Small-scale dynamics of secondary dispersal in a seagrass associated fish: a caging study

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ABSTRACT: Secondary planktonic dispersal potentially alters recruitment patterns of marine organisms, but little is known about whether this process occurs in temperate fishes. This study investigated whether disturbance in seagrass beds, caused by onshore winds that induce high wave action, facilitated the resuspension and secondary dispersal of post-larval King George whiting *Sillaginodes punctata* (Cuvier). Cage inclusion experiments were conducted in seagrass beds within Port Phillip Bay, Australia. Live post-larvae were released into cages during 3 different wind conditions (onshore, alongshore and offshore) and their positions in the cage relative to the shoreline were recorded after 1 h. Significantly higher numbers of post-larvae were collected on the seaward side of cages during high waves associated with onshore winds. Of these post-larvae, higher numbers were collected with increasing onshore wind speed. Our results suggest that physical disturbance, at the seagrass-bed scale, has the potential to alter recruitment patterns of *S. punctata* by facilitating secondary dispersal.

KEY WORDS: Physical disturbance · Secondary dispersal · Seagrass · *Sillaginodes punctata* · Post-larvae

INTRODUCTION

For many marine organisms a critical stage in the recruitment process is the successful settlement from the pelagic environment into a benthic habitat. The settlement of larvae to such habitats can strongly shape recruitment patterns, and plays an important role in structuring population dynamics (Keough 1984, Roughgarden et al. 1988, Doherty & Fowler 1994, Caley et al. 1996, Underwood & Keough 2001). However, settlement is not necessarily the sole determinant of recruitment censused some time after settlement; for some taxa, post-settlement factors such as predation, food availability, habitat complexity, and disturbance also act to alter recruitment (Keough & Downes 1982, Doherty & Williams 1988, Connell & Jones 1991, Connolly 1994b, Levin & Hay 1996, Hixon 1998, Booth & Hixon 1999). An additional process that can be important in structuring assemblages shortly after settlement is secondary planktonic dispersal (Rijnsdorp et al. 1985, Olivier et al. 1996, Turner et al. 1997, Etherington & Eggleston 2000).

Most examples of secondary planktonic dispersal, characterised as the re-entrainment of settlement-stage larvae into the surrounding water column from a benthic habitat, have come from marine invertebrates inhabiting soft-bottom environments relatively devoid of structure (Butman 1987, Commito et al. 1995), and seagrass beds (Etherington & Eggleston 2000, Blackmon & Eggleston 2001). The process of secondary planktonic dispersal has the potential to re-distribute larvae to new locations and alter initial recruitment patterns (Commito et al. 1995, Palmer et al. 1996, Thiebaut et al. 1996). Such re-entrainment into the water column can be passive, influenced by physical processes (Butman 1987, Commito et al. 1995, Turner et al. 1997) or an active behavioural response (Martel & Chia 1991, Blackmon & Eggleston 2001). To date, however, few examples of secondary planktonic dispersal have been found in fishes (but see Rijnsdorp et al. 1985).

The recruitment of fish to seagrass beds has been widely studied in temperate and tropical waters world-

wide (Orth et al. 1984, Bell & Pollard 1989, Orth 1992, Jenkins et al. 1996a). Much of this research has focused on how the effects of habitat structure (Heck & Orth 1980, Jenkins et al. 1998a), predation (Levin et al. 1997, Hindell et al. 2000a,b), food availability (Connolly 1994a, Jenkins & Hamer 2001) and larval supply (Hamer & Jenkins 1996) influence fish recruitment and abundance. An early hypothesis by Bell & Westoby (1986) suggested that fishes and invertebrate larvae settle indiscriminately among seagrass beds regardless of physical structure, and stay within that seagrass bed for up to a few months. This 'settle and stay' hypothesis, however, has been contradicted by evidence that suggests that fauna are highly mobile among seagrass beds (Sogard et al. 1989, Edgar & Robertson 1992).

Recent studies in shallow seagrass beds suggest that wave disturbance generated by onshore winds may facilitate secondary dispersal for a number of seagrass-associated fishes (Jenkins et al. 1997, Moran et al. 2003). One species that may be particularly susceptible to secondary dispersal is the King George whiting *Sillaginodes punctata*. High-frequency sampling has shown that numbers of post-larval *S. punctata* declined in seagrass beds during high wave disturbance compared to calm conditions (Moran et al. 2003). Post-larvae of *S. punctata* enter Port Phillip Bay between September and November each year (Jenkins 1986). On arrival in the bay, post-larvae are between 90 and 150 d post-hatch and range between 16 and 20 mm in length (Jenkins & May 1994, Jenkins et al. 1996b). Post-larvae are defined as having a full compliment of fin elements, but as yet to take on juvenile characteristics of pigmentation, gut-coiling and scale formation (Bruce 1995). The post-larvae of *S. punctata* have a number of similarities with pre-settlement larvae of tropical reef fishes. For example, *S. punctata* is a percoid, has a full compliment of fin elements, and falls within a size-range similar to that of reef fishes studied. However, Jenkins & Welsford (2002) found the swimming capabilities of *S. punctata* post-larvae to be relatively weak, which supports the contention (gained through hydrodynamic dispersal models) that recruitment into Port Phillip Bay is largely a passive process (Jenkins et al. 1997, 1999).

