Spatial variation in the use of seagrass and unvegetated habitats by post-settlement King George whiting (Percoidei: Sillaginidae) in relation to meiofaunal distribution and macrophyte structure

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ABSTRACT: Post-settlement King George whiting *Sillaginodes punctata* and meiofauna were collected from seagrass and unvegetated habitats at 9 sites within Port Phillip Bay, Australia, in October and November 1997. Sites varied considerably in sediment characteristics, macrophyte structure and meiofauna distribution. We hypothesised that the relative use of seagrass and unvegetated habitat by post-settlement *S. punctata* would vary with the characteristics of sites. Overall, the abundance of *S. punctata* on seagrass relative to unvegetated habitats varied greatly among sites, ranging from an almost complete association with seagrass to an almost complete association with unvegetated habitat. The pattern of habitat use among sites by *S. punctata* was reflected by the distribution of small crustacea; differences in habitat use across sites for *S. punctata* and small crustaceans were highly correlated. Relative habitat use across sites by post-settlement *S. punctata* was also negatively correlated with length of seagrass plants. Results suggest a role for prey distribution and seagrass structure in producing these patterns. When data for habitats were pooled, abundance of *S. punctata* at sites was significantly correlated with meiofaunal crustacean abundance, suggesting that prey distribution was an important factor in broad-scale variability in recruitment

KEY WORDS: Spatial variation · *Sillaginodes punctata* · Post-settlement fish · Seagrass · Unvegetated sand · Meiofauna · Macrophyte structure

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INTRODUCTION

Habitat usage by juvenile fish may be influenced by a number of factors. At broad scales, the initial distribution of newly settled fish is largely determined by circulation patterns delivering larvae (Bell et al. 1988, Jenkins et al. 1997a, Hannan & Williams 1998), possibly modified by larval behaviour (Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997). However, at finer scales, distinct patterns of habitat usage may be apparent, influenced by factors such as physical exposure (Jenkins et al. 1997a), food levels (Connolly 1994a, Levin 1994), habitat selection (Bell & Westoby 1986a,

Edgar & Robertson 1992) and predation (Jordan et al. 1996, Tupper & Boutilier 1997). Seagrass is often cited as an important near-shore habitat for juvenile fish, offering increased food and protection from predation and physical exposure, especially compared with unvegetated habitats (Bell & Pollard 1989). The relative importance of different factors in determining habitat usage by juvenile fish in seagrass beds is, however, not clearly understood.

A paradigm in research on the habitat relations of juvenile fish is that, with few exceptions, diversity and abundance of fishes in seagrass are higher than in unvegetated habitats (Bell & Pollard 1989). Research shows, however, that while this generalisation appears to be true for fish diversity (Hakenom & Baird 1984, Humphries et al. 1992), the results for abundance (or

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biomass) are equivocal. While a number of studies support the contention that diversity and abundance of juvenile fish are higher in seagrass (Bell & Pollard 1989, Sogard & Able 1991, Connolly 1994b, Edgar & Shaw 1995a, Gray et al. 1996, Mattila et al. 1999), other studies contradict this assumption. Heck & Thoman (1984) found no significant difference in fish abundance between vegetated and unvegetated habitats in Chesapeake Bay. Ferrell & Bell (1991) found similar numbers of fish on eelgrass, *Zostera* and adjacent sand, although numbers were lower on distant sand. Jenkins et al. (1997b) found that juvenile fish abundance and biomass were higher in the subtidal eelgrass *Heterozostera tasmanica* than in adjacent unvegetated habitat, but abundance was not significantly different for the intertidal eelgrass *Zostera muelleri* and adjacent unvegetated habitat. Thus, there are situations where, in terms of abundance and biomass of fishes, seagrass is not preferred over unvegetated habitat. Understanding the underlying factors that cause such variation in habitat usage is crucial to the rational management of coastal habitats in terms of fisheries production. Where such variation in habitat usage exists, it will not be a simple case of protecting 1 habitat to sustain a certain fish species; management will need to account for spatial variation in habitat use.

Individual species that show spatial variation in habitat usage would be of most value in understanding the underlying factors in habitat selection. There is increasing evidence that usage by juvenile fish of different habitats depends on the environmental context and that gross physical attributes of habitats may not always be of predictive value in fisheries ecology. For example, growth rates of 2 species of juvenile fish in a range of habitats was found to vary in space and time and was dependent on the environmental context of the habitat (Phelan et al. 2000)

A species that appears to show spatial variation in habitat use in southern Australia is the King George whiting *Sillaginodes punctata*, an important recreational and commercial species that is associated with seagrass beds in the early juvenile stage. Broad-scale patterns of settlement and early recruitment are largely determined by hydrodynamics and larval supply (Hamer & Jenkins 1996, Jenkins et al. 1996, Jenkins et al. 1997a, Jenkins et al. 1998). Finer-scale patterns of habitat use by post-settlement fish, however, appear to show spatial variability. In Barker Inlet, South Australia (Connolly 1994b), and Western Port (Robertson 1977) and Port Phillip Bays (Jenkins et al. 1997b, Jenkins & Wheatley 1998) in Victoria, newly settled *S. punctata* are more abundant in seagrass than in adjacent unvegetated habitats. However, in Swan Bay, a small embayment interconnected with Port Phillip Bay, post-settlement *S. punctata* are much more abundant in unvegetated habitats (Jenkins et al. 1997b). A number of factors may show spatial variation that might lead to variation in habitat usage. For example, Swan Bay is a shallow, low energy embayment with muddy, highly organic sediment, while sites that have been sampled in Port Phillip Bay are generally higher energy with coarser sediments (Shaw & Jenkins 1992). Newly settled *S. punctata* feed on meiofauna, predominantly epibenthic harpacticoid copepods and gammaridean amphipods (Connolly 1995, Jenkins et al. 1996). Meiofauna abundances in unvegetated habitats in Swan Bay are much higher than in equivalent habitats in Port Phillip Bay (Shaw & Jenkins 1992), possibly making this habitat more attractive for feeding.

