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Spatial and temporal variability in the effects of fish predation on macrofauna in relation to habitat complexity and cage effects

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ABSTRACT: The effects of predation by fishes, in relation to habitat complexity and periodicity of sampling, on abundances of fishes and macroinvertebrates were investigated using controlled caging experiments during summer 1999/2000 at multiple locations (Blairgowrie, Grand Scenic, and Kilgour) in Port Phillip Bay, Australia. A second experiment evaluated biological and physical cage effects. Sites and habitats, but not caging treatments, could generally be differentiated by the assemblage structure of fishes. Regardless of species, small fishes were generally more abundant in seagrass than unvegetated sand, although the nature of this pattern was site- and time-specific. Depending on the site, abundances of fishes varied between cage treatments in ways that were consistent with neither cage nor predation effects (Grand Scenic), strong cage effects (Kilgour) or strong predation or cage effects (Blairgowrie). The abundance of syngnathids varied inconsistently between caging treatments and habitats within sites through time. Although they were generally more abundant in seagrass, whether or not predation or cage effects were observed depended strongly on the time of sampling. Atherinids and clupeids generally occurred more commonly over seagrass. In this habitat, atherinids varied between cage treatments in a manner consistent with strong cage effects, while clupeids varied amongst predator treatments in a way that could be explained either by cage or predation effects. Macroinvertebrates were closely associated with seagrass, palaemonid shrimps varied little with cage structure, and abundance of cephalopods appeared to be influenced by predation. Neither environmental (particle size and organic content) nor biological (abundances of meiofaunal crustaceans) attributes appeared to be altered by cage structure, but the statistical power of these experiments was sometimes low. Patterns in the abundances of fishes and macroinvertebrates are discussed in relation to predation and cage effects, habitat type, and the time of and location within which experiments were conducted.

KEY WORDS: Predation · Exclusion cages · Cage artefacts · Cephalopods · Crustaceans · Fish · Meiofauna · Seagrass · Unvegetated sand · Australia · Temperate

INTRODUCTION

Seagrass beds generally have more diverse and abundant faunas than adjacent, unvegetated areas (Bell & Pollard 1989, Orth 1992), and they are particularly important as nursery sites for juvenile fishes and crustaceans (Connolly et al. 1999). While the reasons for these patterns are debatable, they are generally thought to reflect habitat complexity and refuge from predation (Orth et al. 1984), increased food supplies (Connolly 1994), larval supply (Bell et al. 1987, Jenkins et al. 1997) and stable substrates (Orth 1992).

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The importance of vegetation characteristics in modifying predation patterns has received considerable attention (Orth et al. 1984). Survival is positively related to the density, biomass and species of vegetation (Stoner 1982, Gotceitas et al. 1997), and structural complexity may hinder foraging of predators (Heck & Thoman 1981) because visual cues can be obstructed by complex relief (Mattila 1992, Lindholm et al. 1999). While the most unequivocal results have been demonstrated in laboratory or mesocosm studies, results from field-based research are generally more complex. For example, Levin et al. (1997) showed that predation influenced the size distribution of fishes but could not explain preferential recruitment to seagrass. Bell & Westoby (1986a) found that both crustacean and fish prey decreased when seagrass was removed, regardless of whether predators were present or not, and while they suggested that predation might be the agent driving habitat preference, it was not the direct cause of low prey abundance amongst sparse cover. Additionally, Sala (1997) concluded that untested complex interactions were responsible for contradictory results in algae from which predatory fishes had been excluded. Clearly, more research is needed to evaluate the importance of predatory fishes in relation to the provision of structure in seagrass beds.

Dietary information and direct measures of abundance of predatory fishes in relation to their prey are useful in determining the importance of predation in structuring assemblages of marine fishes (Choat 1982, Connell & Kingsford 1997). As a result, there is much correlative and circumstantial evidence which implies that predatory fishes influence assemblages of marine animals (see review by Hixon 1991). However, while observational studies can address broad questions, they are more open to alternative interpretations. The strongest inferences regarding the impact of predatory fishes will be made from controlled manipulative experiments that alter abundance of predatory fishes using artificial structures (Sih et al. 1985, Hall et al. 1990). In vegetated marine habitats, the abundance of predatory fishes and decapods are most commonly manipulated using exclusion cages (Levin et al. 1997, Sala 1997). However, even though cage controls, which mimic the physical effects of cages without the exclusion effect, can help to isolate cage effects from treatment effects (Sih et al. 1985), there may still be problems interpreting the results from caging experiments because of cage artefacts (Virnstein 1978, 1980). Subsequently, direct tests of cage effects are necessary to make the results from caging studies more easily interpretable (Steele 1996). Direct measurements of changes in sediment composition, such as particle size and organic content, provide some estimate of how the cages alter the local environment (Kennelly 1991). However, it is hard to say how biologically meaningful changes to these attributes may be, and it may be useful to measure biological attributes directly. For example, cage structure can facilitate increases in meiofauna (Kennelly 1991), which may subsequently influence fish abundances (Connolly 1994) in ways that mimic predation effects (Steele 1996). Therefore, combining measures of variability in meiofaunal abundances and sediment characteristics with cage structure potentially affords researchers a better understanding of how cage artefacts influence the biological and physical parameters that potentially complicate the interpretation of predation effects.

Our study measured whether the abundance of fishes and macroinvertebrates varied between habitats of widely different structural complexity, seagrass and unvegetated sand, and through time, in relation to cage and predation effects. We also assessed whether cage structure per se influenced the assemblage structure of meiofauna and physical aspects of the environment.

MATERIALS AND METHODS

Study sites. The predator exclusion experiment and the experiment to assess cage artefacts were carried out in Port Phillip Bay between November 1999 and January 2000. The exclusion experiment was conducted at 3 sites; Blairgowrie, Grand Scenic, and Kilgour (Fig. 1). The cage artefact experiment was conducted at Blairgowrie. All 3 sites contain mosaics of the

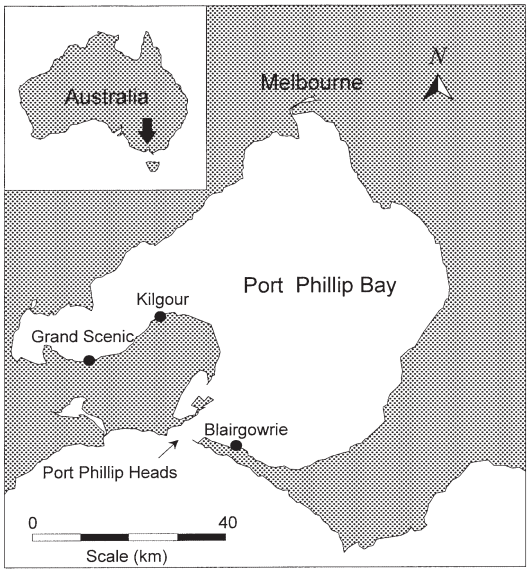

Fig. 1. Location of study sites within Port Phillip Bay. Inset: location of Port Phillip Bay within Australia (arrow)

seagrass *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog interspersed with variable-sized patches of unvegetated sand and some algae. The beds of *H. tasmanica* become progressively more extensive moving from the more exposed site at Blairgowrie (where the substrate is a well-sorted 'gravelly' sand and the currents close to shore may reach 0.5 m s^{-1}) to the sheltered location at Grand Scenic (where sediments contain higher amounts of clay and silt and currents are generally less than 10 cm s^{-1}) (Anonymous 1973, Black et al. 1993). The northerly orientation of all 3 locations affords them protection from the prevailing southwesterly winds. Tides throughout Port Phillip Bay are semidiurnal, and their range is less than 1 m. Jenkins & Wheatley (1998) have shown that relatively high, but inter-annually variable numbers of fishes, particularly King George whiting (Sillaginidae: *Sillaginodes punctata* Cuvier), settle at all sites during spring and summer. Sites also contain varying abundance of predatory fishes, particularly juvenile (length <20 cm) Western Australian salmon (Arripidae: *Arripis truttacea* Cuvier), which consume a variety of small fishes in shallow water close to seagrass beds (Hindell et al. 2000a).

Predator exclusion experiment. Each exclusion and cage control treatment was constructed from 4 steel stakes, 1 of which was hammered into the substrate at each corner of a 4 × 4 m plot. A 16 m length of black polypropylene mesh netting (15 mm knot-to-knot) was attached around these stakes, giving each exclusion cage a height of 1.5 m, which prevented submersion and subsequent fish entrance during spring high tides. The bottom of each cage wall was weighted with a 3 m length of 20 mm diameter steel rod. This weight ensured that the base of the walls of each cage settled into the substrate to a depth of up to 5 cm, and thereby prevented the free movement of larger animals between caged and uncaged areas. The exclusion cages used in our study were designed primarily to exclude predatory fishes which, in Port Phillip Bay, commonly include *Arripis truttacea*, rock flathead (Platycephalidae: *Platycephalus laevigatus* Cuvier), yank flathead (Platycephalidae: *P. speculator* Klunzinger) and longnose weedfish (Clinidae: *Heteroclinus tristis* Klunzinger). Piscivorous birds, such as the black-faced cormorant *Phalacrocorax fuscescens* and the Australasian gannet *Morus serrator*, also occurred in the vicinity of our study locations. Our exclusion cages and cage controls were left open on top to minimise potential changes to bird foraging, and despite the potential for the structure of our cages to provide perches, *P. fuscescens* were rarely observed close to cages during our study; not placing mesh on top of the cages also reduced the likelihood of shading effects. Our sites also contained various species of portunid and leucosiid crabs (Portunidae: common shore crab *Carcinus maenas* Linnaeus, red swimmer crab *Nectocarcinus intergrifrons*; Leucosiidae: pebble crab *Ebalia intermedia* Miers). The small size of the mesh prevented these crabs moving freely between caged areas, and although they could easily burrow under walls, their abundances did not appear to increase inside caged areas (J. S. Hindell pers. obs.). Therefore, the design of our cages appeared to be useful in manipulating abundance of fishes, which, at least in our system, are likely to be the most abundant suite of predators on other small fishes. Partial cages (cage controls) were built from exactly the same materials as exclusion cages, but only half of the wall of each side was filled along the top and bottom on each side of the cage alternatively. Cage controls assessed whether artificial structure per se influenced abundance of animals given 'natural' levels of predation. Uncaged areas were simply unmanipulated 4 × 4 plots of habitat. Replicate caging treatments were arranged in haphazardly chosen patches of seagrass and unvegetated sand. Four replicates of each habitat × cage treatment were constructed at each site. A more detailed description of the caging design is given in Hindell et al. (2000b).

