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Variability in the numbers of post-settlement King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) in relation to predation, habitat complexity and artificial cage structure

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Abstract

The importance of predation by fish in altering abundances of juvenile King George whiting (*Sillaginodes punctata*) was examined at multiple locations in Port Phillip Bay, Australia, by manipulating the numbers of piscivorous fish in unvegetated sand and seagrass habitats using cages. Additional information regarding the local abundances of, and habitat use by, the most common piscivorous fish, Western Australian salmon (Arripidae: *Arripis truttacea*, Cuvier), was gathered using netting surveys and underwater video. Regardless of habitat, abundances of *S. punctata* were similar in partial cages and uncaged areas. In unvegetated sand, *S. punctata* were more abundant inside cages than partial cages or uncaged areas. In seagrass, there was no difference in the numbers of *S. punctata* between caging treatments. Patterns in abundances of *S. punctata* between cage treatments in each habitat were consistent between sites, but the relative difference in the abundances of *S. punctata* between habitats was site specific. Abundances of *A. truttacea* varied significantly between sites, and they consumed a variety of epibenthic fishes including atherinids, clupeids, gobiids, syngnathids and pleuronectids. At one site in Port Phillip Bay (Blairgowrie), *A. truttacea* occurred more commonly in patches of unvegetated sand than seagrass. Over unvegetated sand, abundances of *A. truttacea* varied little between partial cages and uncaged areas. The numbers of *S. punctata* varied between caging treatments and habitats in a manner that was consistent with a model whereby seagrass interferes with foraging by predatory fish and provides juvenile fish with a refuge from predation. The almost total absence of *A.*

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truttacea in seagrass habitats and the lack of *S. punctata* in their diets implies, however, that patterns in *S. punctata* in seagrass/unvegetated sand mosaics are driven by processes other than direct predation.

Keywords: *Arripis truttacea*; Cage experiment; Habitat complexity; Predation; Seagrass; *Sillaginodes punctata*; Temperate; Underwater video; Unvegetated sand

1. Introduction

Predation is thought to be a major determinant of the assemblage structure of fishes in marine ecosystems, and amongst the most common predators in marine systems are other fishes (Choat, 1982). The importance of predatory fishes has commonly been inferred from gut contents and the relative abundances of predatory fish in relation to their prey (Hall et al., 1995; Connell and Kingsford, 1997; Hansson, 1998). In the past decade, manipulative experiments have demonstrated that predatory fishes influence assemblages of fish by altering survival and recruitment (Steele, 1999), densities of adults (Tupper and Boutilier, 1997), sizes and growth of juveniles (Levin et al., 1997), and habitat selection (Gotceitas and Brown, 1993; Lindholm et al., 1999). Most research about predation on fish has been in coral reefs (see review by Hixon, 1991).

Structural complexity is thought to influence the potential for predatory fish to alter assemblages of fish. The shape and size of crevices and their location in relation to alternative habitats have received considerable attention (Sale, 1991; Friedlander and Parrish, 1998; Steele, 1999). Algae and seagrasses also provide structural complexity in many marine systems (Carr, 1994; Tupper and Boutilier, 1997; Gillanders and Kingsford, 1998). Amount (Heck and Thoman, 1981; Gotceitas et al., 1997) or type (Stoner, 1982) of plants can influence numbers of fish (Orth et al., 1984; Orth, 1992), efficiency of predators (Mattila, 1995) and choice of prey (Stoner, 1982). There has been little study of predatory fish in seagrass habitats, despite the often quoted importance of these vegetated areas as nurseries for juvenile fish (Connolly et al., 1999).

Seagrass beds generally have greater species diversity and larger numbers of fishes than adjacent unvegetated areas (Orth, 1992; Butler and Jernakoff, 1999). This is thought to reflect the provision of refuge from biological and environmental perturbations, greater levels of food and more stable substrata (Orth, 1992; Keough and Jenkins, 1995). Heck and Orth (1980) and Orth et al. (1984) suggested that the larger numbers of fish associated with seagrass may reflect reduced predation. Gotceitas et al. (1997) have shown that predation decreases (as the latency to capture increases) with increasing density of eelgrass. Bell et al. (1987, 1988), Bell and Pollard (1989) and Ferrell et al. (1993) presented an alternative model that processes influencing recruitment, particularly larval supply, are important in determining the initial, broad-scale variability in assemblages of fish amongst locations with seagrass. Following recruitment, variability in abundances of fish amongst alternative habitats is due to fish selecting particular regions within a seagrass bed which favours survival (Bell and Westoby, 1986a,b)—for example, areas that provide adequate levels of food or relief from environmental or biological perturbations.

Manipulative field experiments potentially provide the most rigorous and persuasive tests of hypotheses in predation studies (Raffaelli and Moller, 2000). Cages are commonly used to manipulate abundances of predatory fishes (Doherty and Sale, 1985; Hall et al., 1990; Steele, 1996; Connell, 1997; Levin et al., 1997). The artificial structure used to exclude predators, however, may mask or mimic predation effects by altering abundances of fish (Bell et al., 1985; Bohnsack et al., 1997; Carr and Hixon, 1997; Clarke and Aeby, 1998). Physical (e.g. particle size and organic composition of sediment) and biological (e.g. abundances of epifauna/meiofauna that are sources of food for small fish) attributes of the environment may also be altered by cage structure (Virnstein, 1978; Hall et al., 1990). Partial cages (cage controls), which allow predatory fishes to forage in areas enclosed by cage structure, are necessary to separate predation effects from effects caused by artificial structure (Virnstein, 1978; Steele, 1996; Connell, 1997). Research by ourselves (Hindell et al., in press), Schrijvers et al. (1998) and Mattila and Bonsdorff (1989) have shown that caging materials do not always alter meiofaunal abundances or sediment characteristics. Direct observations are needed, however, to determine whether caging materials attract fishes or differentially alter foraging by predatory fishes inside cage controls compared to uncaged areas (see Connell, 1997). Underwater video affords researchers an opportunity to quantify predatory fish whose temporal patchiness and transient nature often precludes the use of divers (Burrows et al., 1994; Hixon and Carr, 1997; Morrisey et al., 1998).