Previous studies have suggested that food levels may be a primary determinant of habitat usage by post-settlement *Sillaginodes punctata* (Connolly 1994a,c, Jenkins et al. 1996). We hypothesised that variation in habitat usage by *S. punctata* is related to the distribution of food. We predicted that in more exposed environments where sediments in unvegetated habitats are relatively coarse and have a low organic content, meiofauna would be more concentrated in seagrass, and correspondingly, *S. punctata* would be more abundant in seagrass. In contrast, sheltered, muddy environments where unvegetated sediments have high organic content are likely to have a much greater concentration of meiofauna relative to seagrass, and this would be reflected in habitat usage by *S. punctata*. Further factors likely to influence habitat selection are seagrass length and density. Studies with artificial seagrass have shown that long seagrass is less preferred by *S. punctata* than shorter seagrass (Jenkins et al. 1998). Thus, long seagrass that occurs in protected, muddy habitats may impede foraging by *S. punctata* and increase usage of unvegetated habitats in these environments.

The aim of the present study was to examine variation in the habitat association of post-settlement *Sillaginodes punctata* at sites that encompass a range of exposure levels from sheltered muddy to exposed sandy environments. We predicted that both meiofauna and *S. punctata* abundances would be higher in unvegetated than in seagrass habitat in sheltered environments, providing evidence for a relation between food distribution and habitat association. We also examined the relation between seagrass structure and relative use of different habitats by post-settlement *S. punctata*.

MATERIALS AND METHODS

Study area. Port Phillip Bay is a large (2000 km^2), semi-enclosed, predominantly tidal embayment linked to the ocean of Bass Strait by a narrow entrance

(Fig. 1). The hydrodynamics are characterised by an entrance region where fast (3 m s^{-1}) ebb and flood jets dominate the circulation, a large flood-tidal delta, known as the Sands region, where strong currents occur in the major channels and an 'inner' zone where tidal currents are weak (Black et al. 1993). On the western side of Port Phillip Bay, tidal currents drop to below 10 cm s^{-1} around the entrance to the Geelong Arm. Tides are semidiurnal and the amplitude inside the bay is less than 1 m. Salinity in Port Phillip Bay is essentially marine (Longmore et al. 1990).

The dominant seagrass in Port Phillip Bay, *Heterozostera tasmanica*, occurs mainly in the southern and western regions of the bay (Fig. 1). These areas are relatively protected from the predominant south-westerly winds (Bulthuis 1981, Bulthuis et al. 1992). *H. tasmanica* in Port Phillip Bay occurs from the lower intertidal to depths of up to 9 m in areas of clear water (Bulthuis 1981). In the southern part of the bay *H. tasmanica* occurs in narrow (20 m wide) bands parallel to shore in the shallow subtidal area; however, in the Geelong Arm the distribution is more widespread.

Sampling sites. Sampling was conducted at 9 sites in the southern and western areas of Port Phillip Bay (Fig. 1). Four sites (Rosebud, Blairgowrie, St Leonards and Grassy Point) are located in the southern part of the bay, and 5 sites (Point Richards, Spray Farm, Kilgour, Clifton Springs and Grand Scenic) are located in the Geelong Arm (Fig. 1).

At each site, sampling was conducted in seagrass and unvegetated habitats averaging approximately 0.5 m below MLWS. The 9 sites were sampled twice, during October 20 to 23 and November 17 to 21, 1997. Two to 3 sites were sampled each day. Samples were collected within 3 h from either side of low tide.

Field methods. *Sediment:* Samples for sediment analyses were collected with a 400 mm long, 32 mm diameter PVC tube. The tube was inserted into the sediment to a depth of 50 mm, a cap was placed over the upper end, and the sample was removed from the water. The sample was poured directly into a sample jar and formalin was added to make up an approximate 10% solution.

Plant structure: Replicate samples of seagrass and associated algae were collected from each site for measurement of plant characteristics. A 250 × 250 mm quadrat was used to take 6, haphazardly placed, replicate samples at each site. Scissors were used to cut the seagrass stems at the sediment interface within the quadrat. Samples were placed in plastic bags and stored on ice for transport to the laboratory where they were frozen for later analysis.

Fish: Post-settlement *Sillaginodes punctata* were sampled with a seine net of 10 m length, with a 2.5 m drop and a mesh size of 1 mm^2. Two 10 m ropes were
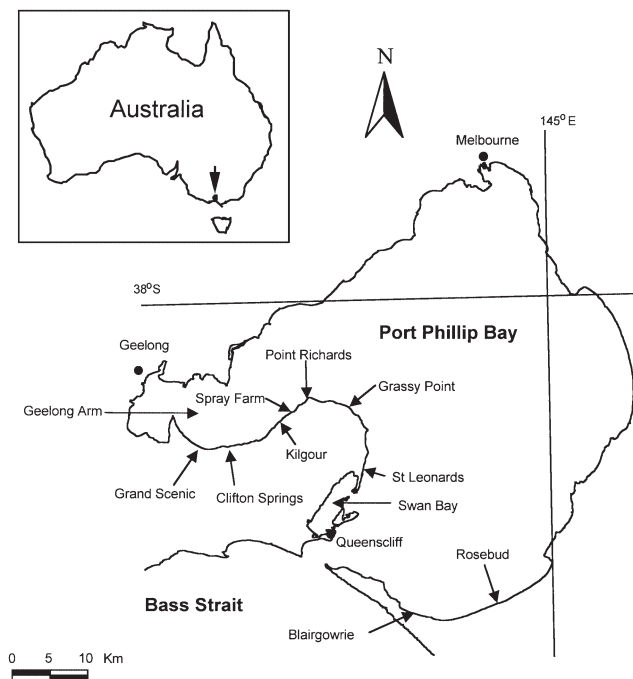