Settlement of *Sillaginodes punctata* occurs in shallow reef and seagrass habitats (Jenkins & Wheatley 1998). Early in the recruitment period, most post-larvae are close to the entrance of Port Phillip Bay, but over time numbers decrease in this area and increase in seagrass beds further inside the bay towards the Geelong Arm (Jenkins et al. 1996b). At present, hydrodynamic dispersal models and known larval behaviours have failed to explain the settlement of *S. punctata* to seagrass beds located in the Geelong Arm on the western side of Port Phillip Bay (Jenkins et al. 1997, 1999). The aim of this study, using cage inclusion experiments, was to assess whether wave disturbance generated by onshore winds can facilitate secondary dispersal in *S. punctata* post-larvae. This study quantitatively examined fine-scale fish movements during varying physical disturbance regimes, and has the potential to further explain recruitment dynamics of demersal fishes.

MATERIALS AND METHODS

Study site. This study was done at Grassy Point, situated on the NE shore of the Bellarine Peninsula of Port Phillip Bay (Fig. 1). Port Phillip Bay is a large semi-enclosed, predominately tidal embayment in SE Australia that is connected to the oceanic waters of Bass Strait (Fig. 1). Tidal currents in the region of our site are generally weak (0.1 to 0.2 m s^{-1}) compared to the strong tidal currents at the Bay's entrance (3 m s^{-1}) (Black et al. 1993). Tides in Port Phillip Bay are semidiurnal, with a range of less than 1 m. In the shallow subtidal at Grassy Point, beds of eelgrass *Heterozostera tasmanica* (Martens ex Aschers) den Hartog run parallel to the shoreline. These narrow bands of seagrass (20 m wide) are interspersed amongst patches of bare sand. Wave height in the study area ranged from less than 5 cm in offshore winds to 0.4 m in the strongest onshore winds of approximately 10 to 11 m s^{-1}.

Cage experiment. We positioned 3 replicate 5 × 5 m fine-mesh cages within *Heterozostera tasmanica* beds at Grassy Point at an average depth of 0.8 m below mean low-water spring tide. Each cage was con-
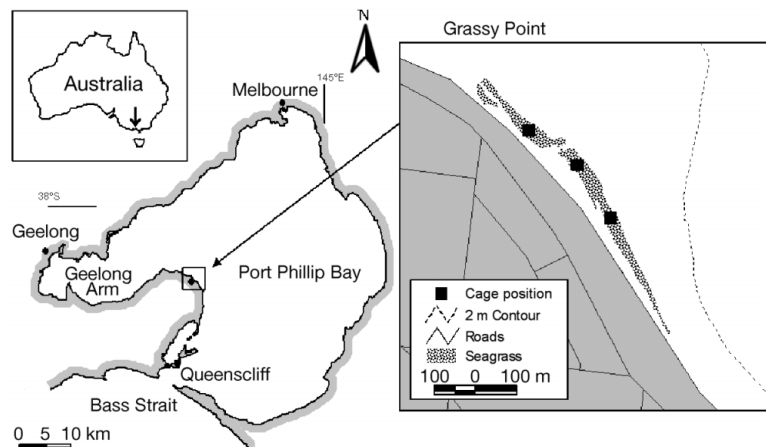

Fig. 1. Port Phillip Bay, SE Australia. Inset: Grassy Point showing positions of cage structures in seagrass

structed of 12 evenly spaced, 2.1 m-long galvanised steel poles hammered into the substrate. Around these poles we attached a 20 m length of 1 mm^2 black fibre-glass netting (1.6 m in height), enclosing an area of 25 m^2. The mesh was tightened at the top and bottom and tied to each pole with 5 mm nylon cord and plastic clamps. The bottom of the net was weighted with a lead rope to prevent fishes swimming between the bottom of the cage walls and the top of the substrate. At all times throughout the experiment, the water level did not exceed the top of the cage walls, and the substrate remained submerged. The placement of each cage was selected at the beginning of the experiment, and plots were sampled repeatedly during each wind condition through time. Cages were separated from each other by approximately 75 m. Cages were oriented parallel to the shoreline, with the shoreward side of the cage approximately 3 m from the shoreward edge of the seagrass bed (Fig. 2). A gradient of less than 3° was measured between the shoreward and seaward edges of each cage.