In Port Phillip Bay, recruitment of juvenile King George whiting, *Sillaginodes punctata*, to seagrass beds varies considerably between locations (Jenkins et al., 1997b, 1998; Jenkins and Wheatley, 1998). Larval supply and environmental disturbance (wave action) explain a significant amount of this broad-scale variability (Jenkins and Black, 1994; Jenkins et al., 1997a). Hindell et al. (2000) have shown that sites with high numbers of predatory fish, such as Western Australian salmon (*Arripis truttacea*), correspond to sites where the recruitment of juvenile *S. punctata* is low. This pattern implies that predatory fish may influence abundances of small fish in seagrass beds.

In this study, we assessed whether (a) numbers of juvenile *S. punctata* varied between areas with and without predatory fish, and (b) patterns in numbers of *S. punctata* across caging treatments were consistent between seagrass and unvegetated sand, and at different locations. To answer these questions, we manipulated the numbers of predatory fish using cages in patches of seagrass and unvegetated sand at several locations in Port Phillip Bay. We also measured the numbers of piscivorous *A. truttacea* in seagrass and unvegetated sand at different locations, and amongst caging treatments to assess how the potential for predation varied.

2. Materials and methods

2.1. Study sites

The caging experiments and predator surveys were carried out at three sites in Port Phillip Bay: Blairgowrie, Grand Scenic and Kilgour (Fig. 1). At each site, there are large contiguous beds of the seagrass *Heterozostera tasmanica* (Martens ex Ascherson) den

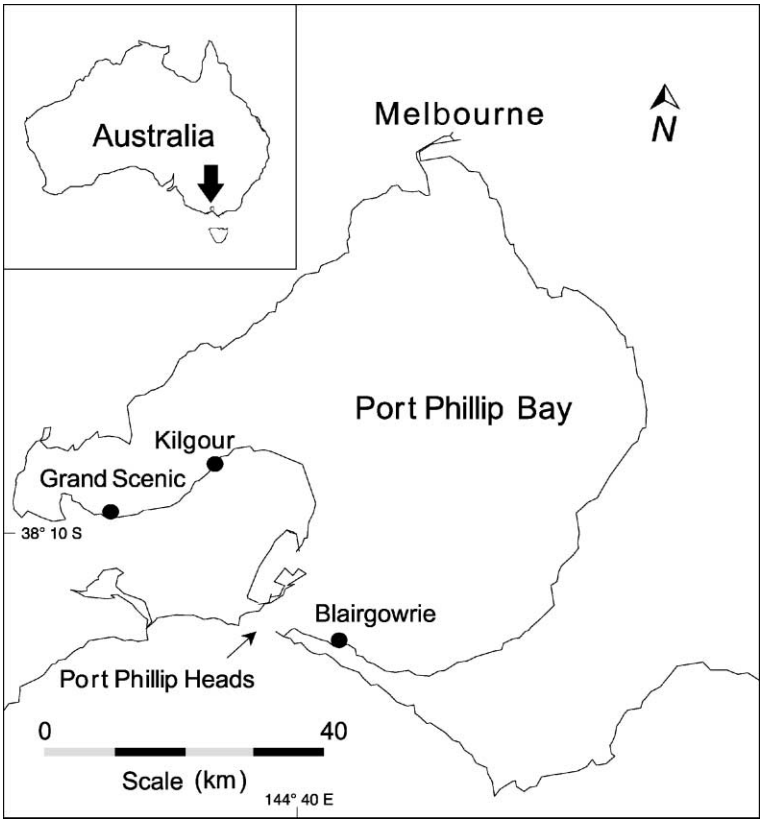

Fig. 1. Locations of study sites in Port Phillip Bay. Inset: Location of Port Phillip Bay within Australia.

Hartog, which are interspersed with patches of unvegetated sand and rocky reef in shallow (<3 m) water close to the shoreline. The currents around Grand Scenic and Kilgour are weak ($\approx$10 cm s^{-1}), but currents in the vicinity of Blairgowrie may reach 50 cm s^{-1}, depending on the local wind direction (Black et al., 1993). The substratum at each site strongly reflect these exposure regimes; fine silty clays at Grand Scenic and well-sorted 'gravely' sand at Blairgowrie (Anonymous, 1973). All three sites have a northerly orientation and are protected from the prevailing southwesterly winds. Tides throughout Port Phillip Bay are semidiurnal with a range of less than 1 m. Despite the variation in assemblage structure of fishes between sites, relatively high, but inter-annually variable, numbers of *S. punctata* settle to all sites during spring (Jenkins et al., 1997a; Jenkins and Wheatley, 1998).