Each habitat × cage treatment was sampled using a large dip net, 4 m wide × 1 m high with 0.5 mm mesh, which was operated by 2 people. The net was placed inside and at one end of the experimental plot and hauled through the water to the opposite end, where it was lifted from the water to trap macrofauna (fishes and invertebrates). Captured macrofauna were anaesthetised prior to preservation in ethanol. The same experimental plots (i.e. each habitat × cage treatment) within each site were sampled repeatedly for 4 consecutive weeks. The net used to sample macrofauna did not appear to detrimentally alter the habitat in experimental plots by breaking or ripping-out aspects of the benthos such as seagrass fronds (Hindell pers. obs.). All cage treatments within a site were sampled on the same day in a randomly chosen order, and all sites were sampled within the same week. In the laboratory, fishes and macroinvertebrates (cephalopods and crustaceans) were counted and the fishes were identified to family and, where possible, to species.

Assessment of cage artefacts related to changes in assemblage structure of meiofauna. To ensure that differences in the abundance of small fishes between cage treatments were not due to cage artefacts that alter sediment characteristics or meiofaunal distributions, we conducted an experiment to evaluate whether abundance of meiofauna (animals such as harpacticoid copepods, amphipods, polychaetes, nematodes and other crustaceans which were retained on a sieve with 180 µm mesh) and particle size and organic content of the sediment varied between cage treat-

ments. We were most interested in these animals because they are commonly consumed by small fishes, and variability in their abundances potentially contributes to the small-scale variability in the abundance of small fishes (Connolly 1994, Jenkins et al. 1996). The design of the cages was identical to those used in the exclusion experiment. This experiment was carried out at Blairgowrie on unvegetated sand, which had a coarser sediment than the seagrass (Jenkins & Hamer in press) and therefore was more likely to show a response of increases in fine particle composition due to baffling by cage walls.

Meiofauna were collected with a 9.5 cm diameter Perspex corer, pushed into the substrate to a depth of 5 mm, 1 wk before and 1 wk after building cages. To prevent the sediment falling out when the core was lifted, a metal plate was placed under the corer to enclose the sample until it could be washed into a sample jar. Ethanol mixed with Rose Bengal was then added to the sample to preserve and stain animals. Sediment samples were collected using a 20 mm diameter corer. Sediment samples were placed in plastic bags and stored in a cooler. For the measurement of each component (i.e. of meiofauna, organic composition and particle size distribution) 5 separate subsamples of sediment were collected, before and after the caging treatments were built, from non-overlapping, randomly selected positions within a cage treatment. Subsamples were subsequently pooled for particle size and organic composition but not for meiofauna.

In the laboratory, meiofauna were counted. The organic content of sediment samples was measured by calculating the loss of weight, after drying, of the organic material burnt off the sample in a muffle furnace for 4.5 h at 550°C. Particle size distribution was estimated by washing the sediment sample through a series of progressively finer sieves (355, 250, 180, 125 and 63 µm) and measuring the dry weight of each size component. Sediments did not contain any particles finer than 63 µm.

Univariate analyses. All data were assessed for homogeneity of variance and normality, using box plots and plots of residuals. Data that failed to meet these assumptions were transformed and reassessed.

Variability in abundance of fishes and macroinvertebrates was analysed using repeated measures analysis of variance (ANOVA). Site, habitat type and cage treatment were treated as fixed factors. Site was treated as a fixed rather than random factor because our choice of site was based on previous sampling of small fishes at these sites over a number of years (Jenkins et al. 1996, 1998, Hindell et al. 2000a). Sampling time was the repeated factor. The Greenhouse-Geisser (G-G) epsilon value (ε) was used to assess the degree to which sphericity influenced our analyses (Winer et al. 1991). However, where the adjusted p-value did not alter the significance of the unadjusted p-value, the unadjusted p-value was used. Tukey's tests and *a priori* planned comparisons were used to test for differences between levels of the site and cage treatments respectively. To control for the experimentwise Type I error rate, the number of planned comparisons of cage treatments was kept below the degrees of freedom for the main caging effect. In the first test, uncaged areas were compared to partially caged areas. If there was no significant difference (i.e. no cage effect), exclusion cages were then compared to the average of cage controls and uncaged areas. If there was a significant difference between uncaged areas and cage controls (i. e. cage effect), exclusion cages were compared to cage controls. Where interactions were found between main effects, separate single factor ANOVAs were conducted for 1 main effect in order to determine where the levels of the interacting main effects varied.

Variability in the abundance of categories of meiofauna was analysed using partially nested, repeated-measures ANOVA. Time of sampling was the repeated factor, cage treatment was treated as a fixed factor, and location (the plot to which a cage treatment was applied) was treated as a random factor. Comparisons of cage treatments were carried out as described for the exclusion experiment. Variability in the percentage composition of organic matter and each of the particle size classes was analysed using 2-factor repeated-measures ANOVA, where cage and time were treated as fixed factors. Where there was a non-significant effect of cage treatment for meiofauna and sediment characters, the power ($1 - \beta$) of the statistical test was measured using G*Power (Buchner et al. 1997: How to use G*Power. Available at: www.psycho.uni-duesseldorf.de/aap/projects/gpower/howtousegpower.html). All other statistical analyses were carried out using SYSTAT statistical software (Wilkinson et al. 1992).

Multivariate analyses. The relationships between sites, habitats and cage treatments (for the fish assemblage), and between cage treatments and times (for meiofauna), based on their frequencies of taxa, were examined using non-metric multidimensional scaling (nMDS). Similarity matrices on abundance of species of fishes or categories of meiofauna were constructed using the Bray-Curtis similarity coefficient. Data were $\sqrt[4]{}$-transformed to reduce the influence of numerically dominant species. Two-dimensional ordinations were produced (Clarke 1993). Stress values less than 0.20 allowed interpretable nMDS patterns (see Clarke 1993, Anderson & Underwood 1994). Analysis of similarities (ANOSIM) was used to test whether habitats (pooled across cage treatments) and cage treatments

(pooled across habitats) varied statistically ($p < 0.05$) in their assemblages of meiofauna (Clarke 1993). ANOSIM was also used to determine whether the assemblage structure of meiofauna in each of the cage treatments varied statistically between the 2 sampling times (pre- and post-caging). Where the number of *a priori* tests exceeded the degrees of freedom (df) for the effect being tested, the significance level (α) was adjusted using the Dunn-Sidak procedure: $(1-(1-\alpha)^{1/c})$, where c = number of comparisons. All multivariate analyses were carried out using PRIMER Version 4.0 (Carr & Clarke 1994).

Table 1. Abundances of fishes sampled in each regime of site (Blairgowrie, Grand Scenic and Kilgour), habitat (seagrass and unvegetated sand) and cage treatment (C: exclusion cage; CC: cage control; UC: uncaged; –: not present). Data pooled across sampling times

Taxa	Blairgowrie						Grand Scenic						Kilgour					
	Seagrass			Unveg. sand			Seagrass			Unveg. sand			Unveg. sand			Seagrass		
	C	CC	UC	C	CC	UC	C	CC	UC	C	CC	UC	C	CC	UC	C	CC	UC
Apogonidae																		
Siphaemia cephalotes	–	–	–	–	–	–	–	–	–	–	–	–	18	2	1	–	–	–
Atherinidae																		
Leptatherina presbyteroides	484	196	–	32	1	–	14	17	24	1	2	7	–	–	1	–	–	–
Kestratherina esox	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Clinidae																		
Heteroclinus eckloniae	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Heteroclinus heptaeolus	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	1	1	–
Heteroclinus perspicilatus	–	–	–	–	–	–	3	10	1	1	1	–	–	1	1	4	1	–
Cristiceps australis	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clupeidae																		
Spratelloides robustus	921	13	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gobiesocidae																		
Parvicrepis sp.1	5	2	4	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gobiidae																		
Favonigobius lateralis	1	1	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gobiidae larvae	3	2	2	17	6	1	–	–	–	–	–	–	–	–	–	8	1	1
Monacanthidae																		
Acanthaluteres spilomelanurus	24	10	9	5	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Meuschenia freycineti	–	–	–	–	1	–	1	3	2	–	–	–	–	1	6	–	1	–
Scobinichthys granularis	3	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mugilidae																		
Aldrichetta forsteri	–	–	–	–	–	–	3	–	–	6	–	–	21	–	–	–	–	–
Odacidae																		
Neoodax balteatus	–	–	–	–	–	–	–	–	–	–	–	–	2	1	3	2	–	–
Pleuronectidae																		
Ammotretis rostratus	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Rhombosolea tapirina	8	9	–	1	–	1	–	1	2	9	9	6	–	–	–	1	1	3
Scorpaenidae																		
Gymnapistes marmoratus	3	–	3	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Sillaginidae																		
Sillaginodes punctata	145	112	138	66	3	2	18	8	12	3	1	1	7	17	17	83	9	1
Syngnathidae																		
Hippocampus breviceps	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–
Hypselognathus rostratus	1	–	–	–	–	–	–	–	–	–	–	1	4	–	2	1	1	1
Lissocampus runa	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	3	–	–
Lissocampus caudalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Mitotichthys semistriatus	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stigmatopora nigra	118	126	122	7	8	1	–	–	–	5	1	2	45	66	30	81	29	13
Stigmatopora argus	5	11	5	3	–	–	516	274	386	230	182	219	248	107	87	142	69	25
Stipecampus cristatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Urocampus carinirostris	–	–	–	–	–	–	3	6	5	–	3	1	–	–	–	–	–	–
Vanacampus phillipi	–	–	1	–	–	–	32	13	42	3	6	1	10	9	10	9	1	1
Tetradontidae																		
Contusus rishei	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Triglidae																		
Lepidotrigla papilio	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–

RESULTS

Exclusion experiment

A wide variety of fishes, representing 15 families and at least 31 species, were recorded in our exclusion experiment (Table 1), including benthic (Scorpaenidae, Syngnathidae) epibenthic (Odacidae, Monacanthidae) and pelagic forms (Clupeidae, Atherinidae). Syngnathidae was the most abundant family of fishes caught, and represented 55.7% of all fishes (Table 1). Clupeidae (15.6%) and Atherinidae (13%) were also highly abundant, but because they were mainly collected at Blairgowrie, analyses for these fishes have been restricted to this location. Interestingly, fishes normally closely associated with seagrass, such as Monacanthidae and Syngnathidae, were commonly caught over unvegetated sand in association with caging structures. No predatory fishes were observed or caught in exclusion cages at any stage during our study.

