differences were clearer when pelagic species were excluded. A similar pattern was found for numbers of *S. punctata*. The disturbance associated with eelgrass removal (habitat P) on its own had no marked effect on fish numbers.

If the eelgrass canopy itself is the characteristic of eelgrass habitat important in attracting an increased abundance of small fish compared with adjacent unvegetated areas, then fish numbers should have declined in the treatment from which eelgrass was removed. In this experiment fish numbers over habitat R were a little lower than in habitat P, but did not match the much lower number found in habitat U. Moreover, when considering only non-pelagic species, for which benthic habitat was expected to be especially important, numbers over habitat R were not lower than in habitats C and P. It must be concluded that over the length of this experiment, removal of eelgrass canopy did not cause fish to distribute themselves in a way consistent with the predictions of a model in which the eelgrass canopy alone is of major importance to small fish.

Two other possible explanations for the failure of fish numbers to fulfil expectations need examining. Firstly, the duration of the experiment was short relative to the seasonal settlement patterns of fish, and longer term manipulations of habitat, provided that they deal adequately with seagrass regrowth, may allow time for changes in physical factors such as sediment grain size affected by the presence of seagrass. As a test of the importance of seagrass canopy per se, however, the duration of this experiment was satisfactory, because fish were forced away from the area on every low tide, and could be expected to redistribute themselves semi-diurnally. Secondly, since patches of habitat U did not receive the disturbance inflicted on patches of R during eelgrass removal, the greater abundance of fish in habitat R compared with that in habitat U could be the result of the difference in degree of disturbance. Another treatment in which unvegetated patches received the disturbance of simulated eelgrass removal could have been used. The same disturbance in eelgrass patches did not alter fish numbers, generating some confidence that disturbance was not important when comparing habitat R with habitat U; that possibility has not, however, been altogether removed.

Epifaunal abundance and production were lowest in habitat U, intermediate in habitats P and R, and highest in habitat C. If fish are directly attracted to seagrass areas by the higher levels of epifaunal production, rather than selecting seagrass habitat per se and as a consequence gaining access to the greater abundance of prey, then fish abundance in the treatments of this experiment should match epifaunal production. Although no correlation between fish abundance and epifaunal production was demonstrated by patch, mean fish abundances by habitat did match epifaunal production when pelagic fish species were included. When pelagic species were excluded, fish abundances by habitat matched epifaunal production less closely, but still more closely than the match with seagrass cover.

The evidence from this experiment does not support a model in which small fish select seagrass habitat because of the presence of seagrass canopy. The evidence better supports, but does not alone demonstrate, the importance of food in the role of eelgrass as habitat for increased numbers of fish compared with unvegetated habitat.

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