2.2. Caging experiment

We used a caging experiment in seagrass and unvegetated sand to assess several predictions about how the effects of predation varied with habitat and cage structure. If

predatory fish reduce the numbers of fish prey, the numbers of prey should be larger inside cages (areas from which predators are excluded) than uncaged areas. If the artificial structure used to build cages does not facilitate the attraction of prey or change the foraging efficiency/movements of predators, then areas enclosed by partial cages (cage controls) should contain similar numbers of predators and prey to uncaged areas. If the structure of seagrass beds provides prey with a refuge from predation, there should be little difference between caging treatments in seagrass, but cages over unvegetated sand should contain more prey than partially caged or uncaged areas in this habitat. Finally, if the only role of seagrass is as a refuge for prey, the numbers of prey in seagrass, regardless of caging treatment, should be similar to the numbers of prey inside cages over unvegetated sand.

Predatory *A. truttacea* were excluded from 16 m^2 (4×4 m) patches of unvegetated sand and seagrass at each site using cages during spring, 1999. *A. truttacea* is a perennially abundant predatory fish in Port Phillip Bay and consumes juvenile fishes associated with seagrass (Robertson, 1982; Hindell et al., 2000). Other predatory fishes were also excluded but were relatively sparse-*A. truttacea* represent 87 % of all predatory fish likely to consume juvenile *S. punctata* at the sites studied (Hindell et al., 2000).

Each cage was constructed from steel stakes hammered into the substratum at each corner of a 4×4-m square plot. Around this, a 16-m-length black polypropylene net, 1.5 m high with a mesh size of 15 mm, was attached (Fig. 2a). The top of each cage (1.5 m high) was not enclosed with mesh because it was never underwater. To prevent predatory fish swimming into the cages, the bottom of each wall was weighted using a 3-m-length steel rod (10 mm diameter). Cage controls were built exactly the same as cages, but the top or bottom half was cut out of each wall (Fig. 2b). Uncaged areas were simply 16 m^2 plots marked with stakes at each corner.

At each site, four replicates of each cage treatment (exclusion cage, cage control and uncaged) were applied to haphazardly chosen plots of unvegetated sand and seagrass. All cages were constructed at all sites within 8 days and left for 1 week before sampling.

2.3. Sampling juvenile S. punctata

Juvenile *S. punctata* in the caging treatments at a site were sampled on the same day during low tide. The water was too deep to sample fish at high tide. The remaining sites were sampled on consecutive days in the same week. This sampling protocol was repeated weekly for four consecutive weeks to get an estimate of the average effects of predation.

S. punctata in caging treatments were sampled using a large net, 4 m wide $\times$ 1.5 m high $\times$ 1.5 m deep, with 0.5 mm black mesh. The net was attached to a rectangular frame (4×1.5 m) made from 20 mm PVC pipe. The net was placed inside, and at one end, of the 16-m^2 area, and hauled through to the opposite end by two people, where it was lifted from the water and returned to a boat so that the fish could be removed. Captured fish were anaesthetised in Benzocaine and preserved in ethanol. Pilot studies, in which each caging treatment was sampled 10 consecutive times, showed that >90 % of the *S. punctata* in a plot were caught on the first haul; therefore, only one haul was conducted

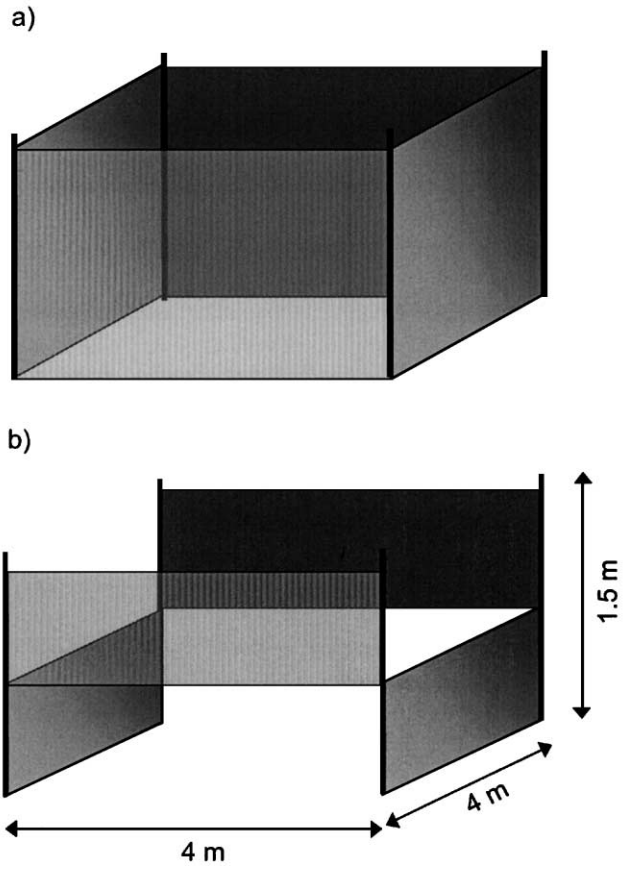

Fig. 2. Design of (a) cage used to exclude fish from areas of seagrass or unvegetated sand, and (b) partial cage used to assess artefacts associated with cages.

per plot on any given sampling occasion. Visual estimates of netting effectiveness showed that *S. punctata* rarely avoided capture by swimming outside the sampling area (J. Hindell, pers. obs.). In the laboratory, the standard length (SL—from the tip of the snout to the posterior end of the caudal peduncle) of fish was measured (mm) and fish were counted.

2.4. Sampling and dietary analysis of piscivorous fish

The numbers of *A. truttacea* were measured at each study site to assess whether predatory fish actually occurred in the vicinity of caging experiments. The dietary composition of *A. truttacea* was assessed to see how commonly *S. punctata* were preyed upon.