Table 2. Multivariate analysis of similarity comparing the assemblages of fishes between sites (BG: Blairgowrie; GS: Grand Scenic; KG: Kilgour), between habitats (seagrass versus unvegetated sand) within each site, and between cage treatments (C: exclusion cage; CC: cage control; UC: uncaged) within each site × habitat regime. R: sample statistic/global R; p: significance level; ns: not significant after adjusting α using Dunn-Sidak procedure ($p < 0.017$); (in all tables values in **bold** are statistically significant at $p = 0.05$)

Source	R	p
Site (stress = 0.18)	0.593	**<0.001**
BG vs GS	0.836	**<0.001**
BG vs KG	0.558	**<0.001**
GS vs KG	0.426	**<0.001**
Within BG (stress = 0.11)	0.705	**<0.001**
Seagrass		
Cage	0.303	**0.046**
C vs CC	0.010	0.371
C vs UC	0.542	0.057
CC vs UC	0.365	0.114
Unvegetated sand		
Cage	0.271	**0.011**
C vs CC	0.375	0.057
C vs UC	0.469	**0.029**^{ns}
CC vs UC	<0.000	0.514
Within KG (stress = 0.13)	0.469	**<0.001**
Seagrass		
Cage	0.100	0.223
C vs CC	0.146	0.257
C vs UC	0.302	0.086
CC vs UC	−0.125	0.771
Unvegetated sand		
Cage	0.137	0.080
C vs CC	0.177	0.143
C vs UC	0.302	0.057
CC vs UC	−0.042	0.629
Within GS (stress = 0.15)	0.538	**<0.001**
Seagrass		
Cage	0.359	**0.040**
C vs CC	0.052	0.429
C vs UC	0.521	0.057
CC vs UC	0.563	**0.029**^{ns}
Unvegetated sand		
Cage	0.368	**0.020**
C vs CC	−0.302	0.971
C vs UC	0.708	**0.029**^{ns}
CC vs UC	0.615	0.057

Predator exclusion experiment

Assemblage structure

The nMDS ordination and pairwise comparisons using ANOSIM for fishes at the 3 sites, averaged across sampling times, showed that each site had significantly distinct assemblages of small fishes (Table 2, Fig. 2a). In each of the site-specific habitat comparisons, assemblages of small fishes associated with unvegetated sand habitats were significantly different from those in seagrass (Table 2, Fig. 2b,d. The assemblage structure of small fishes did not vary between cage treatments in either seagrass or unvegetated sand at any of the sites after adjusting the p-values to reduce the experimentwise Type I error rate (Table 2). The location of a site and the habitat within a site appear to be more important determinants of the assemblage structure of small fishes than predation.

Total fishes

Abundance of fishes, regardless of species, varied inconsistently between habitats for each site through time (Table 3, Fig. 3). At the first sampling time, fishes were much more abundant in seagrass than unvegetated sand at Blairgowrie ($df_{1,162}$, MS = 3.104, $p < 0.001$) and Grand Scenic ($df_{1,162}$, MS = 1.740, $p < 0.001$), but only marginally greater in unvegetated sand than seagrass at Kilgour ($df_{1,162}$, MS = 0.493, $p = 0.017$). At the second sampling time, fishes were more abundant in seagrass than unvegetated sand at Kilgour ($df_{1,162}$, MS = 1.247, $p < 0.001$) and Blairgowrie ($df_{1,162}$, MS = 8.293, $p < 0.001$), but not at Grand Scenic ($df_{1,162}$, MS = 0.011, $p = 0.722$). During the final 2 sampling times, fishes were more abundant in seagrass than unvegetated sand at Blairgowrie (Time 3: $df_{1,162}$, MS = 6.543, $p < 0.001$, Time 4: $df_{1,162}$, MS = 5.579, $p < 0.001$) and Grand Scenic (Time 3: $df_{1,162}$, MS = 1.638, $p < 0.001$, Time 4: $df_{1,162}$, MS = 1.078, $p < 0.001$) but not at Kilgour (Time 3: $df_{1,162}$, MS = 0.161, $p = 0.169$, Time 4: $df_{1,162}$, MS = 0.160, $p = 0.169$). Abundance of fishes also varied differently between cage treatments depending on the

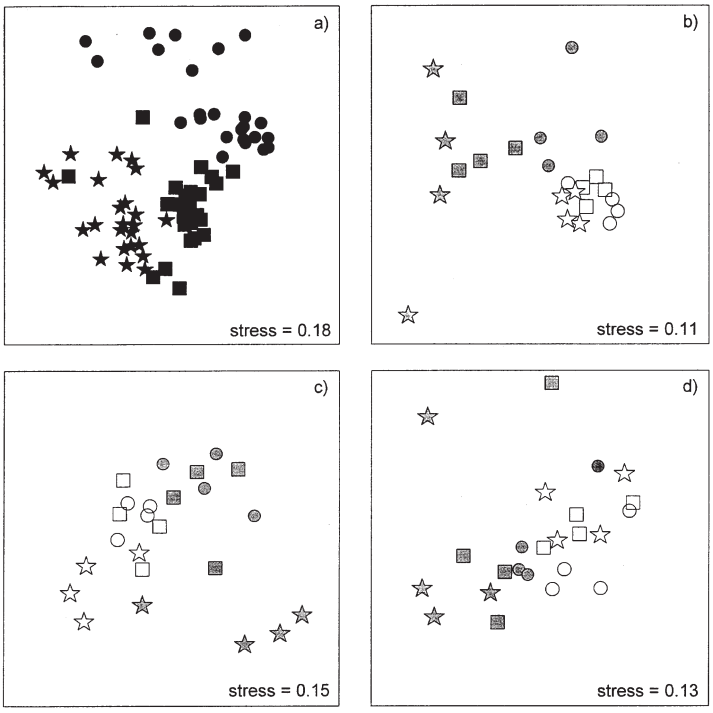

Fig. 2. Two-dimensional MDS ordination of assemblages of fishes at (a) Blairgowrie (●), Grand Scenic (■), and Kilgour (☆), and similar plots of fishes associated with exclusion cages (○), cage controls (⋆), and uncaged areas (□) in seagrass (open symbols), and with exclusion cages (●), cage controls (★) and uncaged areas (■) in unvegetated sand (filled symbols) at (b) Blairgowrie, (c) Grand Scenic, and (d) Kilgour

site (Table 3, Fig. 3). At Blairgowrie, abundance of fishes did not vary significantly between cage controls and uncaged areas ($df_{1,54}$, MS = 0.063, p = 0.246), but were much higher in exclusion cages than the average in cage controls and uncaged areas ($df_{1,54}$, MS = 1.832, p < 0.001). At Kilgour, fishes varied significantly between cage treatments ($df_{2,54}$, MS = 0.825, p < 0.001), more fishes were associated with cage controls than uncaged areas ($df_{1,54}$, MS = 0.307, p = 0.013), and fishes were more abundant in exclusion cages than in cage controls ($df_{1,54}$, MS = 0.528, p = 0.001). At Grand Scenic, the abundance of fishes did not vary with cage treatment ($df_{2,54}$, MS = 0.094, p = 0.138).

Syngnathids

This family was composed of 10 species, the most abundant of which was the spotted pipefish *Stigmatopora argus* Richardson (75.2%), and the widebody pipefish *S. nigra*, Kaup (19.6%) (Table 1). Variability in the abundance of syngnathids between cage treatments depended more on the time of sampling and the site. During the first sampling time, the abundance of syngnathids varied significantly between cages ($df_{2,162}$, MS = 2.128, p = 0.017); cage controls contained similar numbers of fishes to uncaged areas ($df_{1,162}$, MS = 0.019, p = 0.753), and exclusion cages contained significantly more fishes than the average recorded in cage controls and uncaged areas ($df_{1,162}$, MS = 4.236, p < 0.001) (Fig. 4). Also, during this sampling period, there were significantly more syngnathids associated with seagrass than unvegetated sand for all 3 sites; Blairgowrie ($df_{1,162}$, MS = 12.265, p < 0.001), Grand Scenic ($df_{1,162}$, MS = 9.914, p < 0.001) and

Table 3. Three-factor repeated-measures analysis of variance comparing the numbers of total fishes, syngnathids, *Macrobrachium* sp. and *Idiosepius notoides* at each site (Blairgowrie, Grand Scenic and Kilgour) within each cage treatment (exclusion cage, cage control and uncaged) in each of seagrass and unvegetated sand habitats through time (n = 288). Data were log(x + 1) transformed prior to statistical analysis. Total fishes, Syngnathidae, *Macrobrachium* sp. and *I. notoides* Greenhouse-Geisser epsilon values were 0.9616, 0.8777, 0.8898 and 0.8965 respectively. The table shows, for each category of animals, the probabilities (p) associated with each of the terms in the model (Source) and the residual MS

Source	df	Total fishes	Syngnathidae	*Macrobrachium* sp.	*Idiosepius notoides*
Between subjects					
Site (S)	2	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Habitat (H)	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Cage (C)	2	**<0.001**	**<0.001**	0.086	**0.002**
S × H	2	**<0.001**	**0.003**	**<0.001**	**<0.001**
S × C	4	**0.001**	**0.002**	0.060	0.131
H × C	2	0.242	0.799	**<0.001**	0.388
S × H × C	4	0.203	0.344	**<0.001**	0.444
Residual MS	54	0.184	0.983	0.356	0.162
Within Subjects					
Time (T)	3	**<0.001**	**<0.001**	**<0.001**	0.497
T × S	6	**0.001**	**0.001**	**0.002**	0.660
T × H	3	0.911	0.348	**<0.001**	0.095
T × C	6	0.087	**0.035**	0.890	0.713
T × S × H	6	**<0.001**	**0.013**	**0.013**	0.132
T × S × C	12	0.370	0.652	0.301	0.124
T × H × C	6	0.916	0.927	0.957	0.765
T × S × H × C	12	0.266	0.858	0.174	0.066
Residual MS	162	0.084	0.507	0.037	0.023