Fig. 1. Location of sampling sites in Port Phillip Bay. Inset: Location of Port Phillip Bay on the Australian coast

attached at each end of the seine. Fish were collected in 4, haphazardly placed, non-overlapping hauls from each habitat. Replicate samples were taken from interspersed patches of seagrass and unvegetated habitat at each site. Hauls were made by 2 people walking out to the appropriate depth, 1 person walking 10 m further, setting the net parallel to the shore and returning to the position of the second person where the net was then hauled into the bucket. *S. punctata* were sorted from the net contents, anaesthetised in benzocaine and preserved in 95% ethanol.

Meiofauna: Six replicate samples of meiofauna were taken from each habitat in the same area as the seine netting. Sediment, seagrass and associated meiofauna were sampled using a 400 mm long, 95 mm inner diameter plexiglass tube with a 63 μm mesh covering 1 end. The open end of the tube was pushed approximately 5 mm into the sediment before sliding a 2 mm thick, 200 × 200 mm steel plate under the opening and pressing the plate against the tube as the sample was inverted and removed from the water. In seagrass habitat, stems were cut at the sediment interface with scissors before placing the plate under the tube—this action was simulated in unvegetated habitat to keep sample treatment consistent. The sample was washed from the tube into a jar for transport to the laboratory.

Laboratory methods. *Sediment:* The percentage silt-clay fraction of sediments was determined by wet sieving the sediment through a 63 μm sieve and drying the

2 fractions at 60°C for 2 d in a drying oven. The percentage organic content was determined by placing dried samples in a muffle furnace at 550°C for 2 h and determining ash-free dry weight.

Plant structure: Samples were thawed, and seagrass and algae were separated. The length of 10 randomly selected seagrass plants was measured. The biomass of the seagrass and algal components was determined after drying for 2 d at 60°C.

Fish: The standard length (tip of the snout to tip of the caudal peduncle) of *Sillaginodes punctata* was measured under a dissecting microscope fitted with an ocular micrometer. For larger samples of *S. punctata*, a random subsample of 25 individuals was measured.

Meiofauna: Samples were preserved immediately upon return from the field. The sample was washed though a 63 µm mesh sieve and seawater was drained off. The sample was then washed back into the jar with freshwater and left for 2 min so that epifaunal crustacea would release their grasp on seagrass blades. The freshwater was then sieved off and replaced with 99% ethanol. A solution of ethanol and rose bengal stain was then added to increase the visibility of animals during sorting.

For sorting, samples were washed through a series of stacked sieves of 2.6, 1.0, 710, 500, 333 and 250 mm mesh. Animals from the 1.0 mm sieve downwards were identified to broad taxonomic categories and counted. Although we use the term meiofauna, our samples also included small macrofauna that would not be included in a strict definition of meiofauna. For larger samples we used the sample divider described by Elmgren (1973) to produce sub-samples of approximately 50 to 100 animals. This generally meant that a sub-sample of $\frac{1}{2}$ of the 333 µm sample and $\frac{1}{8}$ of the 250 µm sample was counted.

Data analysis. Assumptions of ANOVA were examined using box and normal probability plots. Data were transformed to $\log(x + 1)$ where necessary. Variation in the abundance of post-settlement *Sillaginodes punctata* was analysed with a 3 factor ANOVA, with main effects of site, habitat and month. Habitat was treated as a fixed factor while site and month were treated as random factors. In statistical terms, our hypothesis that usage of habitat by *S. punctata* would vary with the characteristics of the site would be supported by a significant interaction between site and habitat. Because the ANOVA model had 2 random factors, it was not possible to construct an *F* ratio for the habitat main effect without resorting to a quasi *F* ratio (Underwood 1997). In the situation where our hypothesis was correct, and the site by habitat interaction was significant, the significance of the habitat main effect was rendered meaningless and did not need to be estimated (Underwood 1997). Relations between relative usage

of habitats (the abundance or biomass in unvegetated habitat subtracted from that in seagrass habitat) and site characteristics were examined with simple correlation and backward stepwise regression analysis.