Following construction, each cage was cleared of fishes and drift algae with a 6 m long × 2 m high × 1 mm^2 mesh beach seine net; 2 people deployed the seine net. Seine-net techniques and methods used to catch post-larvae are described in detail by Jenkins et al. (1996b). On removal of the fishes, the cages were left undisturbed for at least 15 min prior to beginning the experiment.

At approximately 5 to 7 d intervals, *Sillaginodes punctata* post-larvae were collected from *Heterozostera tasmanica* beds in the vicinity of experimental cages at Grassy Point. These fish were caught during calm weather conditions along the same depth contour as the cage structures. Post-larvae were collected on calm days to eliminate any bias in the behaviour of individual fish during different weather conditions. Fish were collected with a 10 m long × 2 m high × 1 mm^2 mesh beach seine net; 2 people slowly hauled in the net until a small enclosed circle remained. The fish were then carefully transferred to 20 l plastic tubs filled with seawater and transported to the Queenscliff Marine Station (20 min by road). On arrival, the fish were transferred to a series of 200 l holding tanks filled with re-circulating seawater at ambient temperature (19°C) and fed brine shrimp daily until used in the caging experiment. No fish were kept in the holding tanks for longer than 4 d.

Fish were introduced to cages at approximately 1 to 4 d intervals from mid-September to early November 2001; 2 cages were used on each sampling day; 1 person slowly released 25 fish in the centre of each cage. Visual observations during pilot studies suggest that fish introduced in this manner were not subjected to increased turbulent forces that could have affected
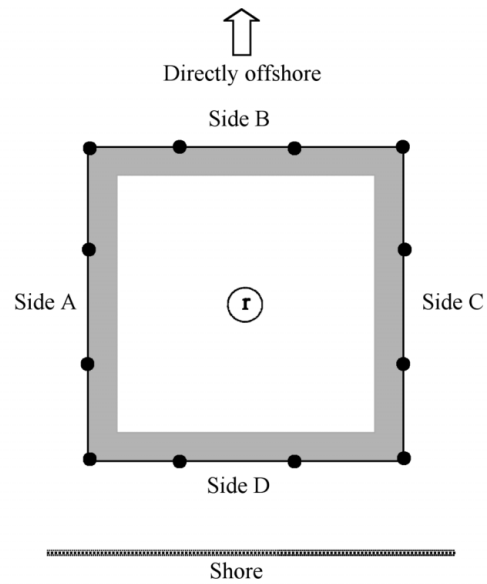

Fig. 2. Structure of cages (5 × 5 m) used in recapture experiment. Shaded area represents section of cages sampled. Diagram also shows cage sides (A-D), orientation of cages relative to shoreline, and the fish-release point, r

their swimming capability or caused physiological damage. Fish were left in cages for 1 h before sampling. As the mean currents in the sampling area range from approximately 2 to 30 cm s^{-1} (K. P. Black et al. unpubl. data), this would allow more than enough time for passive transport of post-larvae to the side of the cage. Each side of the cage was sampled with a 1.5 m long × 0.4 m wide × 0.25 m deep dip-net. The dip-net was made from a 25 mm diameter PVC rectangle frame with 1 mm^2 black mesh attached. The bottom of the net was weighted with lead and the top buoyed with small floats. Sampling was conducted by placing the net at a corner of the cage (long side held vertically), and then walking the net along each side of the cage to the next corner (maintaining the side of the net against the side wall of the cage). Each cage wall was sampled 4 times (i.e. 4 rotations) on each sampling date to ensure that no fish were missed during sampling. The first side sampled was chosen randomly, and all sides of the cage were sampled once before the next round of sampling started. Underwater visual observations during pilot studies had suggested that the operation of this type of dip net accurately represented fish numbers along the sides of cage structures (i.e. capture efficiency for 1 sweep averaged 90% success rate). All fish collected on each side were removed, anaesthetised in benzocaine and placed in ethanol. In the laboratory, standard lengths (SL; tip of snout to the tip of caudal peduncle) were recorded.