Kilgour ($df_{1,162}$, MS = 3.241, p = 0.012). During the second sampling time, cage treatment again had a significant influence on the abundance of syngnathids ($df_{2,162}$, MS = 4.101, p < 0.000); syngnathids were significantly more abundant in cage controls than in uncaged areas ($df_{1,162}$, MS = 1.275, p = 0.012), and exclusion cages contained more fishes than cage controls ($df_{1,162}$, MS = 2.940, p < 0.001). Syngnathids were also more abundant in seagrass than unvegetated sand at Blairgowrie ($df_{1,162}$, MS = 12.562, p < 0.001) and Kilgour ($df_{1,162}$, MS = 6.473, p < 0.001), but did not vary between habitats at Grand Scenic ($df_{1,162}$, MS = 0.035, p = 0.793). During the third sampling time, abundance of syngnathids did not vary between cage treatments ($df_{2,162}$, MS = 0.378, p = 0.149), and they were more abundant in seagrass habitats during the third sampling time at Blairgowrie ($df_{1,162}$, MS = 19.135, p < 0.001) and Grand Scenic ($df_{1,162}$, MS = 11.167, p < 0.001) but not at Kilgour ($df_{1,162}$, MS = 1.215, p = 0.124). during the final sampling time, the abundance of syngnathids varied strongly between cages ($df_{1,162}$, MS = 5.878, p < 0.001); like the second sampling time, cage controls contained more fishes than uncaged areas ($df_{1,162}$, MS = 3.014, p < 0.001), and exclusion cages

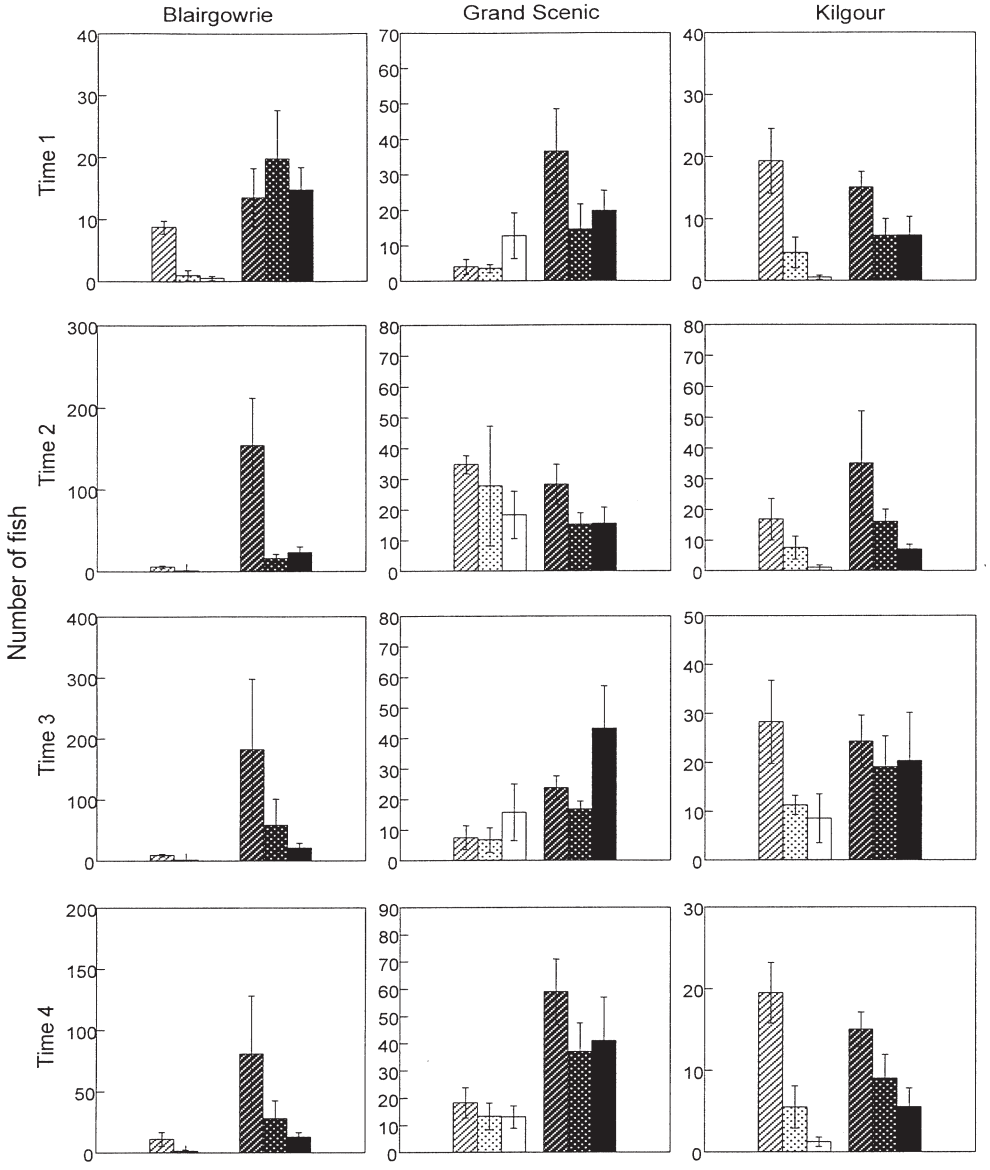

Fig. 3. Mean (±SE) numbers of fishes (regardless of species) associated with exclusion cages, cage controls and uncaged areas in seagrass (= last 3 bars, from left to right respectively) and with exclusion cages, cage controls and uncaged areas in unvegetated sand (= first 3 bars, from left to right respectively) at each site on each sampling occasion (once a week over 4 consecutive weeks)

contained more fishes than cage controls ($df_{1,162}$, MS = 11.756, $p < 0.001$). As at the third sampling time, abundance of syngnathids varied significantly between habitats at Blairgowrie ($df_{1,162}$, MS = 20.281, $p < 0.001$) and Grand Scenic ($df_{1,162}$, MS = 4.683, $p = 0.003$), but not at Kilgour ($df_{1,162}$, MS = 1.091, $p = 0.144$).

Atherinids

The atherinids were comprised almost exclusively of silverfish *Leptatherina presbyteroides* Richardson (Table 1). Atherinids varied significantly between both habitats and cage treatments (Table 4, Fig. 5). Abundances did not vary significantly between cage controls and uncaged areas ($df_{1,18,}$ MS = 0.226, $p = 0.222$), but were significantly higher inside exclusion cages than the average recorded inside cage controls and uncaged areas ($df_{1,18,}$ MS = 0.795, $p = 0.029$). Atherinids were also more abundant over seagrass than unvegetated sand (Table 4, Fig. 5).

Clupeids

Only a single species of Clupeidae, the blue sprat *Spratelloides robustus* Ogilby, was captured during this study (Table 1). Like the atherinids, this species occurred almost exclusively at Blairgowrie, where it as only sampled during the final 3 sampling times; therefore, analyses are restricted to this location and these times. Variability in abundance of clupeids between cages depended on the type of habitat (Table 4, Fig. 5). In unvegetated sand habitats, clupeids only occurred

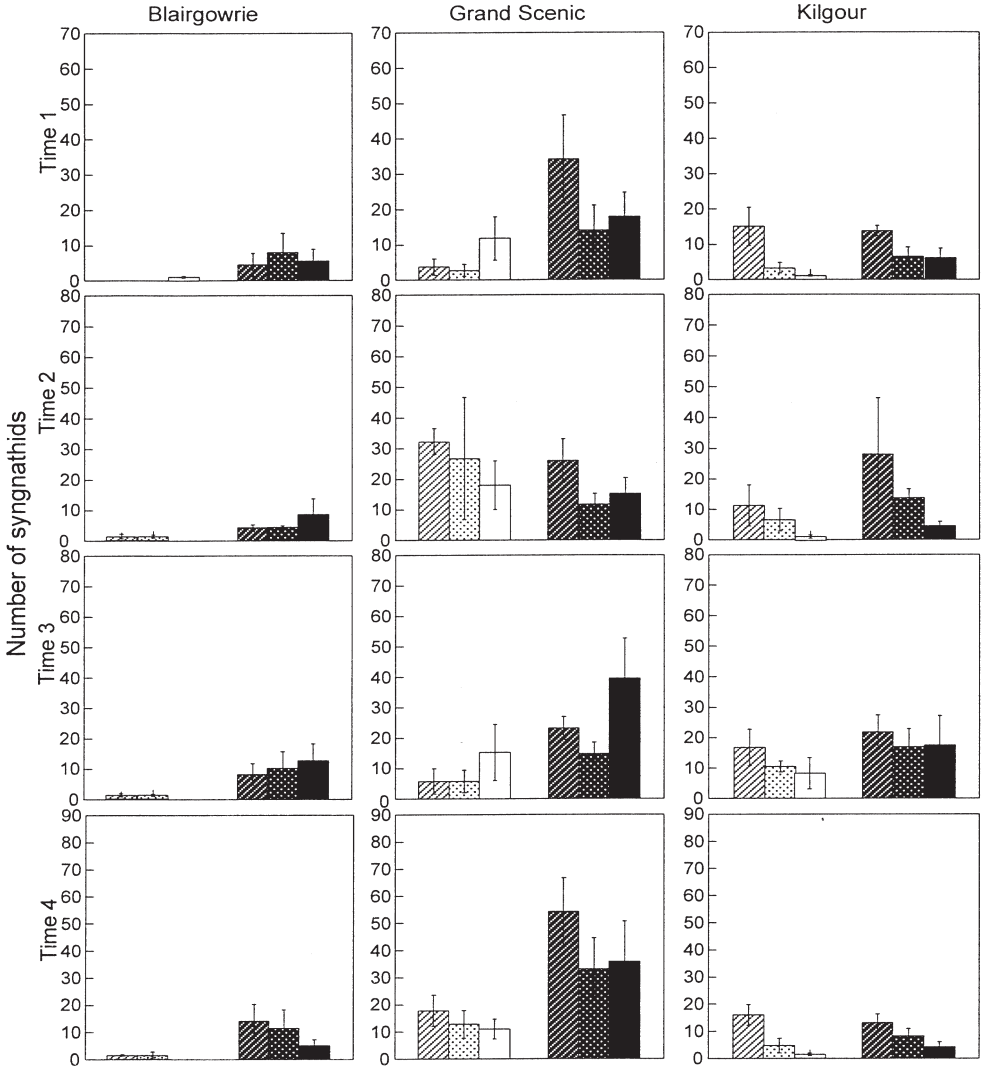

Fig. 4. Syngnathids. Mean (±SE) numbers. Further details as in Fig. 3

Table 4. Two-factor repeated-measures analysis of variance (ANOVA) comparing the abundances of fishes associated with different habitats (seagrass and unvegetated sand) and cage treatments (exclusion cage, cage control and uncaged) over 4 consecutive sampling periods at Blairgowrie (n = 24). Data were $\log_{10}(x+1)$-transformed prior to statistical analysis. G-G ε: Greenhouse-Geisser epsilon; H-F ε: Huynh-Feldt epsilon. *df: 2, 2, 4, 4 and 36 for time, time × habitat, time × cage, time × habitat × cage, error Within Subjects respectively