Analyses involving meiofauna were restricted to crustacea because this group forms the dominant prey of post-settlement *Sillaginodes punctata* (Robertson 1977, Connolly 1995, Jenkins et al. 1996). The biomass of meiofaunal crustaceans was estimated by determining the mean weight of crustaceans in each sieve from the equation in Edgar (1990), multiplying by the num-
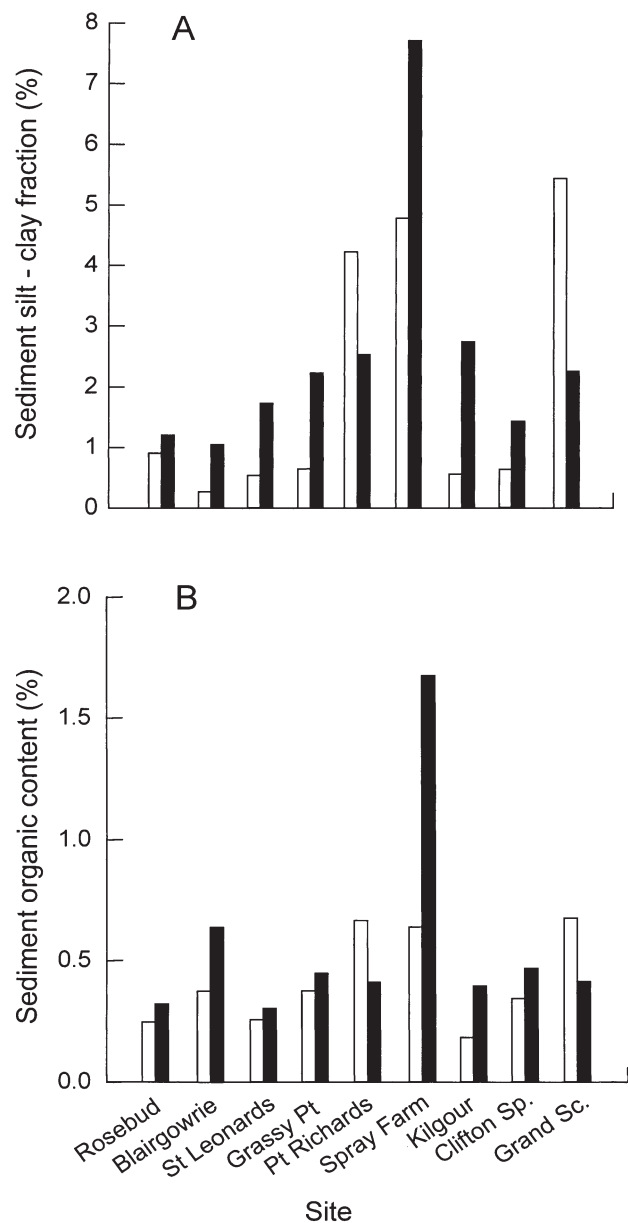

Fig. 2. Characteristics of sediment at 9 sites in Port Phillip Bay. (A) Percentage silt-clay fraction; (B) Percentage organic content. Open bars: unvegetated; closed bars: seagrass

ber of crustaceans in the sieve and summing over all the sieve classes.

RESULTS

Sediment characteristics varied widely among the 9 sites. In seagrass, the percentage silt-clay fraction and organic content were much higher at Spray Farm than at other sites (Fig. 2). In unvegetated habitat, the percentage silt-clay fraction and organic content were
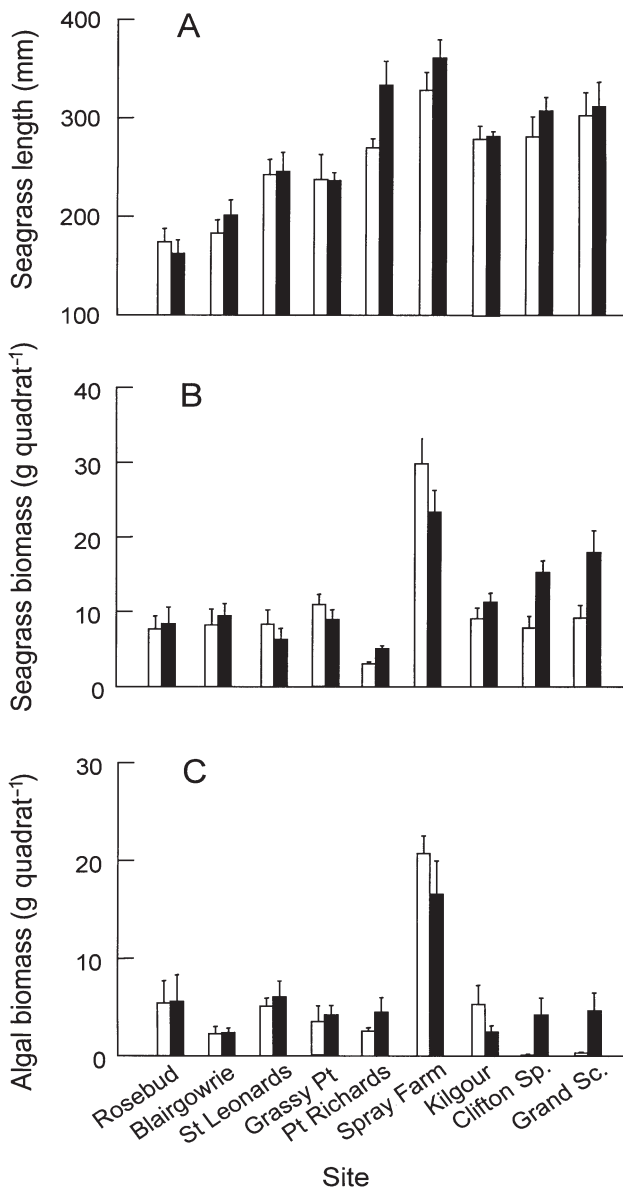

Fig. 3. Characteristics of seagrass beds at 9 sites in Port Phillip Bay. (A) Mean seagrass plant length; (B) mean seagrass biomass; (C) mean algal biomass. Open bars: October; closed bars: November. Error bars are SE

higher at Point Richards, Spray Farm and Grand Scenic than at other sites (Fig. 2). For the Kilgour and Clifton Springs sites within the Geelong Arm, the percentage silt-clay fraction and organic content in unvegetated habitat were as low as for sites near Port Phillip Heads (Fig. 2).

Plant characteristics also varied considerably among sites. In general, epiphytic algal growth on seagrass was minimal; however, finely branched genera such as *Gracelaria*, *Laurencia* and *Jeannerettia* grew *in situ* within the seagrass beds. Average length of seagrass plants varied significantly among sites (df = 8/90, $F = 26.829$, $p < 0.001$), but not between months (df = 1/8, $F = 4.350$, $p = 0.070$), and there was no significant interaction (df = 8/90, $F = 1.061$, $p = 0.398$). In general, seagrass was shorter at sites near Port Phillip Heads, and the longest seagrass in both months was at Spray Farm (Fig. 3A). Seagrass biomass showed a significant interaction between month and site (df = 8/90, $F = 2.874$, $p = 0.007$). The highest and lowest values for seagrass biomass occurred at adjacent sites: Spray Farm and Point Richards, respectively (Fig. 3B). Seagrass biomass increased markedly between sampling times for Clifton Springs and Grand Scenic (Fig. 3B). Algal biomass also showed a significant interaction between month and site (df = 8/90, $F = 2.274$, $p = 0.029$). The pattern of variation in algal biomass was similar to that in seagrass: the biomass of algae was much higher at Spray Farm than at other sites and there was a marked increase between sampling times at Clifton Springs and Grand Scenic (Fig. 3C).