Cage effects. Physical measurements were taken to assess the effects of the cage on flow. On 14 November 2001, an S4 current meter was deployed in the centre of a cage. The current meter was mounted on a concrete block and stainless steel pole, with measurements taken approximately 0.5 m above the substrate (0.35 to 0.4 m above the seagrass canopy). The water depth was approximately 1.25 m, the tide was at the top of the flood, and winds were light (2 to 3 m s^{-1}) from the southeast. Measurements were taken at 1 min intervals for 10 min periods. We alternated 10 min periods of measurements taken with the cage mesh in place with periods without the cage mesh, until 3 periods each of cage mesh and no cage mesh were recorded.

At the end of the cage experiment on 22 August 2000, a fast-response 3-dimensional Acoustic Doppler Velocimeter (ADV, Sontek) was deployed on a stainless steel frame in the centre of a cage to examine the effect of the cage mesh on wave and turbulence characteristics. The frame was carefully levelled so that the horizontal (u, v) velocity components did not contaminate the vertical (w) component.

The ADV was set to record at 16 Hz and the water temperature was measured with a submersible thermometer at the start of each profile and set in the instrument's software. The water depth was approximately 1.35 m, winds were onshore at approximately 5 m s^{-1}, and the tide was in the mid- to late flood. Measurements were taken for 5 min with and without the cage mesh at approximately 0.45 m above the substrate (0.3 to 0.35 m above the seagrass canopy).

The ADV records a signal-to-noise ratio and correlation coefficient for each signal beam that can be used to assess the quality of each measurement. With the manufacturer's software, filtering was achieved with the correlation coefficient for each signal beam set to a threshold level of 70% and 5 dB for the signal-to-noise ratio. The data was then further de-spiked, assuming that any natural acceleration could not exceed 1 G. The filtering generally eliminated less than 10% of the time series recorded in the water column.

Environmental variables used in study. Wind directions were recorded at the time of sampling. We assigned 3 classifications of wind direction: onshore, offshore and alongshore. Because the shoreline at Grassy Point is orientated approximately NW–SE (see Fig. 1), winds from the north around to the E–NE were therefore classified as onshore winds. Wind from the south to W–SW quadrant was subsequently classified offshore. All other wind directions were categorised as alongshore. At this site, onshore winds are highly correlated with high wave disturbance, while offshore winds represent calm weather associated with low wave heights. Furthermore, due to the orientation of the coastline, alongshore winds tend to wrap around the headland and direct waves shoreward, resulting in similar wave disturbance to that generated by onshore winds. Wind speeds were collected from a meteorological weather station located at Point Cook, approximately 20 km from our study site.

Statistical analysis. The cage experiment was analysed as a repeated-measures 3-factor analysis of variance (ANOVA), with wind condition (onshore, alongshore, offshore), cage side and cage location as fixed factors. The side of cages was the repeated factor. Cages were placed in specific positions to ensure that they related to a parallel hydrodynamic study conducted at this location at Grassy Point (K. P. Black et al. unpubl. data). In all, 6 replicate days for each wind condition were used throughout the experiment. Data were proportions of the original number of fish collected on each cage side, which were arcsine-transformed to satisfy the assumptions of normality and homogeneity of variances. Not all fish were recaptured on each sampling occasion, so data were not constrained to sum to 1. The assumption of sphericity was checked by the Greenhouse-Geisser (G-G) epsilon value (ε). A separate analysis of variance was used for each location to explain significant interactions between main effects from the repeated measures ANOVA model. Tukey's tests ($p < 0.05$) were used for post-hoc comparisons of significant main effects in the above models. Regression analysis was used to investigate how the proportion of fish collected along cage sides varied with wind speed.

Variation in standard length (SL) on different cage sides was investigated with a 2-factor ANOVA, with wind condition and cage side treated as fixed factors. Unlike the above analyses, a repeated-measures model could not be used because of the large number of 'missing cells' in our data (e.g. when no fish were collected on a particular cage side on a given day). Significant main effects were investigated with Tukey's test ($p < 0.05$).

Power spectra for speed components in the u, v and w from the ADV measurements were obtained from the acquired 5 min time series using the fast fourier transform (FFT) technique. A window of 1024 data points was used.

RESULTS

The proportion of *Sillaginodes punctata* post-larvae recaptured from different cage sides varied with wind direction (Table 1, Fig. 3). Overall, 62% of released post-larvae were recaptured during onshore winds, while 51 and 23% were recaptured during alongshore and offshore wind conditions respectively. Separate

Table 1. *Sillaginodes punctata.* Results of 3-factor repeated measures analysis of variance (ANOVA) comparing numbers of fish amongst cages and wind conditions (onshore, offshore and alongshore). Data were arcsine-transformed prior to analysis. **Bold** values indicate significance at p < 0.05