Source	df	Atherinidae MS	Atherinidae p	Clupeidae MS	Clupeidae p
Between subjects					
Habitat (H)	1	2.923	**0.035**	2.608	**0.018**
Cage (C)	2	2.041	**0.048**	2.161	**0.013**
H × C	2	0.790	0.271	1.707	**0.028**
Error	18	0.563		0.388	
Within subjects					
Time (T)	3*	0.595	**0.005**	0.242	0.197
T × H	3*	0.260	0.113	0.182	0.291
T × C	6*	0.259	0.071	0.316	0.086
T × H × C	6*	0.175	0.228	0.294	0.106
Error	54*	0.125		0.142	
G-G ε		0.8351		0.9652	
H-F ε		1.0000		1.0000	

Table 5. Multivariate analysis of similarity comparing the assemblage structure of meiofauna between cage treatments (C: exclusion cage; CC: cage control; UC: uncaged) over unvegetated sand at Blairgowrie. Sampling times were pooled across cage treatments. R: sample statistic/global R; p: significance level; ns: not significant after adjusting α using Dunn-Sidak procedure (p = 0.017). Stress = 0.07

Source	R	p
Sampling times (pooled)	0.302	**<0.008**
Within sampling times		
Pre-cage construction (Cpre)		
Cage	0.023	0.349
C vs CC	−0.052	0.686
C vs UC	−0.063	0.629
CC vs UC	0.115	0.200
Post-cage construction (Cpre)		
Cage	0.102	0.196
C vs CC	0.146	0.200
C vs UC	−0.010	0.371
CC vs UC	0.240	0.114
Between sampling times		
Cpre vs Cpost	−0.052	0.486
CCpre vs CCpost	0.125	0.229
UCpre vs UCpost	0.583	**0.029**^{ns}

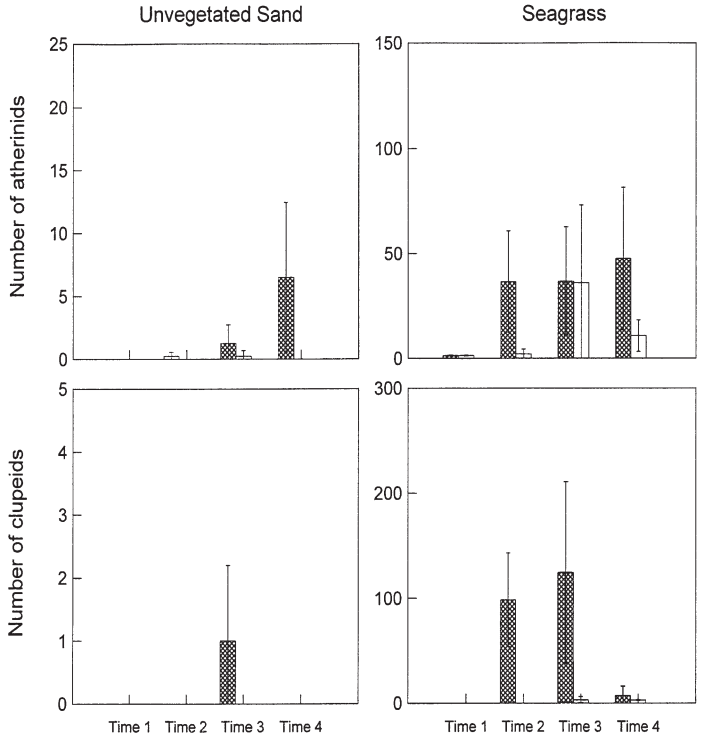

Fig. 5. Atherinids and clupeids. Mean (±SE) numbers associated with exclusion cages (▩), cage controls (□) in seagrass and unvegetated sand at each sampling time. Analysis was restricted to Blairgowrie

once, in association with exclusion cages (Fig. 5). Conversely, the numbers of clupeids varied strongly between cage treatments in seagrass habitats ($df_{2,18}$, MS = 0.723, p = 0.001). In seagrass, abundance of clupeids did not vary significantly between uncaged areas and those enclosed by cage controls ($df_{1,18}$, MS = 0.026, p = 0.559), but exclusion cages contained higher numbers of clupeids than the average recorded in uncaged areas and cage controls ($df_{1,18}$, MS = 1.420, p < 0.001).

Macroinvertebrates

The 2 most abundant macroinvertebrates sampled in our study were an idiosepiid (the southern pygmy squid *Idiosepius notoides*, Berry) and a palaemonid shrimp (*Macrobrachium* sp.). Both of these commonly occur in shallow and sheltered seagrass beds along the southern Australian coast (Edgar 1997).

Abundance of *Macrobrachium* sp. varied inconsistently between sites and habitats through time (Table 3, Fig. 6). Overall, its abundance at Grand Scenic was very low. At the other 2 sites, *Macrobrachium* sp. was associated almost exclusively with seagrass, and was significantly more abundant in this habitat at all times for both sites (Blairgowrie—Time 1: $df_{1,162}$, MS = 7.455, p < 0.001; Time 2: $df_{1,162}$, MS = 10.365, p < 0.001; Time 3:

$df_{1,162}$, MS = 16.886, p < 0.001; Time 4: $df_{1,162}$, MS = 8.365, p < 0.001. Kilgour—Time 1: $df_{1,162}$, MS = 7.455, p < 0.001; Time 2: $df_{1,162}$, MS = 10.365, p < 0.001; Time 3: $df_{1,162}$, MS = 16.886, p < 0.001; Time 4: $df_{1,162}$, MS = 8.356, p < 0.001). Abundance of *Macrobrachium* sp. did not vary significantly between caging treatments (Table 3, Fig. 6).

Abundance of *Idiosepius notoides* varied differently between habitats at different locations, and varied significantly between cage treatments (Table 3, Fig. 7). Regardless of site or habitat type, abundance of *I. notoides* did not vary between cage controls and uncaged areas ($df_{1,54}$, MS = 0.008, p = 0.329). However, there were significantly more *I. notoides* associated with exclusion cages compared with the average recorded in cage controls and uncaged areas ($df_{1,54}$, MS = 0.099, p = 0.001). Additionally, *I. notoides* were significantly more abundant in seagrass than unvegetated sand at Blairgowrie ($df_{1,54}$, MS = 1.534, p < 0.001) and Kilgour ($df_{1,54}$, MS = 0.205, p < 0.001) but not at Grand Scenic ($df_{1,54}$, MS < 0.001, p = 0.864), where numbers were generally very low regardless of habitat type.

Biological cage artefacts

Assemblage structure

The assemblage structure of meiofauna varied significantly between the 2 sampling times, i.e. pre-