The range of standard lengths of *Sillaginodes punctata* collected in October was 17.5 to 26.0 mm, and for November it was 18.0 to 36.0 mm. There were extreme differences in the relative use of seagrass and unvegetated habitats among sites by post-settlement *S. punctata*, with most individuals occurring in seagrass at Rosebud, Blairgowrie and St Leonards in contrast to most individuals occurring in unvegetated habitat at Spray Farm (Fig. 4). This pattern is reflected in the highly significant site by habitat interaction (Table 1).

Table 1. ANOVA of $\log(x + 1)$ transformed abundance of *Sillaginodes punctata*

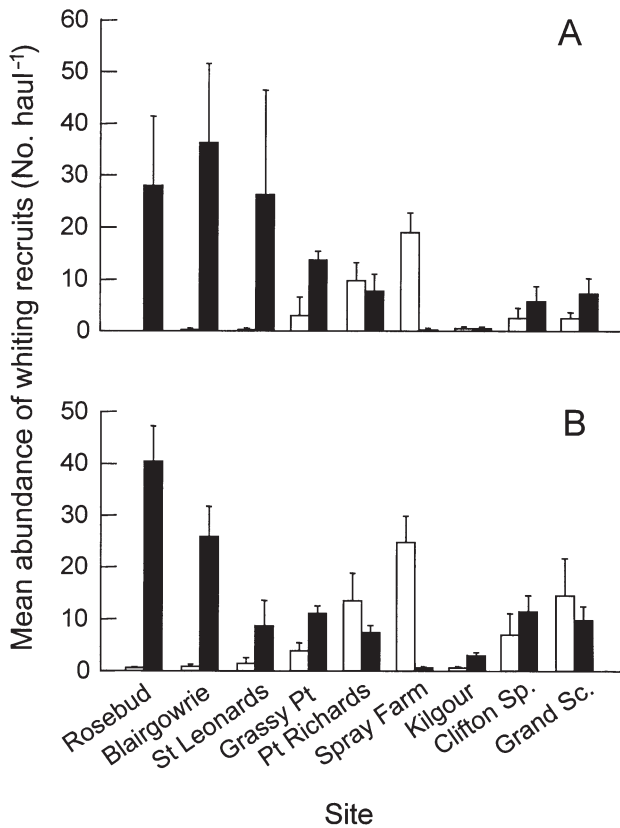| Source	df	MS	F	p
Month	1	2.30	9.64	0.015
Site	8	0.80	3.35	0.105
Habitat	1	5.35		
Month × site	8	0.24	2.40	0.020
Month × habitat	1	0.20	1.15	0.315
Site × habitat	8	2.52	14.84	0.005
Month × site × habitat	8	0.17	1.71	0.104
Error	108	0.10		

Fig. 4. Mean abundance of *Sillaginodes punctata* in seagrass and unvegetated habitat at 9 sites in Port Phillip Bay. (A) October; (B) November. Open bars: unvegetated; closed bars: seagrass. Error bars are SE
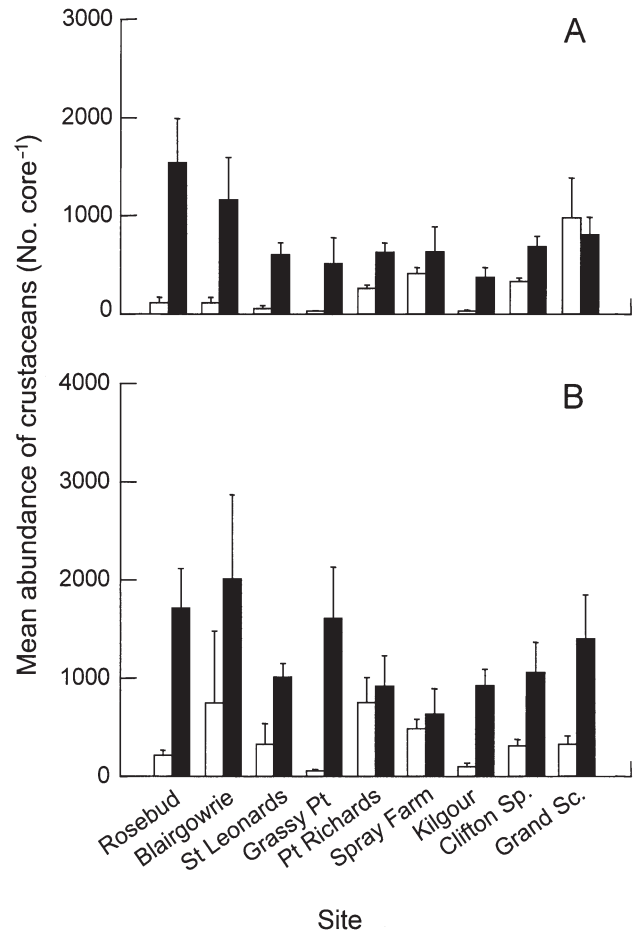

Fig. 5. Mean abundance of crustaceans in seagrass and unvegetated habitat at 9 sites in Port Phillip Bay. (A) October; (B) November. Open bars: unvegetated; closed bars: seagrass. Error bars are SE