Abundances of *A. truttacea* and other predatory fishes were measured using a beach seine net, 100 m long $\times$ 2 m high with 20 mm mesh in the wings and 15 mm mesh in the

bag and middle, with 50-m-long hauling ropes attached to each end. The seine net was set parallel to the shoreline, 50 m offshore and hauled directly onto the beach. Three replicate hauls of the seine net were made in haphazardly selected areas on two separate occasions at each site. All *A. truttacea* were kept for diet analysis.

The SL of each *A. truttacea* was measured, and their stomachs, not including intestines, were removed and preserved. The stomach contents of *A. truttacea* were identified to various taxonomic levels, individual dietary items were counted, and dietary categories were weighed. The importance of a dietary component can vary with its weight, abundance and frequency of occurrence, therefore, the percentage of these parameters was calculated for each dietary item found.

2.5. Underwater observations of A. truttacea

Partial cages are supposed to provide a control for effects caused by the artificial structure in cages. The structure used to build cages in our study did not alter sediment parameters (particle sizes or amount of organic matter) or numbers of meiofauna (Hindell et al., in press). Partial cages should also allow predators to forage or move as they would in uncaged areas, but this is rarely tested. If partial cages are appropriate controls, the numbers of predators observed inside should be similar to those observed in uncaged areas.

Sony standard 8 mm Handycam video recorders enclosed in underwater housings were used to measure numbers of *A. truttacea* in caging treatments in each habitat. In either unvegetated sand or seagrass, a replicate of each caging treatment was recorded. A video camera was placed inside each caging treatment. The videos were linked using Cameratalk software, JK Instruments, which enabled the user to pre-program recording regimes. Videos were set to simultaneously begin recording 3 h before mean high water and record the first 10 min of each half-hour time interval for 6 h. In this way, we 'captured' the movement/abundance of fish during flood and ebb tides. This procedure was replicated twice in each habitat at Blairgowrie. Video footage was taken around the same time as the predator survey and the caging experiment. The numbers of *A. truttacea* observed in each combination of habitat and cage were counted.

2.6. Statistical analysis

Assumptions of homogeneity of variance and normality were assessed by viewing box plots and plots of residuals. Non-normal data or data with heterogeneous variances were transformed and reassessed. Variability in numbers of *S. punctata* was analysed using a three-factor analysis of variance (ANOVA). Habitat and caging were treated as fixed factors. Site was treated as a random factor. Numbers of *S. punctata* were averaged across the four sampling times. A priori planned comparisons were used to determine how the levels of the cage effect varied amongst habitats at each site. Initially, we compared the numbers of *S. punctata* in uncaged areas to those associated with partial cages to assess for a cage effect. If there was no statistical difference ($P = 0.05$), and therefore no cage effect, then the average of these was compared to cages. If, however, numbers of *S. punctata* varied significantly between partially and uncaged

areas, the numbers in cages were compared to those inside partial cages to provide some measure of the importance of predation versus cage structure in determining abundances of fish. Tukey's tests were used to determine which sites differed. Lack of replication ($n = 1$ at the level of fish) in some habitat × caging treatments precluded a fully orthogonal analysis of the variability of sizes of *S. punctata* between sites, caging and habitats. We compared variability in sizes of *S. punctata* between sites for fish sampled in cages, and we provide a figure that summarises the remaining size-related data. Variability in numbers of *A. truttacea* in the netting survey was analysed using a two-factor partially nested ANOVA. Variability in numbers of *A. truttacea* between treatments in unvegetated sand was analysed using a one-factor ANOVA and Tukey's test.

3. Results

The numbers of *S. punctata* varied in a complex way between sites, habitats and caging treatments (Table 1). There was a significant three-way interaction between sites, caging and habitats, averaging data across times (Table 1, Fig. 3). The numbers of *S. punctata* were, on average, larger in unvegetated sand than seagrass at Kilgour, but smaller in unvegetated sand than seagrass at Blairgowrie (Fig. 3). There was no difference in the

Table 1
Summary of 3-factor analysis of variance and multiple planned comparisons of mean ($\log_{10}$ transformed) numbers of *S. punctata* at each site (Blairgowrie, Kilgour and Grand Scenic) within each treatment (cage — c, cage control — cc and uncaged — uc) and habitat (seagrass and unvegetated sand) averaged through time ($n = 288$)

Source	*df*	MS	*P*
Site = S	2	5.310	< **0.001**
Habitat = H	1	4.285	**0.377**
Cage = C	2	1.364	**0.055**
S × H	2	3.380	**0.045**
S × C	4	0.210	**0.762**
H × C	2	1.298	**0.169**
S × H × C	4	0.451	**0.001**
Blairgowrie			
seagrass	c = cc = uc	0.084	0.826
unvegetated sand	cc = uc	0.004	0.926
	c > cc = uc	4.555	**0.002**
Grand Scenic			
seagrass	c = cc = uc	0.071	0.850
unvegetated sand	c = cc = uc	0.006	0.986
Kilgour			
seagrass	c = cc = uc	0.132	0.739
unvegetated sand	cc = uc	0.131	0.586
	c > cc = uc	5.283	**0.001**
Error	54	0.082	