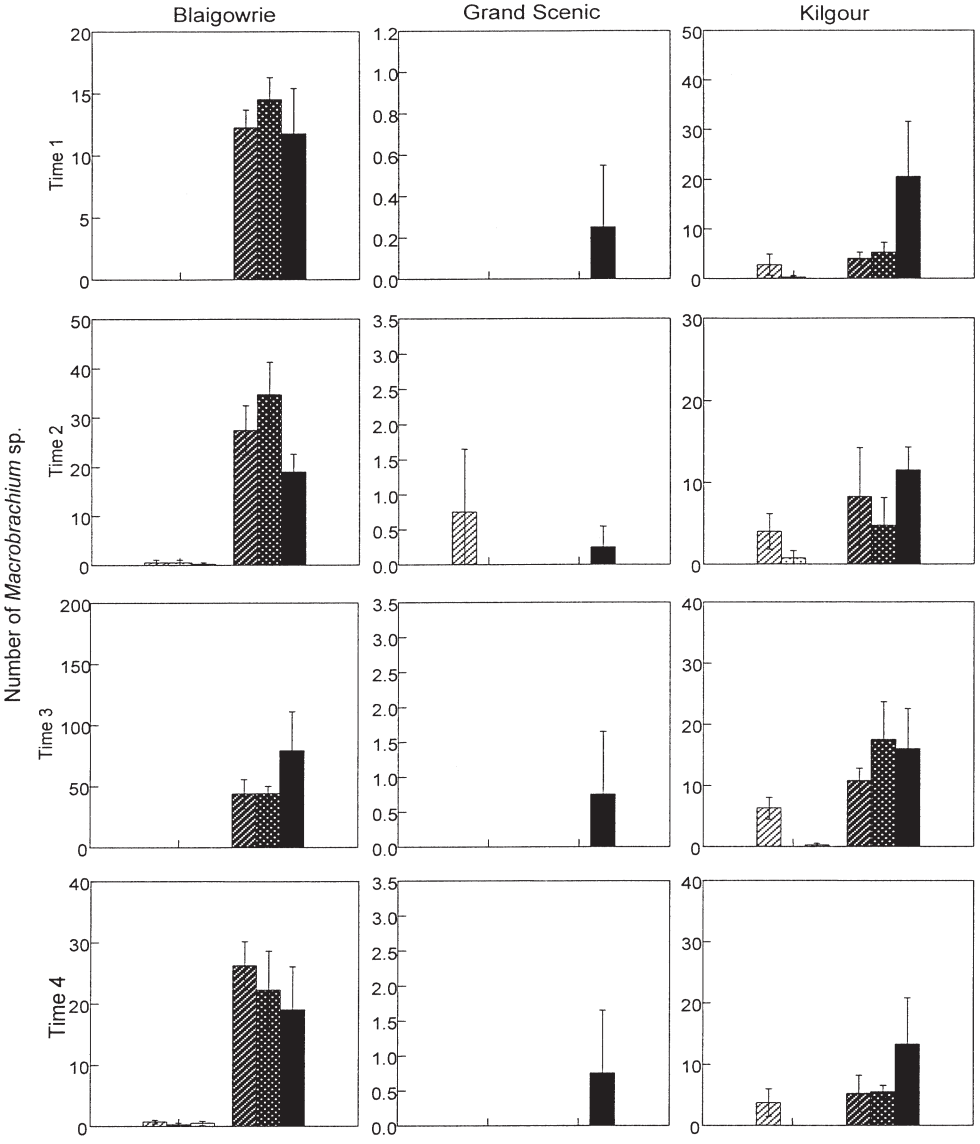

Fig. 6. *Macrobrachium* sp. Mean (±SE) numbers. Further details as in Fig. 3

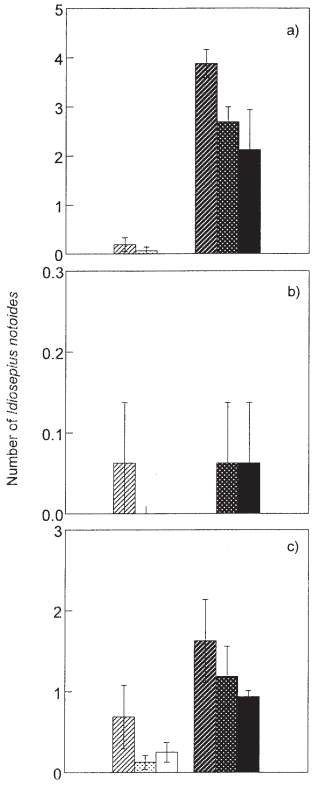

Fig. 7. *Idiosepius notoides*. Mean (±SE) numbers pooled across sampling times. Further details as in Fig. 3

and post-treatments (Table 5, Fig. 8), but did not appear to vary with cage structure; neither before nor after building cages could the experimental plots be differentiated by their assemblages of meiofauna (Table 5, Fig. 8). Similarly, plots to which exclusion or cage controls were applied could not be differentiated from those prior to adding structure (Table 5). Interestingly, the assemblage structure of meiofauna in unmanipulated areas varied significantly between sampling times.

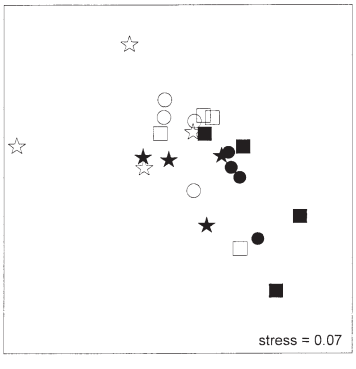

Fig. 8. Two-dimensional 2-factor MDS ordination describing assemblages of meiofauna associated with plots of unvegetated sand at Blairgowrie before and after the construction of cages, (□) pre-exclusion cage; (☆) pre-cage control; (○) pre-uncaged; (■) post exclusion cage; (★) post-cage control; (●) post-uncaged

Individual groups

Five groups of meiofauna, nematodes (Fig. 9a), polychaetes (Fig. 9b), 'other' crustaceans (including tanaids, mysids, ostracods and cumaceans) (Fig. 9c), harpacticoid copepods (Fig. 9d) and amphipods (Fig. 9e) were analysed separately because of their relative abundance in our study samples. While some of the groups varied significantly between sampling times and between locations within which a particular cage treatment was applied, their abundances did not vary between cages treatments (Table 6). There was a trend for the numbers of animals in all taxonomic categories to increase between the first and second sampling times. Most important however, from the point of view of identifying effects related to the provision of artificial structure, their abundances did not vary inconsistently between cage treatments through time (there was no interaction between time and cage) (Table 6, Fig. 9). However, the power for these statistical analyses was sometimes low. For the 'other' crustaceans, there was only a 7% chance of detecting a significant difference ($p = 0.05$) if the numbers of animals doubled in the cage treatments (exclusion and cage controls) compared to the uncaged area; the change in abundance of other crustaceans in exclusion cages and cage controls was actually 75 and 61% fewer respectively compared with uncaged areas. For the polychaetes, there was an 81% chance of detecting a significant difference ($p = 0.05$) if their numbers doubled in the cage treatments (exclusion and cage controls) compared to the uncaged area; the change in the numbers of polychaetes in exclusion cages and cage controls was actually 0.8 and 66% fewer compared with uncaged areas. For the nematodes, there was a 21% chance of detecting a significant difference ($p = 0.05$) if the numbers of animals doubled in the cage treatments (exclusion and cage controls) compared to the uncaged area; the change in numbers of nematodes in exclusion cages and cage controls was actually 21 and 73% greater respectively than for uncaged areas. For harpacticoids, there was a 20% chance of detecting a significant difference if the numbers doubled in the cage treatments (exclusion and cage controls) compared to the uncaged area; the change in the numbers of harpacticoids was actually 84% less in exclusion cages and 9% greater in cage controls compared to uncaged areas. For amphipods, there was an 18% chance of detecting a significant difference if the num-

Table 6. One-factor repeated measure ANOVA comparing the abundance of each taxonomic category of meiofauna, organic composition (%Org) and mass of each particle size class (>355 to 63 µm) of sediment between cage treatments in unvegetated sand habitats at Blairgowrie. N: nematodes; P: polychaetes; H: harpacticoid copepods; A: amphipods; O: other crustaceans. The table shows, for each of the 5 categories of meiofauna,%Org and each of the 5 particle size classes, the probabilities (p) associated with each of the terms in the model (Source) and the residual MS

Source	df	N	P	H	A	O	%Org	Particle size class (µm) 63>125	125>180	180>250	250>355	>355
Between												
Cage (C)	2	0.331	0.073	0.554	0.872	0.617	**0.043**	0.286	0.161	0.644	0.916	0.382
Residual MS	9	0.134	0.255	1.280	0.368	0.363	0.004	<0.001	0.002	0.007	0.006	0.017
Within												
Time (T)	1	**0.003**	**<0.001**	**0.048**	0.051	0.330	0.600	0.281	0.647	0.155	0.957	0.252
T × C	2	0.478	0.495	0.537	0.7486	0.716	0.110	0.196	0.991	0.159	0.316	0.150
Residual MS	9	0.057	0.056	0.087	0.107	0.078	0.004	<0.001	<0.000	0.001	0.001	0.002

bers doubled in the cage treatments (exclusion and cage controls) compared to the uncaged area; the change in the numbers of amphipods was actually 40% greater in exclusion cages and 76% lower in cage controls compared with uncaged areas.

None of the 5 sediment size classes varied significantly between cage treatments or inconsistently between cages through time (Table 6, Fig. 10a). For the 2 smallest size classes of sediment (63 to 125 and 126 to 180 µm), there was a 5 and 7% chance respectively of detecting a 100% change in the amount of sediment in exclusion and cage controls compared with uncaged areas; the proportions of the 63 to 125 µm sediment class in exclusion cages, cage controls and uncaged areas changed by +0.02, −0.17 and −0.007% respectively. The 126 to 180 µm sediment size class in exclusion cages, cage controls and uncaged areas changed by +0.3, +0.5 and +0.2% respectively. For the 181 to 250 µm size class of sediment, there was a 7% chance of detecting a 100% change in the amount of sediment in cages (exclusion and cage controls) compared with uncaged areas; this size class in exclusion cages, cage controls and uncaged areas changed by +4.3, +1.7 and −1.2% respectively. For the 2 largest size classes of sediments (251 to 355 and >355 µm), there were 5 and 6% chances, respectively, of detecting a 100% change in the amount of sediment in cages (exclusion and cage controls) compared with uncaged areas; the proportion of sediments between 251 and 355 µm in exclusion cages, cage controls and uncaged areas changed by +2.1, −1.8 and −0.1% respectively. The proportion of sediments >355 µm in exclusion cages, cage controls and uncaged areas changed by −6.7, −0.2 and +1.1 respectively.

The amount of organic matter varied significantly between cage treatments (Table 6, Fig. 10b); however, it did not vary inconsistently between plots through time (no cage × time interaction) (Table 6, Fig. 10b). For the organic composition of sediments, there was a 15% chance of detecting 100% changes in the percent composition of sediment in cages (exclusion and cage controls) compared with uncaged areas; the proportion of organic material inside exclusion cages, cage controls and uncaged areas actually changed by +0.03, +0.05 and −0.05 respectively.

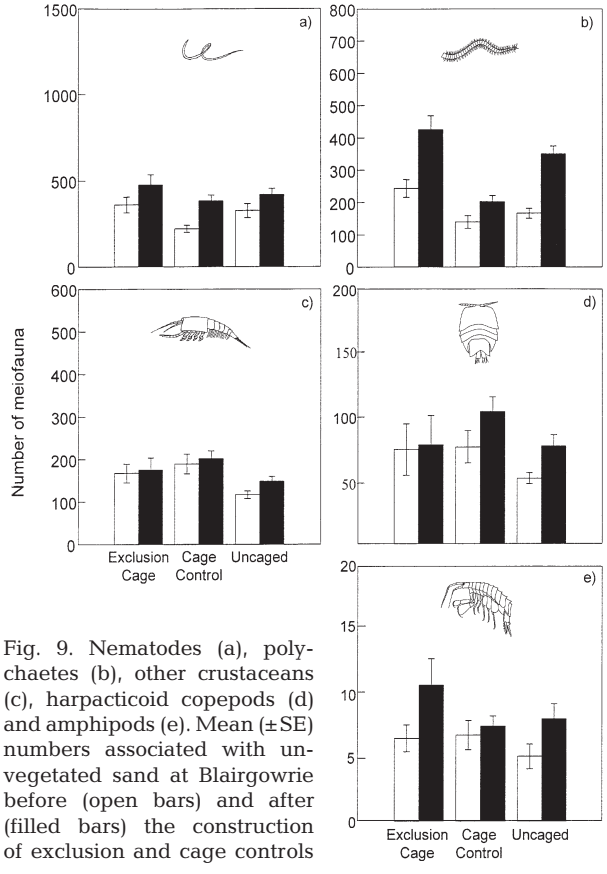

Fig. 9. Nematodes (a), polychaetes (b), other crustaceans (c), harpacticoid copepods (d) and amphipods (e). Mean (±SE) numbers associated with unvegetated sand at Blairgowrie before (open bars) and after (filled bars) the construction of exclusion and cage controls