Source	df	MS	*F*	p
Between subjects				
Wind (W)	2	0.246	7.502	**0.003**
Cage (C)	2	0.018	0.510	0.606
W × C	4	0.024	0.684	0.609
Residual	27	0.035		
Within subjects				
Side (S)	3	1.288	32.462	**<0.001**
S × W	6	0.089	2.239	**0.048**
S × C	6	0.052	1.314	0.261
S × W × C	12	0.042	1.051	0.412
Residual	81	0.040		

Fig. 3. *Sillaginodes punctata.* Effects of wind condition (alongshore, onshore, offshore) and cage side (A–D) on mean proportion of post-larvae recaptured in cage structures. Means (±1 SE). For each wind condition, a total of 300 post-larvae were placed in cage structures

2-factor ANOVAs used to investigate the significant interaction between wind direction and cage sides showed the proportion of fish at the seaward side (Side B) varied significantly amongst wind conditions (Table 2). Post-hoc tests showed that more larvae were concentrated on the seaward side of cages (Side B) during onshore than offshore wind conditions (Tukey's test, p = 0.003; Fig. 3), with numbers falling by ~75%. Additionally, the proportion of recaptures along the seaward side (Side B) did not vary between onshore and alongshore wind conditions (Tukey's test, p = 0.372) and, although a trend suggests otherwise, alongshore and offshore wind conditions also did not vary (Tukey's test, p = 0.071; Fig. 3). Furthermore, the proportion of larvae recaptured did not vary amongst cages at Grassy Point (Table 1). Recapture rates of post-larvae along Side B varied in response to wind strength, with a significant relationship between the proportion of post-larvae recaptured and onshore wind strength (n = 12, r^2 = 0.451, p = 0.017; Fig. 4). However, a similar relationship was not found for offshore (n = 12, r^2 = 0.015, p = 0.705) or alongshore (n = 12, r^2 = 0.147, p = 0.218) wind conditions.

A high proportion of fish (>60%) were re-captured on 5 sampling days. On 2 of these days, winds were onshore, while on the other 3 d winds were alongshore. The highest recapture rates were found during onshore winds on 10 and 22 October, when 98 and 96% of fish were re-caught respectively (Fig. 5). Of these fish re-captured, 90 and 72% were collected along Side B respectively (Fig. 5). On these dates, wind strength was >10 m s^{-1} from the NE, which was the strongest onshore wind strength observed throughout our study. During alongshore winds, the highest recapture rates were on 1, 18 and 25 October, when 66, 80 and 68% of the fish were re-caught respectively. On 1 and 18 October, the
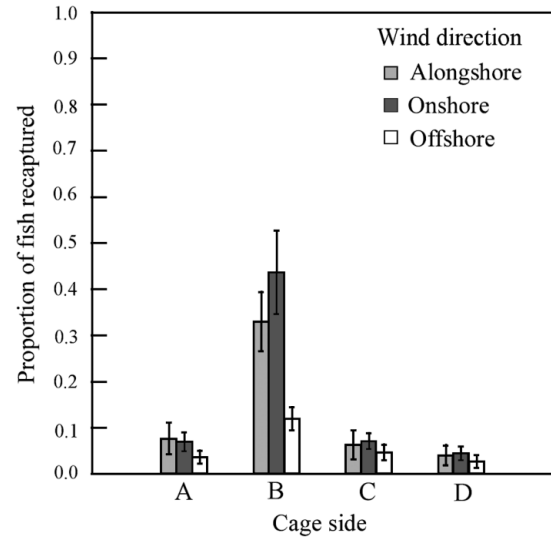
proportion of recaptures along Side B dominated this result (52 and 54% respectively; Fig. 5), while on October 25 the proportion of recaptures along Side B was lower (26%) and similar to that for Side C (24%; Fig. 5).

The standard lengths of recaptured *Sillaginodes punctata* did not vary significantly amongst cage sides

Table 2. *Sillaginodes punctata.* Results of 2-factor analysis of variance of proportions, with side analysed separately for effects of cage and wind direction (onshore, offshore, alongshore). Data were arcsine-transformed prior to analysis. **Bold** values indicate significance at p < 0.05