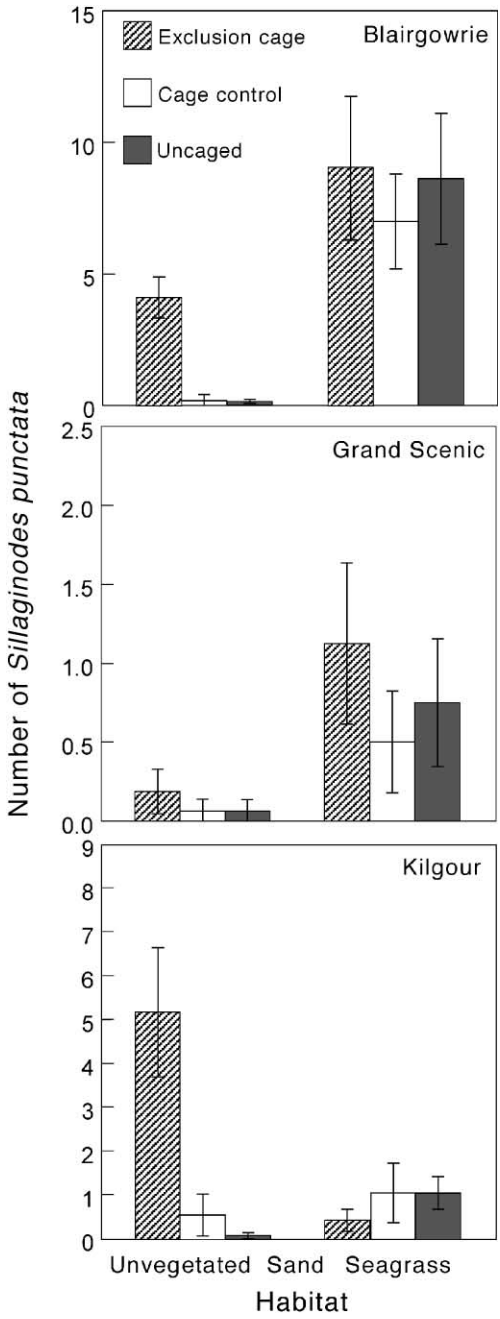

Fig. 3. Mean abundance (± S.E.) of *S. punctata* at Blairgowrie, Grand Scenic and Kilgour in cages, partial cages and uncaged areas in seagrass or unvegetated sand habitats.

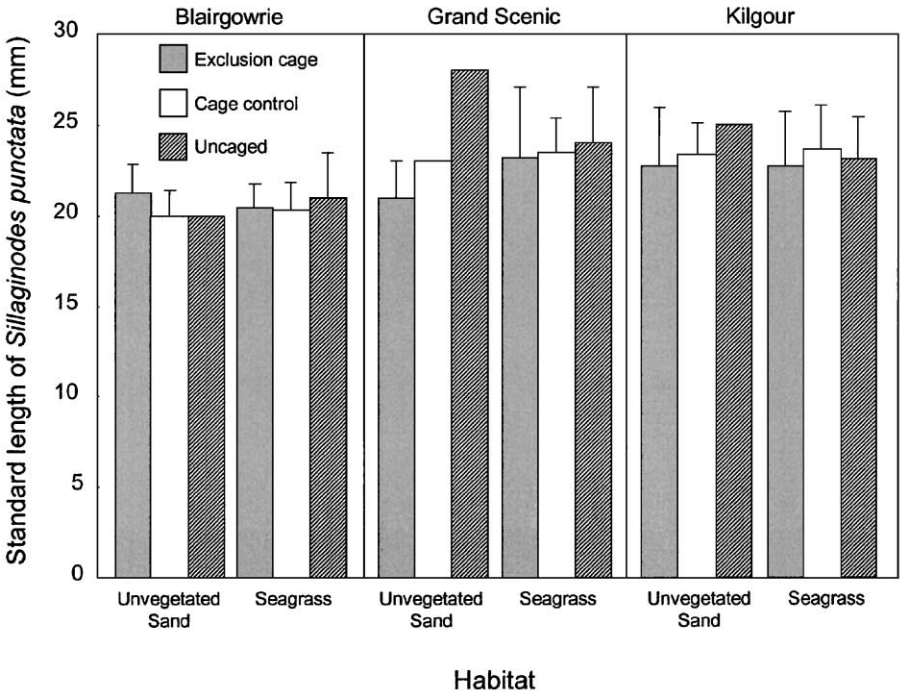

Fig. 4. Mean standard length (± S.E.) of *S. punctata* in cages, partial cages and uncaged areas at Blairgowrie, Grand Scenic and Kilgour.

numbers of *S. punctata* between cage treatments in seagrass at either Kilgour or Blairgowrie, but there was a strong caging effect in unvegetated sand (Table 1, Fig. 3). Partial cages contained similar numbers of fish to uncaged areas, and cages contained significantly more *S. punctata* than the average of partial cages and uncaged areas over unvegetated sand (Table 1, Fig. 3). More fish were associated with seagrass than unvegetated sand at Grand Scenic. In seagrass, the numbers of *S. punctata* did not vary between cage treatments (Table 1, Fig. 3). Despite a larger average number of *S. punctata*

Table 2
Summary of nested analysis of variance and Tukey's test of mean ($\log_{10}$ transformed) numbers of *A. truttacea* at each site (Blairgowrie — Bg, Kilgour — Kg and Grand Scenic — Gs) ($n = 6$)

Source	*df*	MS	*P*
Site	2	2.700	**0.008**
Bg > Kg			**0.010**
Bg > Gs			**0.012**
Gs = Kg			0.953
Day{Site}	3	0.077	0.982
Error	12	1.408	