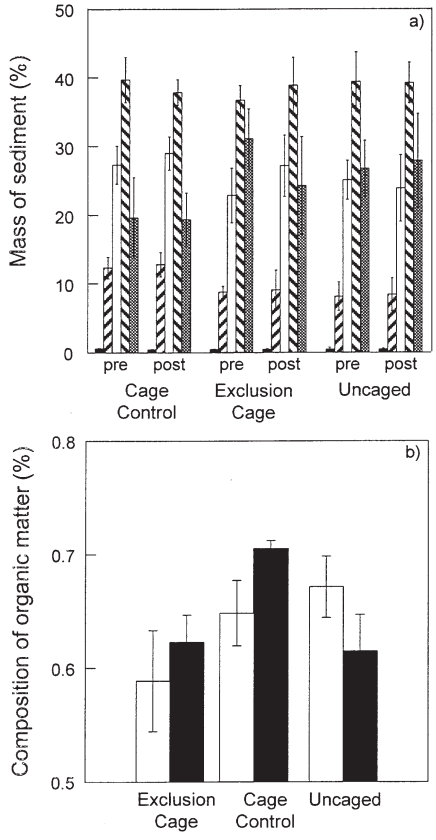

Fig. 10. (a) Mean (±SE) mass of the 63–125, 126–180, 181–250, 251–355 and >355 µm size fractions (bars from left to right) before (pre) and after (post) building cages; (b) mean (±SE) % organic composition of samples of sediment before (open bars) and after (filled bars) building cages in unvegetated sand at Blairgowrie

DISCUSSION

The importance of predation by fishes in structuring assemblages of marine macrofauna in structurally diverse habitats has received considerable attention. However, with the exception of Bell & Westoby (1986a), few studies have measured the impact of predatory fishes on the assemblage structure of fishes and invertebrates in the same experiment, nor addressed the small-scale (several days) temporal dynamics of impacts, be they predator- or cage-induced. Furthermore, little research has directly assessed the importance of cage artefacts in relation to modifying biological or physical attributes inside experimental plots, despite the importance of this information in interpreting results (Virnstein 1978). Our study focused on measuring the impact of predation by fishes in relation to cage artefacts on the variability in abundance of fishes and macroinvertebrates within and between structurally different habitats at different locations through time.

Effects of predation on fishes

Although the higher numbers of fishes in seagrass beds than in unvegetated habitats could be caused by a variety of processes, including habitat complexity (Bell et al. 1985, James & Heck 1994), increased food supply (Connolly 1994, 1997) and hydrodynamic effects on larval supply (Jenkins et al. 1997, 1998), much research has focused on determining the importance of seagrasses as a refuge from predation (Summerson & Peterson 1984, Minello 1993, Jordan et al. 1996). In our study, even though seagrass habitats generally contained more fishes than unvegetated sand, the ways in which the abundance of fishes varied amongst cage treatments depended on the site, regardless of habitat, in which experiments were conducted. For example, at Grand Scenic, total abundance of fishes did not vary between cage treatments, implying that predation was not important. However, at Blairgowrie, fishes were much more abundant inside exclusion cages than either cage controls or uncaged areas, and this implied a strong predation effect. A measurable predation effect at Blairgowrie but not at Grand Scenic agrees well with the much higher abundance of a predatory fish, the Western Australian salmon (Arripidae: *Arripis truttacea* Cuvier), observed at Blairgowrie compared to Grand Scenic (data not shown), and implies that predation effects may be related to local abundance of predatory fishes. Interestingly, at Blairgowrie, regardless of time, the numbers of fishes inside exclusion cages over unvegetated sand were similar to those in uncaged areas over seagrass, and over unvegetated sand; abundance of fishes in cage controls was similar to those over uncaged plots (i.e. very low), so cage effects did not complicate this result. Despite most research showing higher numbers of fishes in seagrass than over unvegetated sand (Orth et al. 1984, Bell & Pollard 1989), caging experiments to assess predation in these habitats show that abundance of small fishes was not influenced by predation (Bell & Westoby 1986a, Bell et al. 1987), and impacts of predation were similar in structurally variable habitats (Levin et al. 1997): habitat preference and/or availability of food may contribute more to the higher abundance of fishes in seagrass compared with unvegetated sand (Bell & Westoby 1986a, Levin et al. 1997). Our conclusions are preliminary because of the limited spatial and temporal scales over which our study was conducted, but we contend that, at least in this location, predation by fishes influences the variability in abundance of fishes between seagrass and unvegetated sand, and seagrass appears to provide an important refuge from predation to small fishes. More research is now needed which assesses: (1) the generality of these results, and (2) the mechanisms, whether

they be interference of predation or avoidance of seagrass by predators, which shape these patterns.

Grand Scenic and Kilgour have similarly low numbers of predatory fishes, and it would be reasonable to expect a similarly low effect of predation; instead, abundance of fishes at Kilgour appear to be positively associated with cage structure per se, suggesting a strong cage effect. This pattern is primarily driven by the strong association of syngnathids with the amount of mesh in the cage walls, and is unique to Kilgour. The use of cages to measure predation effects is often complicated by the attraction of fishes to cage structures (Doherty & Sale 1985, Steele 1999); positive relationships between numbers of fishes and amount of shelter should not be construed as proof of the importance of predation in determining the abundance of fishes (Steele 1999). Similarly, exclusion caging studies in Port Phillip Bay have previously shown that syngnathids respond strongly to structure, although increases in structure above that presented in cage controls did not facilitate further increases in fishes (Hindell et al. 2000b). In the present study, it appeared that the demersal rather than pelagic fishes were responding to cage structure. Underwater video observations of pelagic fishes around cage structures showed that abundance of fishes were no greater on the edges of cage walls than in uncaged areas, evidence that artificial structure probably did not attract pelagic fishes such as clupeids and atherinids (Hindell et al. unpubl.). We suggest that the high relief offered by cage structure may be beneficial in enabling syngnathids to forage further into the water column. Alternatively, the coarser sand and lower level of organic material in the sediments at Kilgour compared with Grand Scenic (Jenkins & Hamer in press) suggest that Kilgour is more susceptible to environmental perturbation. Therefore, the higher numbers of fishes associated with cage controls at this site might reflect fishes seeking refuge from environmental disturbance. Further information is needed that evaluates why syngnathids respond to cage structure per se, particularly in relation to the mediation of environmental disturbance and the provision of enhanced foraging sites.

The overall lack of a significant interaction between habitats and caging treatments (or site × habitat × caging) implies that predation influences the assemblage structure of fishes similarly in both seagrass and unvegetated sand habitats, and, therefore, the higher numbers of fishes in seagrass than in unvegetated sand may not be solely due to the mediation of predation by structural aspects of the habitat. Levin et al. (1997) showed that the impact of predation on the recruitment of pinfish was similar between artificial seagrass and unvegetated sand, and thus differential predation did not facilitate the higher numbers of fish in seagrass than unvegetated sand. Bell & Westoby (1986a) reduced the amount of seagrass with and without predators, and found that fishes decreased in both predator treatments, implying habitat choice. We suggest that, regardless of species, variability in the total numbers of fishes between habitats is more likely to reflect habitat choice than predation, although predation influences abundance of fishes in both seagrass and unvegetated sand habitats.

Atherinids and clupeids rarely occurred in unvegetated habitats at Blairgowrie, generally only in areas from which predatory fishes had been excluded. Even though the abundance of these fishes varied somewhat through time and between replicate patches within a treatment, overall, both atherinids and clupeids appeared to associate with cage treatments in a manner that was consistent with either predation influencing their abundances or attraction to the artificial structure provided by cages. Stomach-contents analyses of predatory fishes, particularly *Arripis truttacea*, sampled at Blairgowrie at the same time as the caging experiment was being conducted, showed that clupeids and atherinids were common dietary items (Hindell et al. unpubl.). Together with the relative differences in abundance of these fishes between cage treatments, the dietary data suggests that predatory fishes influence abundance of these prey fishes by direct predation. Levin et al. (1997) showed that predatory fishes influenced abundance and differentially altered the size structure of fishes within structurally variable habitats, and the coral-reef based literature is replete with research that implicates direct predation as influencing assemblages of fishes (Connell 1996, Beets 1997, Connell & Kingsford 1998, Hixon 1998, Steele 1999). Conversely, studies of fish predation on assemblages of fishes in seagrass suggest that behaviour is more important than direct predation in shaping patterns in abundance between seagrass (mimics) and unvegetated sand (Bell & Westoby 1986a). While direct predation appears to contribute to the variability in abundance of some species of prey fishes, antipredator behaviour and the movement of prey fishes to areas that increase survival (Bell & Westoby 1986b) may also contribute to variability in abundance of fishes amongst areas that vary in predation pressure. Additionally, even though underwater video footage taken during our study did not show fishes congregating around cages (Hindell et al. unpubl.), the structure of cages per se may have influenced abundance of fishes via some, as yet unknown, attraction mechanism. Abundance of pelagic fishes are often positively associated with artificial structure, such as fish attraction devices (Kingsford 1993), and the interpretation of predation effects has previously been complicated by cage effects caused by the attraction of fishes to artifi-

cial structures (Doherty & Sale 1985). Therefore, the attraction of fishes to artificial structures cannot be totally discounted as a process contributing to the patterns in abundance of fishes between cage treatments. While the generality of our results for these species of fishes is largely restricted to a single site, Blairgowrie (because this was the only site where atherinids and clupeids were caught in sufficient numbers for formal analysis), we contend that predation is likely to be a significant contributor to variability in fish abundances. However, these results are preliminary and further research is required that investigates, in a pluralistic manner, the relative contribution of anti-predator mechanisms, habitat selection and cage effects (fish attraction) versus direct predation in determining patterns in the assemblage structure of fishes within seagrass and unvegetated sand habitats.