Crustaceans were dominated by epibenthic harpacticoid copepods, averaging 69% of the crustacea in unvegetated sand and 51% in seagrass, across the 2 sampling months. Like post-settlement *Sillaginodes punctata* abundance, the relative abundance (Fig. 5) and biomass (Fig. 6) of crustacea in the 2 habitats varied among sites, although overall, crustacea had a stronger association with seagrass than did *S. punctata*. At

Rosebud, Blairgowrie, St Leonards, Grassy Point and Kilgour, abundance and biomass were much higher in seagrass than in unvegetated habitat (Figs 5 & 6). In contrast, at Point Richards, Spray Farm and Grand Scenic, although numbers were generally higher in seagrass, the difference between habitats was much lower (Figs 5 & 6). In the cases of abundances at Grand Scenic in October (Fig. 5A) and biomass at Spray Farm in November (Fig. 6B), average values were higher in unvegetated than in seagrass habitat. For both crustacean abundance and biomass, the site by habitat interaction was highly significant (Table 2).

Given the significant interactions between site and habitat for post-settlement *Sillaginodes punctata* and crustacean meiofauna, we used correlation to test for a significant relation between

Table 2. ANOVA of log(*x* + 1) transformed abundance and biomass of meiofaunal crustaceans

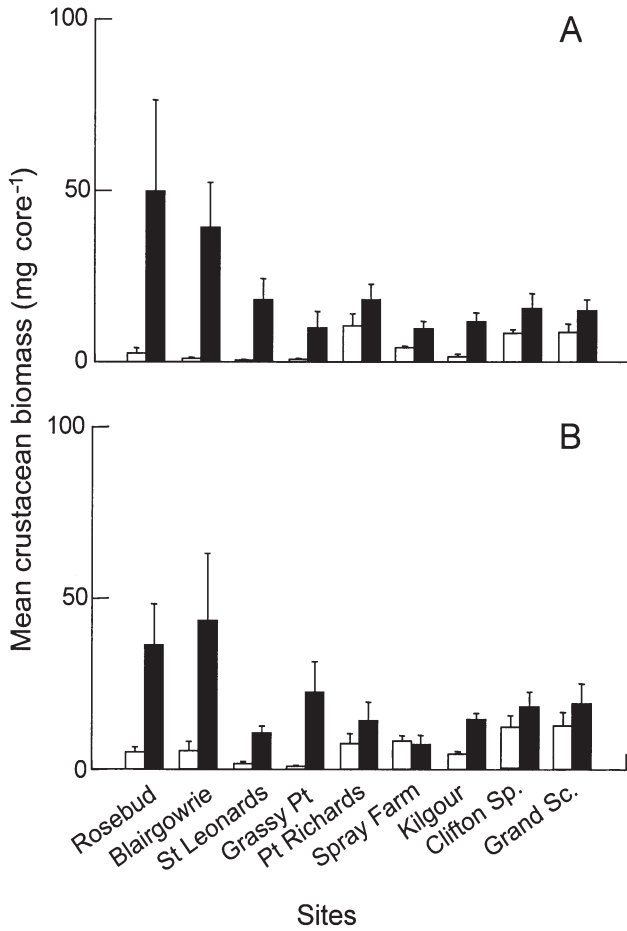| Source	df	Crustacean abundance			Crustacean biomass		
		MS	*F*	P	MS	*F*	P
Month	1	2.00	12.48	0.008	0.39	7.42	0.026
Site	8	0.84	5.28	0.015	0.48	9.19	0.003
Habitat	1	17.78			11.71		
Month × site	8	0.16	2.05	0.047	0.05	1.18	0.317
Month × habitat	1	0.01	0.05	0.824	0.28	4.59	0.065
Site × habitat	8	0.79	6.61	0.002	0.58	9.40	0.002
Month × site × habitat	8	0.12	1.53	0.155	0.06	1.41	0.203
Error	108	0.08			0.04		

Fig. 6. Mean biomass of crustaceans in seagrass and unvegetated habitat at 9 sites in Port Phillip Bay. (A) October; (B) November. Open bars: unvegetated; closed bars: seagrass. Error bars are SE

Fig. 7. Scatterplot of the relative abundance (log abundance in unvegetetated habitat subtracted from the log abundance in seagrass habitat) of *Sillaginodes punctata* versus the relative biomass (log biomass in unvegetetated habitat subtracted from the log abundance in seagrass habitat) of crustacea at 9 sites in Port Phillip Bay. R: Rosebud; B: Blairgowrie; S: St Leonards; G: Grassy Point; P: Point Richards; SF: Spray Farm; K: Kilgour; C: Clifton Springs; GS: Grand Scenic

the relative use of seagrass and unvegetated habitat by fish and their potential prey. Because the abundance and biomass of crustaceans were highly correlated (n = 36, r = 0.907, p < 0.001), we have restricted analyses to crustacean biomass. The relative use of habitat in terms of *S. punctata* abundance and crustacean biomass was highly correlated (n = 18, r = 0.703, p = 0.001; Fig. 7).