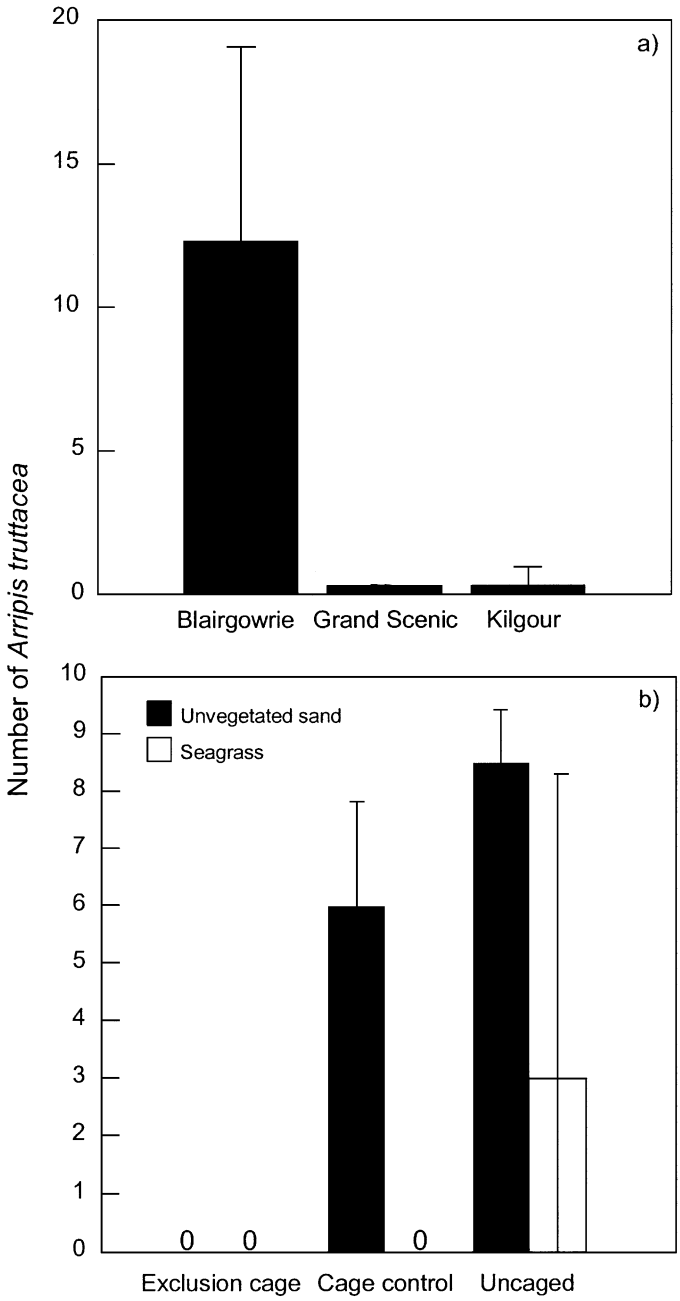

Fig. 5. Mean abundance (± S.E.) of *A. truttacea* (a) caught using a seine net at Blairgowrie, Grand Scenic and Kilgour, and (b) observed using underwater videos in cages, partial cages and uncaged areas within seagrass and unvegetated sand habitats at Blairgowrie.

in cages compared with cage controls or uncaged areas, this pattern was not statistically significant in unvegetated sand (Table 1, Fig. 3).

The SLs of *S. punctata* inside cages were significantly smaller at Blairgowrie than Grand Scenic ($df_{1,50}$, $P<0.001$) or Kilgour ($df_{1,50}$, $P<0.001$). There was no difference in the size of *S. punctata* in cages at Kilgour compared with Grand Scenic ($df_{1,50}$, $P=0.617$) (Fig. 4). Lack of replication (at the level of individual fish within a replicate cage treatment) prevented us from conducting an orthogonal analysis of the sizes of juvenile *S. punctata* between cage and habitat treatments within each site. But graphically, the sizes of *S. punctata* appeared to vary little between caging by habitat treatments within each site (Fig. 4).

3.1. Variability in numbers and diets of *A. truttacea*

Numbers of *A. truttacea* varied significantly between sites (Table 2, Fig. 5a). Larger numbers of *A. truttacea* were caught at Blairgowrie than Kilgour or Grand Scenic (Table 2, Fig. 5a). Numbers of *A. truttacea* did not vary significantly between Kilgour and Grand Scenic (Table 2, Fig. 5a).

Mysids and euphausids dominated the diets of *A. truttacea* at Blairgowrie and Grand Scenic (Table 3). *A. truttacea* sampled from Kilgour had not consumed crustaceans; instead, their diet at this site was composed exclusively of atherinid larvae. The contribution of fish to the diets of *A. truttacea* decreased from Grand Scenic to Blairgowrie. At Grand Scenic, pleuronectids and unknown fish contributed only 3 or 29 and 10 or 40 by percentage abundance and percentage mass, respectively (Table 3). *A. truttacea* at Blairgowrie consumed a more diverse assemblage of fish, although the overall contribution of fish was low. Atherinids, clupeids, gobiids and syngnathids were eaten, but

Table 3
The number of *A. truttacea* caught at each site (*n*), their mean standard length ± standard error (SL ± S.E.), and the percentage abundance (*N*), percentage mass (*M*) and percentage frequency of occurrence (*F*) of their stomach contents