Syngnathids appeared to respond very little to variable predation pressure and varied more with cage structure per se. In fact, there was often an almost linear relationship between the amount of artificial structure and the number of syngnathids. This response to structure by syngnathids was somewhat expected, considering that they are rarely consumed by predatory fishes (Hindell et al. 2000a) and associate strongly with habitat complexity (Gomon et al. 1994, Jenkins & Sutherland 1997), which suggests that artificial structure may actually attract some fishes associated with seagrass. Reise (1985) and Steele (1999) have also shown that positive relationships between some reef fishes may not be caused by lower rates of predation in areas with abundant shelter, but instead may be driven by the attraction of fish to cage structures. Therefore, the utility of controlled exclusion experiments using cages in evaluating predation impacts for some species of fishes, in our case syngnathids, is limited. Our research warns that researchers must have a thorough understanding of the ecology of the study organism to ensure that the manipulative technique used is appropriate to the species and the hypothesis.

As a consequence of the growing emphasis on the importance of spatial (between sites, and between habitats within sites) and temporal (between tides, diel periods and seasons) variability in generating patterns in abundance of small fishes (Chesson 1998, Sale 1998) (in fact temporal variability can actually influence spatial patterns: Ives & Klopfer 1997), the effects of smaller scale temporal variability in determining the magnitude and pattern of experimental effects is gaining attention (Wiens et al. 1986). However, most studies of predation measure an assemblage at a single time and, in the process, record averaged effects even though, as our results for syngnathids show, the time of sampling is important in determining site and caging patterns. At Kilgour, at the first sampling time, regardless of habitat type, variability in the numbers of syngnathids between cage treatments was strongly suggestive of a predation effect—exclusion cages contained more fishes than either cage controls or uncaged areas, which contained similar numbers of fishes. At other times, numbers of syngnathids were linearly related to the levels of artificial structure, and even though exclusion cages contained more fishes than uncaged areas, the intermediate numbers of fishes counted in cage controls suggested strong cage effects. At Blairgowrie and Grand Scenic, the numbers of syngnathids appeared to be unrelated to cage structure at some times but closely associated with it at others. Therefore, the time at which sampling was conducted dictated not only the degree to which cage effects confounded the experimental test of a predation effect, but also the nature of the relationship between these species and structure per se. Whether our study genuinely represents small-scale (several days) temporal variability in habitat/predation/cage effects, or whether it simply indicates transitional stages in abundance of fishes following the initiation of the experiment, is unknown. Further research is required to separate these possibilities. However, given the variability between sampling times, we warn that future research should place more emphasis on determining the temporally dynamic nature of biological effects.

Research has traditionally focused on changes at the individual level rather than at that of the assemblage, probably because of the practical limitations in measuring numerous animals and the need to focus on species that show a positive effect (Sih et al. 1985, Browman 1999). However, if predation is a significant process in the organisation of individual species, then researchers might observe these effects manifested at the level of the community. For example, Connell & Anderson (1999) found that small predatory fishes influenced the assemblage structure of benthic invertebrates. To date, little research has evaluated the impact of fish predation on the assemblage structure of fishes; most attention has been focused at determining impacts on single species. In our study, locations and habitats could be differentiated according to their assemblages of small fishes, but the assemblage structure of small fishes appeared to vary little between caging treatments. Connell & Anderson (1999) highlighted the importance of the specificity in predator-prey relationships in determining predation effects—only small fishes impacted on assemblages of invertebrates. The dietary research by Edgar & Shaw (1995) and Hindell et al. (2000a) suggests that the lack of observed predation effect does not simply represent the manipulation of an inappropriately selected predatory fish, but rather, may reflect some form of 'assemblage inertia'. Connell & Anderson (1999) looked at

largely sedentary benthic animals that are less temporally dynamic in their abundance variability. In the same way that prey movement potentially complicates the interpretation of predation effects (Englund 1997) at the individual level, so too, the short-term variability in abundance of fishes potentially reduces the impact of predation at the level of the assemblage. Despite predatory fish in our study influencing the abundance of fishes overall, these changes do not necessarily facilitate a re-organisation of the community as a whole. We contend that while the location of a site, or the variability amongst habitats within a site, appear to be important determinants of the assemblage structure of small fishes in this region of Port Phillip Bay, biological processes such as predation may not be.

Effects of predation on macroinvertebrates

A significant amount of research has investigated the impact of predators on assemblages of invertebrates (Bell & Westoby 1986a, Martin-Smith 1993, Sala 1997). The general consensus is that predation is less important than habitat preference in determining patterns between habitats, although predation may have a significant influence on habitat preference (Bell et al. 1985, Bell & Westoby 1986a). At our study site, the carid shrimp *Macrobrachium* sp. is a conspicuous element of the seagrass associated fauna, and its numbers were around 2 orders of magnitude higher in seagrass than unvegetated sand. Because *Macrobrachium* sp. is consumed by a variety of predatory fishes, particularly platycephalids and clinids (Hindell et al. 2000a), it could be hypothesised that predation influences inter-habitat patterns. However, these crustaceans varied little between cage treatments, nor between or within habitats. Bell & Westoby (1986a) showed that while numbers of *M. intermedium* were unaffected by excluding predators, reducing the amount of seagrass impacted negatively, and correlations of abundance with shoot density within seagrass could be interpreted as due to habitat preference and not predation, although predation pressure may have selected for habitat preferences. Similarly, Martin-Smith (1993) found a positive correlation between abundance of epifauna and levels of epiphytes. Therefore, in our study, it is possible that higher numbers of *Macrobrachium* sp. in seagrass are a reflection of food availability. Conversely, Sala (1997) found that epiphytic algae showed no relationship with any invertebrate decapods, but that decapod crustaceans were influenced by the exclusion of predators only after 15 wk of manipulating abundance of predators; at this time their numbers were 4.9 times larger than those in control plots. Therefore, in our study, predation may influence abundance of *Macrobrachium* sp. but over greater time frames than those examined. We suggest that variability in abundance of *Macrobrachium* sp. in short-term experiments is unlikely to be influenced by predation, but is more likely to reflect habitat preferences. Further research is needed to evaluate the time scales over which predation effects are manifested for these invertebrates.

The southern pygmy squid *Idiosepius notoides* is a conspicuous element of seagrass habitats in temperate Australian waters (Edgar 1997), and it is readily consumed by predatory fishes (Hindell et al. 2000a). However, in spite of the large amount of research on other types of macro-epifauna, no study has evaluated whether predation can influence the assemblage structure of this macroinvertebrate. In our study, regardless of site, *I. notoides* was rarely sampled in unvegetated sand except in association with high levels of artificial structure, and was most commonly associated with seagrass, where its abundance varied between cage treatments in a manner that was consistent with a predation effect. However, while predation appears to influence the abundance of this cephalopod, it does not appear to be important in determining habitat preferences, as indicated by the lack of a significant cage × habitat interaction. Juvenile fishes are known to increase in abundance where there are high numbers of their prey (Connolly 1994, Levin 1994), and seagrass beds contain higher numbers of small fishes, the prey of cephalopods, than unvegetated sand. Therefore, higher numbers of cephalopods in seagrass may reflect the higher levels of potential prey. Regardless of the mechanisms generating patterns between habitats, this study indicates that predatory fishes influence the abundance of *I. notoides* in seagrass habitats.

Biological and physical cage artefacts

The provision of cage controls to assess the effects of cage structure per se is a necessary element of any exclusion caging experiment. However, even where cage controls are employed, the results can still be equivocal and difficult to interpret (Schmidt & Warner 1984, Kennelly 1991, Martin-Smith 1993) if cage structure baffles water movement or attenuates light and causes changes in sediment regimes or abundance of other animals (McGuinness 1997). Measuring biological and physical attributes of the environment potentially provides a subtle indication of changes in biological and physical characters that may mask predation effects. For example, fish abundances may be positively correlated with food (Levin 1994, Jenkins et al. 1996), and patterns of abundances between seagrass and unvegetated sand are thought to reflect the avail-

ability of their prey (Connolly 1994). If cages facilitate increases in the numbers of meiofauna prey, this could subsequently attract small fishes and thereby mimic a predation effect (more fishes in exclusion cages than uncaged areas). In our study, neither the assemblage structure nor abundance of individual categories of meiofauna varied significantly with the provision of variable amounts of cage structure. Similarly, neither the organic content nor particle size distribution of sediments varied as a function of artificial structure. This implies that cage structure probably did not influence the abundance of fishes. However, the statistical power to detect even 100% differences between areas with and without artificial structure was sometimes low for meiofauna and always low for sediment characteristics. Therefore, changes may actually have occurred as a result of building cages, but these could not be detected. Interestingly, we had 81% confidence in detecting no effect for polychaetes. Abundance of polychaetes vary strongly with sediment characteristics, including particle size and organic content (Hsieh 1995, Mendez & Green-Ruiz 1998), and they are commonly consumed by small fishes (Labropoulou & Papadopoulou-Smith 1999). Therefore, given the results for the polychaetes, we are more confident that the structure of the cages used in our study probably did not alter characteristics of the environment or abundance of animals in ways which confound the interpretation of caging results. However, our results pertaining to cage effects overall should be viewed cautiously because of the possibility of Type II errors, and future studies need to address these issues.

Conclusions

This study is unique in that it measured the impact of predatory fishes on both assemblage and individual level characters of fishes and macroinvertebrates simultaneously, and assessed biological and physical cage artefacts using similar experimental designs. At the assemblage level, the structure of small fishes depends strongly on site and habitat, with a negligible contribution by predation. Predatory fishes appear to contribute directly to the variability in numbers of fishes in seagrass and unvegetated sand habitats, but this result is highly species-specific. Syngnathids varied in no discernible way with regards to predation, but overall appeared to respond more to habitat and cage structure. Additionally, syngnathids showed that the temporal scale over which an experiment is evaluated, particularly in relation to periodicity of sampling, can influence the nature of differences between experimental treatments. Macroinvertebrates were most abundant in seagrass. While behaviour, not predation, may be the proximate cause for variability between habitats in abundance of *Macrobrachium* sp., predation appears to influence abundance of cephalopods, particularly in seagrass. Even though dietary analyses suggests that predation by fishes is a ubiquitous and important process in seagrass (Edgar & Shaw 1995, Hindell et al. 2000a), the strength and nature of its impact, even when assessed with rigorously designed experiments, is strongly influenced by the species of prey measured, as well as, the habitat within which and the temporal scale over which manipulative experiments are conducted. The structure of the exclusion and cage controls used in our study did not appear to influence biological or physical attributes of the environment. However, the power of these tests was generally very low and, therefore, variability in abundance of fishes between cage treatments in relation to biological artefacts should be interpreted cautiously.

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