In terms of the structural characteristics of the seagrass beds, relative use of habitat by *Sillaginodes punctata* showed a significant negative correlation with seagrass length (n = 18, r = −0.830, p < 0.001; Fig. 8). Thus, relatively more *S. punctata* occurred in unvegetated than in seagrass habitat where seagrass was longer. Significant negative correlations also occurred between relative habitat use of *S. punctata* and total plant (n = 18, r = −0.590, p = 0.01) and seagrass (n = 18, r = −0.479, p = 0.045) biomass. However, these correlations were largely dependent on the high biomass values (Fig. 3) and low abundance of *S. punctata* in vegetated habitat (Fig. 4) that occurred at the Spray Farm site.
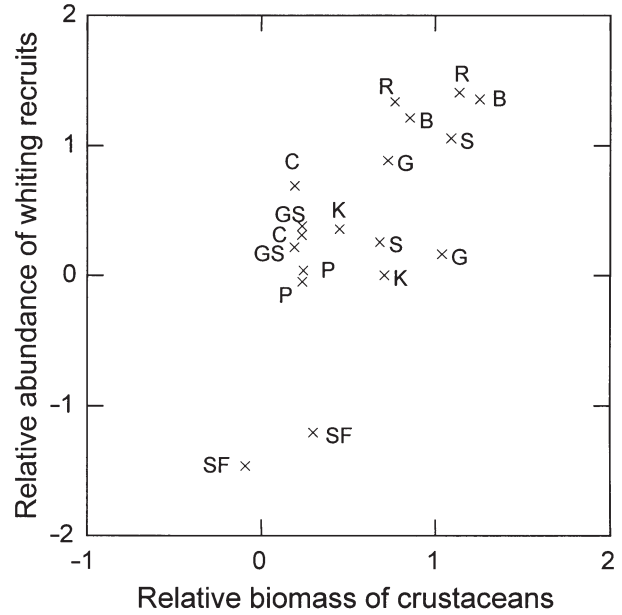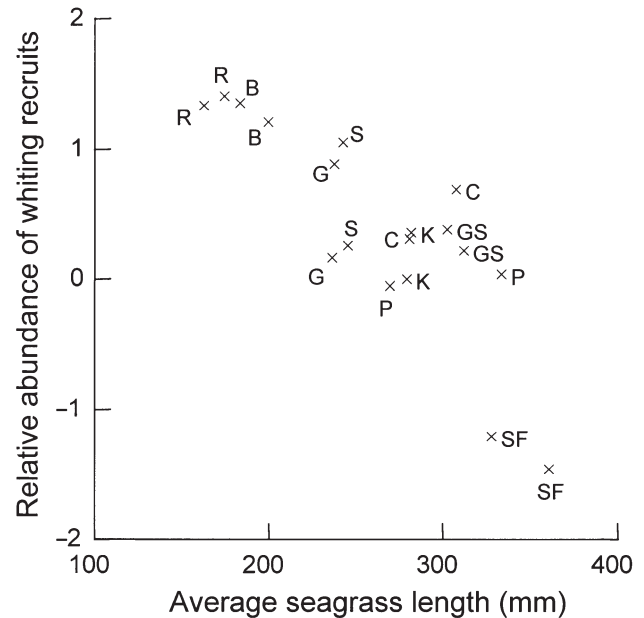

Fig. 8. Scatterplot of the relative abundance (log abundance in unvegetetated habitat subtracted from the log abundance in seagrass habitat) of *Sillaginodes punctata* versus the average length of seagrass plants at 9 sites in Port Phillip Bay. See Fig. 7 for site coding
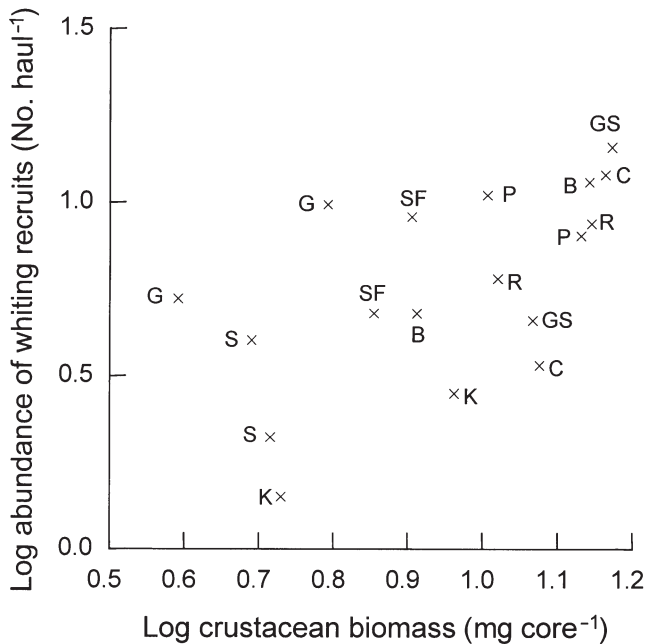
Fig. 9. Scatterplot of the log abundance of *Sillaginodes punctata* versus the log biomass of crustacea (pooled across habitats) at 9 sites in Port Phillip Bay. See Fig. 7 for site coding

If analysis is restricted to seagrass habitat only, abundance of *Sillaginodes punctata* (n = 18, r = −0.392, p = 0.108) and biomass of crustaceans (n = 18, r = −0.449, p = 0.061) were not correlated with total plant biomass at sites. Overall, when habitats were pooled, post-settlement *S. punctata* abundance was significantly correlated with crustacean biomass at sites (n = 18, r = 0.574, p = 0.013; Fig. 9).

DISCUSSION

Our hypothesis, that post-settlement *Sillaginodes punctata* would be more abundant on unvegetated than on seagrass habitat in sheltered, muddy environments compared with more exposed environments with coarser sediments, was supported. The finding that post-settlement *S. punctata* showed a similar pattern of distribution to meiofaunal crustaceans, and that the relative use of habitat by *S. punctata* and crustaceans was highly correlated, suggests a possible role of prey distribution in determining the habitat usage of small fish.

Previous studies suggest that prey distribution may be an important determinant of habitat usage by *Sillaginodes punctata*. In a study by Connolly (1994a), food availability was manipulated in tanks in which juvenile *S. punctata* were offered a choice of seagrass and unvegetated habitats. The distribution of *S. punc-*

tata was primarily determined by food distribution until fish were satiated. In a field study, the distribution of juvenile *S. punctata* in seagrass, unvegetated habitat and areas where seagrass was removed was most consistent with a pattern related to food distribution rather than substrate choice (Connolly 1994c).