	Site								
	Blairgowrie			Grand Scenic			Kilgour		
n	70			2			2		
SL (± S.E.)	16 (3.11)			15			19 (2)		
Prey items	*N*	*M*	*F*	*N*	*M*	*F*	*N*	*M*	*F*
Fish									
Atherinidae	0.3	3.7	4.6	–	–	–	100	100	100
Clupeidae	0.9	24.9	10.8	–	–	–	–	–	–
Rhombosolea	–	–	–	3.3	29.4	50.0	–	–	–
Gobiidae	0.2	2.6	4.6	–	–	–	–	–	–
Syngnathidae	0.1	0.2	1.5	–	–	–	–	–	–
Unknown fish	1.2	11.3	23.1	10.0	40.3	100	–	–	–
Other									
Crustaceans	97.3	57.4	75.4	86.7	30.3	50.0	–	–	–

unknown fish represented the largest dietary component (Table 3). In contrast to Hindell et al. (2000), who found that juvenile *A. truttacea* occasionally ate *S. punctata*, none of the *A. truttacea* sampled in this study could be positively identified as having consumed juvenile *S. punctata*.

3.2. Variability in the use of habitats and caging by A. truttacea

Underwater video showed that *A. truttacea* occurred in seagrass only once in 480 min of footage over 24 h on four separate days. In this case, the small school ($n = 6$) passed through the field of vision in less than 1.5 s. We therefore analysed our data from unvegetated sand habitats only. The design of our exclusion cages ensured that no *A. truttacea* were observed inside cages. The numbers of *A. truttacea* inside partial cages did not differ from those inside uncaged areas over unvegetated sand ($df_{1,3}$, MS = 0.004, $P = 0.333$) (Fig. 5b). Importantly, neither *A. truttacea* nor their potential prey, such as atherinids, clupeids, or sillaginids, appeared to aggregate around the walls of cages.

4. Discussion

Structural aspects of the environment, regardless of whether they are biogenic or not, often provide small fish with a refuge from predation (Heck and Crowder, 1991; Beukers and Jones, 1997), and thereby influence patterns in survival and recruitment (Steele, 1999). In our study, larger numbers of juvenile *S. punctata* in uncaged areas of seagrass than unvegetated sand, and similar numbers of fish inside cages over unvegetated sand and any of the caging treatments in seagrass, implied that seagrass beds were somehow mediating predation. Our observations of habitat preference in predatory fish showed they actually foraged very little in seagrass habitats. Regardless of the potential for the structural complexity in seagrass beds to mediate predation, and the consistency of our results with this model, predatory fish were rarely using seagrass habitats. Differences, therefore, in the numbers of *S. punctata* between seagrass and unvegetated sand do not necessarily reflect the interference of predation by aspects of the seagrass, but may be related to habitat preferences of predatory fish and/or selection by juvenile fishes for areas with low numbers of predators. Why predatory fish occur less in seagrass could reflect some adaptive behaviour to restrict foraging to areas where prey are easiest to catch, or to avoid the risk of predation to themselves from still larger piscivores (Sweatman and Robertson, 1994; Hixon and Carr, 1997). But this is purely speculative. Further research is needed to assess why predator activity varies amongst habitats of variable structure.

Dietary composition of predatory fish and estimates of their abundances provides evidence of their potential to influence the assemblage structure of their prey (Hall et al., 1995; Connell and Kingsford, 1997). *A. truttacea* consumed a variety of fishes including clupeids, atherinids, pleuronectids and gobiids, but despite the predation effect implied by the variability in numbers of *S. punctata* between caging treatments, *S. punctata* were conspicuously absent from the diets of *A. truttacea.* This suggests that predation may not be influencing the numbers of *S. punctata* directly, and our results may represent anti-predator behaviour — the selection of areas with low numbers of predators. Patterns in

recruitment of fish in mosaics of unvegetated sand and seagrass are thought to be caused by behaviourally mediated predator avoidance by recruits rather than direct predation (Sweatman and Robertson, 1994; Jordan et al., 1996). Alternatively, the rapid rate of digestion of early post-settlement fish may have prevented us from identifying *S. punctata* from gut contents. Atherinids and clupeids were common in the diets of *A. truttacea*, and these fish displayed strong associations with cages (Hindell et al., in press). This evidence suggests predation directly influences small-scale spatial patterns in numbers of small fish in our system. We need more information about microsite selection with respect to the local abundance of predatory fish to separate the contribution of direct predation versus anti-predator behaviour in determining numbers of *S. punctata*.

The numbers of fish in seagrass are thought to be due to the availability of larvae prepared to settle indiscriminately into any shelter (Bell and Westoby, 1986b; Bell et al., 1987) rather than settlement preferences based on physical complexity of seagrass or post-settlement predation. Initial patterns may then be modified by the redistribution of fish to microsites that favour survival (Bell and Westoby, 1986b). For our study, such microsites would be areas with low numbers of predators (cages) and/or sufficient refuge from predation (seagrass). If predation is important in structuring assemblages of fish amongst sites, the sites with the most predatory fish would have fewest prey fish (Hixon, 1986, 1991; Connell and Kingsford, 1997). *A. truttacea* were most abundant at Blairgowrie (their numbers were low at the other sites), but *S. punctata* were also most abundant at Blairgowrie. Despite the numbers of *S. punctata* varying between cage treatments in unvegetated sand in a manner consistent with predation, predatory fish did not appear to be influencing the abundance of fish at the site level. Although our study was conducted at relatively few sites, the results suggest that predation effects per se, although consistent between habitats across sites, are less important determinants of large-scale spatial variability in the abundance of small fish. Our results support the paradigms of Bell and Westoby (1986a) and Bell and Pollard (1989), whereby larval supply probably drives the initial broad-scale spatial patterns in numbers of fish in seagrass. Processes such as predation by fish, however, contribute to the inter-habitat variability within a site after settlement. Specifically, predation by *A. truttacea* restricts the distribution of *S. punctata* to habitats where predation pressure is 'low', and this impact is consistent between sites.