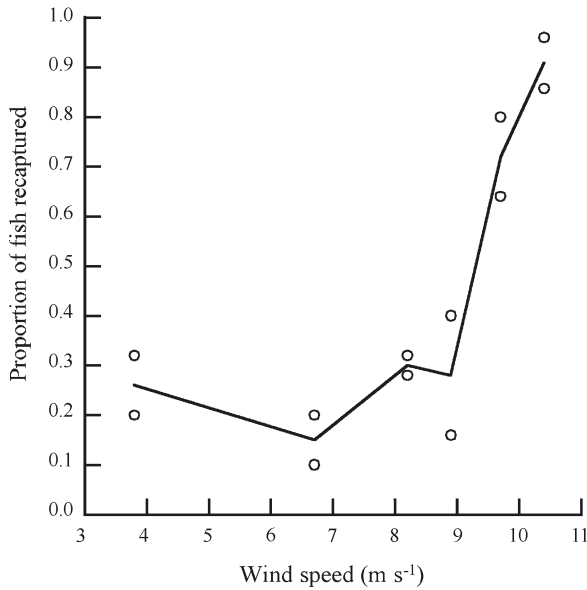| Source	df	MS	*F*	p
Side A				
Wind	2	0.028	0.978	0.389
Cage	2	0.030	1.036	0.368
Wind × Cage	4	0.037	1.298	0.296
Residual	27	0.029		
Side B				
Wind	2	0.485	6.912	**0.004**
Cage	2	0.112	1.590	0.222
Wind × Cage	4	0.058	0.831	0.518
Residual	27	0.070		
Side C				
Wind	2	0.007	0.212	0.811
Cage	2	0.008	0.235	0.792
Wind × Cage	4	0.017	0.520	0.721
Residual	27	0.033		
Side D				
Wind	2	0.010	0.450	0.642
Cage	2	0.025	1.146	0.333
Wind × Cage	4	0.036	1.657	0.189
Residual	27	0.022		

Fig. 4. *Sillaginodes punctata.* Effects of onshore wind speeds on proportion of larvae recaptured along Side B of cage structures. Lowess smoother fitted to regression model. Each data point represents the proportion of post-larvae recaptured out of total 25 originally placed in cage structures
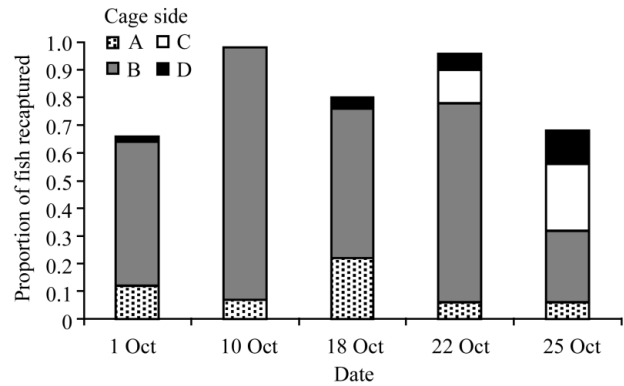

Fig. 5. *Sillaginodes punctata.* Individual sampling days when proportion of recaptured post-larvae was >60% inside cage structures. Total of 50 post-larvae were placed in cage structures on each day

on current speed and direction over the period of the trial (Table 4). Frequency spectra of the velocity measurements taken on 22 August 2000 with the ADV showed that the peak in energy at the dominant wave frequency of approximately 0.4 Hz was very similar with or without the cage mesh (Fig. 7). There was no evidence of a change in high-frequency turbulence in the presence of cage mesh (Fig. 7).

DISCUSSION

This study suggests that *Sillaginodes punctata* post-larvae are transported offshore out of seagrass beds during wave disturbance associated with onshore winds. During onshore winds, recapture rates of post-larvae were high, and larger numbers of fish were collected on the seaward side of cages. A similar pattern, although not significant, occurred during alongshore wind conditions, a condition that also causes wave disturbance through refraction onto the coast. Furthermore, recapture rates along the seaward side of cages were positively related to onshore wind strength. During calm weather conditions associated with offshore winds, recapture rates were lower, and numbers of recaptured fish showed no difference amongst cage sides. The net movement of fish offshore during rough weather conditions is consistent with previous studies conducted at this site, when fewer post-larval *S. punctata* were collected in the seagrass during high wave/ onshore wind conditions (Jenkins et al. 1997, Moran et al. 2003). From these results we suggest that episodic disturbance events operating over relatively short temporal scales, for example high-wave conditions generated by onshore winds, have the potential to re-entrain post-larvae into the plankton, thereby facilitating secondary dispersal.
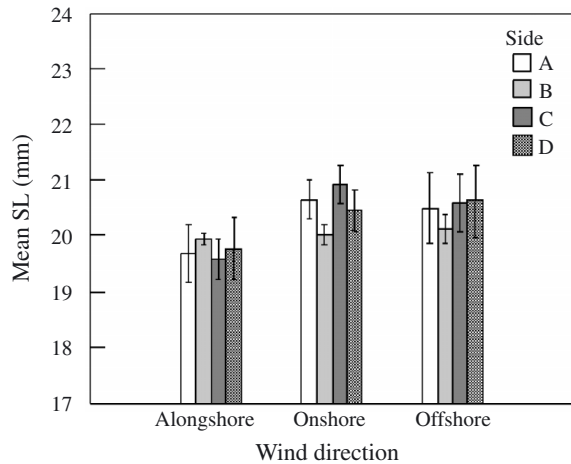
(Table 3). In particular, the seaward side of cages (Side B), where a significantly higher proportion of recaptures was found, had similar length distributions across all wind conditions (Fig. 6). Standard lengths did, however, vary significantly amongst wind conditions during the experiment (Table 3, Fig. 6). The standard lengths of larvae were significantly smaller when the wind was along- rather than onshore (Tukey's test, p = 0.007) or offshore (Tukey's test, p = 0.017). No significant interaction between wind condition and cage side was found.