A number of inter-correlated environmental and habitat factors vary with the degree of exposure of sites. *Heterozostera tasmanica* plants are much longer in sheltered, muddy habitats than in more exposed habitats. Experiments with artificial seagrass in Port Phillip Bay have shown that post-settlement *Sillaginodes punctata* prefer shorter *H. tasmanica* plants (Jenkins et al. 1998). Sampling efficiency of seine nets for small fish is likely to be lower in relatively long, dense seagrass (Pierce et al. 1990, Rozas & Minello 1997). However, in the case of *S. punctata*, experiments on net efficiency in dense seagrass have given recapture rates of 95 to 100% (G. P. Jenkins unpubl. data) probably because the preferred habitat is above the seagrass canopy (S. Moran unpubl. video obs.). A further factor related to seagrass structure is that foraging success of small fish may be lower in long, dense seagrass (Heck & Thoman 1981, Stoner 1982), making the habitat less favourable.

The data, however, do not necessarily support a role for seagrass structure in determining habitat association of post-settlement *Sillaginodes punctata* at sites. The long, dense seagrass at Spray Farm may have had a role in the very low numbers of *S. punctata* collected in seagrass at this site. However, such an explanation would not apply to the Point Richards site, where, although seagrass plants were long, they were also very sparse (the seagrass biomass was very low) and unlikely to reduce sampling efficiency or impede feeding. Nevertheless, abundances of *S. punctata* in unvegetated habitat relative to seagrass at Point Richards were relatively high. Ultimately, determining the relative roles of plant structure and prey distribution in determining relative habitat use by fish will require experiments manipulating seagrass structure and prey availability.

An unmeasured variable that may have contributed to the differences in habitat usage observed is predation. Small fish may change habitat association in response to predation (Sogard & Olla 1993, Jordan et al. 1996). Dietary analysis of piscivorous fish associated with seagrass beds has suggested that *Sillaginodes punctata* are rarely eaten (Hindell et al. 2000). Recently, we have conducted experiments on predation on post-settlement *S. punctata* at the Blairgowrie, Kilgour and Grand Scenic sites (Hindell et al. in press). *S. punctata* numbers at the Blairgowrie and Kilgour sites increased in exclusion cages relative to controls in unvegetated habitats, but the effect was not apparent in

seagrass. No predation effect was found in either habitat at the Grand Scenic site. Numbers of *S. punctata* in the present study were very low at Kilgour, but the use of habitat at the Blairgowrie and Grand Scenic sites was consistent with a greater impact of predation on unvegetated habitat at Blairgowrie. Thus, predation may be an important factor influencing habitat usage at sites. Levin et al. (1997) also found a significant affect of predator exclusion in seagrass and unvegetated habitat for pinfish; however, the effect was constant across habitats. In the future, experiments manipulating both food and predation contemporaneously would be desirable.

A final factor that might lead to relatively higher numbers of *Sillaginodes punctata* on unvegetated habitats at exposed sites is the presence of currents or wave turbulence. Jenkins et al. (1997a) have shown that post-settlement *S. punctata* abundances are reduced on seagrass beds after periods of significant wave action. The impact of wave action may be more severe on unvegetated than on seagrass beds as the latter is known to ameliorate wave turbulence (Fonseca & Cahalan 1992).

Restricting the focus to vegetated (seagrass) habitats only, abundances of *Sillaginodes punctata* and biomass of crustaceans were not correlated with plant biomass, a measure of habitat complexity. Strong correlations between the abundance or biomass of fauna and habitat complexity are often found at the scale of individual macrophyte beds (Heck & Orth 1980, Stoner 1983, Orth et al. 1984, Bell & Pollard 1989, Edgar & Robertson 1992, Orth 1992). However, this correlation often breaks down among macrophyte beds over broad scales (Bell & Westoby 1986b, Bell et al. 1988, Jenkins et al. 1998). This difference has been attributed to variability in larval supply and low post-recruitment migration rates among beds (Bell & Westoby 1986b). Other environmental factors that vary over a broad scale, such as the degree of wave exposure at sites, may also contribute to this pattern (Edgar & Shaw 1995b, Jenkins et al. 1997a).

For some species of small fish the distribution of prey may be more important in determining abundance than macrophyte characteristics (Levin 1994). There is increasing evidence that selection for seagrass beds by fauna may be more related to elevated food levels than to the shelter provided by complex habitat (Bologna & Heck 1999, Bostrom & Mattila 1999). Jenkins et al. (1996) presented evidence that while the distribution of post-settlement *Sillaginodes punctata* was not initially related to food availability on a broad scale, 1 or 2 mo after settlement there was a strong correlation between the abundance on a seagrass bed and average gut fullness. These results imply preference for, or reduced mortality at, sites with more food at a broad

scale. This contention is supported here in that there was a correlation between abundances of *S. punctata* and biomass of crustacea across sites when the data for the 2 habitats were combined.

In summary, across a range of sites, abundance of *Sillaginodes punctata* in seagrass relative to unvegetated habitat varied with site. In general, the relative use of unvegetated habitats increased at sheltered, muddy sites compared with more exposed, sandy sites. This change in relative abundances in habitats was also reflected in the distribution of meiofaunal crustaceans, implicating food distribution as a factor in habitat usage by small fish. Other important factors, however, could have been increased length of seagrass or macrophyte biomass that may have impeded foraging, or spatial variation in predation pressure or wave turbulence. In general, the results suggest that for species such as *S. punctata*, the distribution of prey may be an important factor determining the utilisation of habitat by post-settlement individuals.

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