Predatory fish may influence the size structure of juvenile fishes (Folkvord and Hunter, 1986; Pepin and Shears, 1995; Manderson et al., 1999). The presence of predatory fishes is associated with a higher mean size of fish recruits (Levin et al., 1997) because of size-selective predation (Levin et al., 1997) or altered growth of surviving recruits (Carr and Hixon, 1995). Within sites, SLs of *S. punctata* did not vary between caging treatments or habitats. In view of the implied role of behaviour rather than direct predation in determining habitat patterns of *S. punctata*, it does not appear that susceptibility to predation varies over the sizes measured. The variability in SLs of *S. punctata* between sites is likely to be related to the supply of larvae and their size at settlement, which varies positively with distance into Port Phillip Bay (Jenkins et al., 1996; Jenkins and Wheatley, 1998). Larval *S. punctata* enter Port Phillip Bay from Bass Strait — there is no breeding stock inside the bay (Kailola et al., 1993). Blairgowrie is the closest site to the source of larvae and is the first to receive larvae. Larval *S. punctata* settle at the other sites later, by which time they are larger in size.

Steele (1999) showed that the magnitude and patterns of recruitment for a reef fish were similar among shelter treatments regardless of whether they were open to predation or not. In our study, the relative difference in the numbers of *S. punctata* inside cages between unvegetated sand and seagrass varied inconsistently between sites. For example, the numbers of *S. punctata* were similar between cages in seagrass and unvegetated sand at Blairgowrie. This suggests that the primary role of seagrass was as a refuge from predation. Holbrook and Schmitt (1988) similarly found that fish preferred to forage in areas that provided a refuge from predation, regardless of the levels of food. Conversely, the numbers of *S. punctata* were larger in unvegetated sand than seagrass at Kilgour, which implies that the provision of refuge from predation was not the only role of seagrasses at this site. Other processes, for example, food availability, may influence patterns caused by predation (Kemp, 1989; Keough and Jenkins, 1995). Connolly (1994) and Jenkins and Hamer (in press) have suggested that prey availability was an important contributor to habitat utilisation by juvenile *S. punctata*. At Kilgour, where more *S. punctata* were sampled from cages in unvegetated sand than seagrass, unvegetated sand may actually be a 'preferred' foraging habitat, but *S. punctata* may be restricted to foraging in seagrass because of predatory fish and the associated risk to survival.

Additional structure in marine environments may act as a type of fish attraction device (Kingsford, 1993; Clarke and Aeby, 1998). Predatory fish and their teleost prey may aggregate around the artificial structure of cages and partially obscure or prevent the interpretation of predation effects. We found no evidence that numbers of *S. punctata* were linearly related to the amount of cage structure. Underwater observations showed that atherinids and clupeids, as well as *S. punctata*, did not congregate around cage walls. Differences, therefore, in the numbers of *S. punctata* between caging treatments can be interpreted more confidently in terms of predation rather than cage artefacts caused by the attraction of fish to caging structure.

The successful interpretation of results from studies that use partial cages to control for cage effects is restricted by the usually untested assumption that predatory fish forage inside cage controls with similar frequency to that which they forage in uncaged areas. As Virnstein (1978) suggested, however, it is difficult to conceive of a cage control that provides all the structure of an exclusion cage but allows access to predatory animals. Underwater observations of *A. truttacea* showed that their numbers inside partial cages were similar to those in uncaged areas over unvegetated sand. Connell (1997) has also found that numbers of large predatory fishes were unaffected by partial cages, and predation pressure between open plots and partial cages was commensurable. The predation pattern that is suggested by the variability in numbers of *S. punctata* between treatments is therefore unlikely to be driven by differential predator use of partially caged and uncaged areas.

5. Conclusion

Despite the attention given to determining the importance of predation in structuring assemblages of small fish that live in vegetated marine environments (Bell and Pollard,

1989; Gotceitas et al., 1997; Rangeley and Kramer, 1998), the importance of predation by fish has remained controversial. For juveniles of *S. punctata*, predation strongly influences their inter-habitat distribution within a location, probably through behaviourally mediated antipredator measures rather than direct predation, and these impacts are consistent over relatively large (tens of kilometers) spatial scales. Low variability in numbers of *S. punctata* between cage treatments in seagrass, compared with a strong predation effect in unvegetated habitats, suggests that seagrass beds mediate predation and this could be why juvenile fish preferentially settle into these habitats. However, predatory fish rarely used vegetated habitats, relative to unvegetated areas, and habitat use by predatory fish needs to be considered when assessing the importance of habitat complexity in the provision of refuge from predation. Cages did not attract fishes or interfere with the movements of predatory fish, and therefore variability in abundances of *S. punctata* between cage treatments in unvegetated sand can be attributed more convincingly to predation. Caging experiments are a valuable experimental tool by which to assess predation effects in marine systems. But their interpretation depends on augmenting results with experimental studies and observational data that assess small- (within site) and large- (between sites) scale spatial variability in abundances of predatory fishes and their fish prey in relation to the variable structure of caging treatments and the habitats in which they are applied.

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