Current measurements with and without the cage mesh on 14 November 2001 showed a reversal in current direction over the sampling period associated with a change of tidal direction, and variation in current speed with higher speeds in the middle of the period (Table 4). There was no strong effect of the cage mesh

Table 3. *Sillaginodes punctata.* Results of 2-factor analysis of variance of wind direction (onshore, offshore and alongshore) and side for standard length (SL). **Bold** values indicate significance at p < 0.05

Source	df	MS	*F*	p
Wind	2	5.480	5.824	**0.004**
Side	3	0.633	0.673	0.571
Wind × Side	6	0.768	0.816	0.560
Residual	85	0.941		

Fig. 6. *Sillaginodes punctata.* Standard length (SL) of post-larvae recaptured along cage sides (A–D) during wind conditions. Means (±1 SE) are shown

shore direction. Post-larval *S. punctata* are relatively weak swimmers in the horizontal plane, with swimming speeds in the order of 6 cm s^{-1} (Jenkins & Welsford 2002). Because mean current velocities, and especially orbital velocities, generally exceeded this level in onshore conditions (K. P. Black et al. unpubl. data), passive transport of *S. punctata* during onshore winds seems likely.

One factor that can influence the swimming abilities of fish larvae is their size (Wardle 1997). For fish larvae, general theory suggests a positive relationship between swimming speed and size (Stobutzki & Bellwood 1994, Bellwood & Fisher 2001). This relationship can ultimately influence whether larvae maintain their position in or around a particular settlement habitat, or be subjected to further dispersal in response to physi-

The vertical position of post-larvae in the water column, particularly in reference to their proximity to the tops of seagrass fronds, has important implications for their susceptibility to being re-suspended and dispersed offshore. Active depth selection has been shown to occur in larvae of coral reef fishes in offshore waters and inshore reefs (Leis et al. 1996, Leis 1999). Research on *Sillaginodes punctata* has shown that post-larvae are generally positioned in the lower to middle layer of the water column, directly above the seagrass canopy (Connolly 1994a, S. M. Moran pers. obs.). In this study, a small number (n = 10) of *in situ* observations confirmed that post-larvae occupy the lower to middle layer of the water column, approximately 30 cm above the seagrass canopy. These observations were made during relatively calm weather conditions when visibility was sufficient to follow post-larvae within the seagrass beds. In a closely related study focusing on small-scale hydrodynamics among seagrass beds at Grassy Point, K. P. Black et al. (unpubl. data) found that, during onshore winds, the bulk of the mid-water column was moving in an off-

Table 4. Current speed and direction measured with and without cage mesh

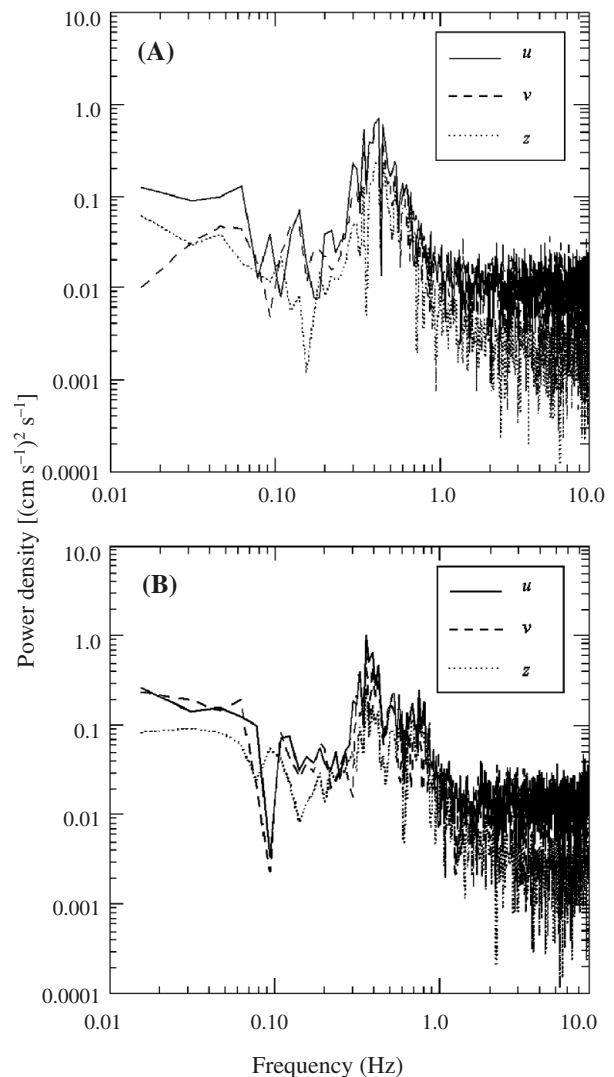| Trial	Time (h)	Speed (cm s^{-1}) Avg.	SD	Avg. direction (°)
Net on	12:40–12:50	2.7	2.32	13
Net off	12:55–13:05	3.5	1.97	324
Net on	13:13–13:23	9.8	2.97	351
Net off	13:26–13:36	9.1	2.51	315
Net on	13:39–13:49	9.9	2.80	260
Net off	13:52–14:02	5.0	1.28	184

Fig. 7. Current speed spectra above seagrass canopy. Continuous line, *u* direction; dashed line, *v* direction; dotted line, *z* direction. (A) Cage net mesh present, (B) cage mesh absent

cal disturbance. Size is important in determining secondary planktonic dispersal for the blue crab *Callinectus sapidus* (Blackmon & Eggleston 2001), where larger instars are more likely to undergo secondary planktonic dispersal. In our study we found no significant difference in size amongst the cage sides that would suggest a differential effect of size on secondary dispersal. However, the relatively narrow size-range of post-larvae used in the experiment makes interpretation of the results difficult.

The patterns of dispersal shown by *Sillaginodes punctata* in our caging experiment, suggesting offshore movements, contradict the 'settle and stay' hypothesis proposed by Bell & Westoby (1986). The first part of this hypothesis predicts that fish larvae should settle indiscriminately in seagrass patches, regardless of patch structure. Previous studies on *S. punctata* were in agreement with this, with settlement of larvae in seagrass beds being largely unrelated to seagrass structure (Jenkins et al. 1998). However, through recent high-frequency sampling in seagrass beds (Hamer & Jenkins 1996, Jenkins et al. 1997) the remaining prediction of the 'settle and stay' hypothesis has come into question. These studies have shown that once *S. punctata* arrive in seagrass patches they do not necessarily stay in that patch for long. However, it was not possible to distinguish between dispersal through resuspension or mortality. Moran et al. (2003) have recently suggested that secondary dispersal is a possible mechanism accounting for the significant reduction of post-larvae collected in seagrass beds during increased physical disturbance, although mortality through physical injury caused by wave action was also discussed. However, the present study has shown that mortality driven by physical injury cannot account for variability in post-larval abundance during physical disturbance associated with rough weather. In this study we found that a high proportion of post-larvae added to experimental cages during rough weather were later recaptured. Furthermore, regardless of calm or rough weather conditions, all post-larvae that were recaptured in cages were still alive. Therefore, these results suggest that mortality in rough weather may not significantly influence this species over the timescales studied.

Experimental cages have been widely used in fish predation studies (Doherty & Sale 1985, Hindell et al. 2000a), and as a consequence much information is available on possible confounding by cage artifacts (e.g. Virnstein 1978, Connell 1997). For example, baffling effects by the materials used to construct cage structures may alter flow patterns, thus artificially confounding experimental results. However, our studies found that flow direction and velocity, wave energy and high-frequency turbulence above the seagrass

were not greatly affected by the presence of cage mesh. Therefore, the results found in this study are a reliable indication of what is actually occurring in the seagrass beds and not simply an artifact of cage structures.

To summarise, the distribution of the post-larvae inside the cages suggests that *Sillaginodes punctata* move in an offshore (seaward) direction during disturbance from high waves generated by onshore winds. The rate of offshore movement increased with increasing wind speed but was not related to post-larval size. Our results suggest that physical disturbance, at the seagrass bed scale, has the potential to alter recruitment patterns of *S. punctata* by facilitating secondary dispersal. The observation that secondary dispersal occurs in settlement-stage *S. punctata*, and potentially redistributes fish amongst seagrass beds, demonstrates that settlement is a dynamic, protracted event, rather than the discrete event often documented in other systems.

LITERATURE CITED

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