

The role of passive transport and the influence of vertical migration on the pre-settlement distribution of a temperate, demersal fish: numerical model predictions compared with field sampling

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ABSTRACT: We compared spatial variation in the abundance of King George whiting *Sillaginodes punctata* post-larvae in the southern part of Port Phillip Bay, Australia, with predictions of hydrodynamic and dispersal numerical models that included passive transport, and vertical migratory behaviour previously observed in the field. Post-larvae were sampled at 20 sites on cruises in the spring of 1994 and 1995. Modelling included a 'passive' case with particles mixed through the water column, 'active' behaviour mirroring diel and tidal variation in the field, and 'day/night' behaviour where behaviour in the field was averaged across tides. Correlations between model simulations and post-larval distribution were highest in 1995 and were similar amongst the 3 simulations (58% of variation explained for both the passive and day/night cases). In 1994, variation in the spatial distribution explained was highest for the passive case, intermediate for the active case and lowest for the day/night case. Prevailing winds were quite different between years, with westerlies prevailing in 1994 but significant periods of easterly winds in 1995. These differences were reflected by particle distributions from simulations including behaviour, but were not reflected in post-larval distributions. A negative correlation was found between post-larval abundances and distance from shore. When model predictions and distance from shore were combined in a multiple regression, approximately 70% of the spatial variation in post-larval abundance was explained in 1995. The results imply that although the passive transport model was an excellent predictor of post-larval abundance in both years, observed vertical migration was not influencing transport, and post-larvae were closer to shore than expected, possibly due to behaviours other than vertical migration. The close association of *S. punctata* post-larvae with the coastline provided a mechanism for transport further into the bay, against the prevailing wind field.

KEY WORDS: Pre-settlement fish · Spatial distribution · Port Phillip Bay · Numerical hydrodynamic model · *Sillaginodes punctata*

INTRODUCTION

Recognition that recruitment can have an important role in controlling the size of marine populations has stimulated great interest in this area of research in recent years (Roughgarden et al. 1988, Doherty & Fowler 1994, Olafsson et al. 1994, Caley et al. 1996).

Recruitment has 5 major components: input of propagules into a given water body, transport of these propagules, planktonic mortality, settlement, and post-settlement growth/survival. The least understood components of recruitment are the transport of propagules and their mortality while in the plankton. In particular, the combination of coastal physical oceanography and marine ecology is thought to be a critical research need in this field (Underwood & Fairweather 1989, Sale 1990), and our lack of understanding of this stage has

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created a substantial barrier to the successful prediction of settlement events.

A wide range of oceanographic processes have been shown to influence larval transport patterns (Norcross & Shaw 1984, Werner et al. 1997). At the broadest scales, variation in ocean currents due to climatic phenomena such as El Niño may influence dispersal of larvae (Cowen 1985, Pearce & Phillips 1988). As larvae are transported in coastal waters they may be strongly influenced by phenomena such as meso-scale current eddies (Hare & Cowen 1996), wind forcing (Farrell et al. 1991, Thorrold et al. 1994, Miller & Emler 1997, Stoner & Smith 1998), tidal currents (Epifanio et al. 1989), and fronts and convergences (Shanks & Wright 1987, Kingsford et al. 1991, Pineda 1994, Kingsford & Suthers 1996, Thiebaut 1996). Larvae in nearshore waters such as estuaries and bays are primarily influenced by tidal currents (Chen et al. 1997, Clancy & Cobb 1997), winds (Bertness et al. 1996, Clancy & Cobb 1997) and estuarine fronts (Eggleston et al. 1998).

Research has shown that many larvae are capable of complex behaviours, and it is assumed that the interaction of these behaviours with coastal oceanography will lead to modified patterns of dispersal and recruitment. The most commonly expressed and widely studied form of behaviour that might influence larval dispersal is vertical migration (Hutchinson 1967, Haney 1988, Neilson & Perry 1990), and even weakly swimming larvae may alter their horizontal movement by varying their vertical position in the water column (Mileikovsky 1973). Vertical migration in phase with tides is commonly found for larvae in bays and estuaries and is assumed to enhance recruitment of larvae to (Creutzberg 1961, Weinstein et al. 1980, Rijnsdorp et al. 1985, Boehlert & Mundy 1988, Rowe & Epifanio 1994, Champalbert & Koutsikopoulos 1995, Forward et al. 1998), or dispersal of larvae from (Queiroga et al. 1997), bay and estuarine habitats. For species with strongly swimming larvae such as lobsters (Phillips & McWilliam 1986, Rooney & Cobb 1991) and coral reef fish (Leis et al. 1996, Leis & Carson-Ewart 1997, Sancho et al. 1997, Stobutzki & Bellwood 1997), horizontal movement may also influence dispersal patterns.

Recently, the use of numerical hydrodynamic models to study the influence of coastal oceanography on dispersal and recruitment has increased (Black & Moran 1991, Richards et al. 1995, Hinckley et al. 1996, Bartsch & Coombs 1997, Jenkins et al. 1997, Kasai et al. 1997). Models can make predictions based on 'passive' dispersal with simulated larvae well-mixed through the water column and, in a number of studies, simulation of passive dispersal has successfully predicted larval distribution or settlement in space or time (McShane et al. 1988, Clancy & Cobb 1997, Jenkins et al. 1997, Van

der Veer et al. 1998). Hydrodynamic numerical modelling can also be coupled with modelled attributes of larval behaviour (Tremblay et al. 1994, Hinckley et al. 1996, Verdierbonnet et al. 1997), providing a possible test of the influence of observed behaviours on larval dispersal by comparing predictions of models, with and without behaviour, with actual larval dispersal/settlement distributions. The strongest tests of the predictive capacity of hydrodynamic models occur when the results can be compared statistically with actual larval distributions in the field.

Study area

Port Phillip Bay is a large marine embayment on the south-east coast of Australia (Fig. 1). Port Phillip Bay is highly variable in a hydrodynamic sense, consisting of 3 broad hydrodynamic zones (Black et al. 1993). The narrow entrance is characterised by fast tidal currents that create an ebb and flood tidal jet each half tidal cycle. Over the sands region in the southern segment of the bay, tidal currents remain strong (up to 1 m s^{-1}) over the banks and channels. Wind-driven circulation in this region is relatively unimportant, and the low frequency circulation consists primarily of the tidal cycle residual currents, and the low frequency currents associated with barometric pressure driven oscillations, wind set-up, and coastal trapped waves in Bass Strait, entering Port Phillip Bay (Black et al. 1993). Beyond the sands, tidal currents in Port Phillip Bay are weak and net circulation is primarily induced by direct local wind-forcing. Thus, there is wide variability in the absolute current strengths and in the dominant mechanisms forcing the circulation. Currents also show considerable vertical stratification, especially where winds are dominant (Black et al. 1993).

Study species

Sillaginodes punctata enter Port Phillip Bay as late-stage (post-) larvae between September and November each year (Jenkins & May 1994). The post-larval stage is characterised by a full complement of fin elements but gut coiling has not begun and scales have not formed (Bruce 1995). At this stage, post-larvae are 15 to 22 mm in length and are 90 to 150 d old (Jenkins & May 1994). No distinct metamorphosis occurs in this species, post-larvae collected offshore in the plankton are morphologically indistinct from those collected in nearshore seagrass beds until gut coiling begins at approximately 23 mm (Bruce 1995). No spawning adults, or eggs and young larvae, have been recorded in Port Phillip Bay (Jenkins 1986). Studies using larval

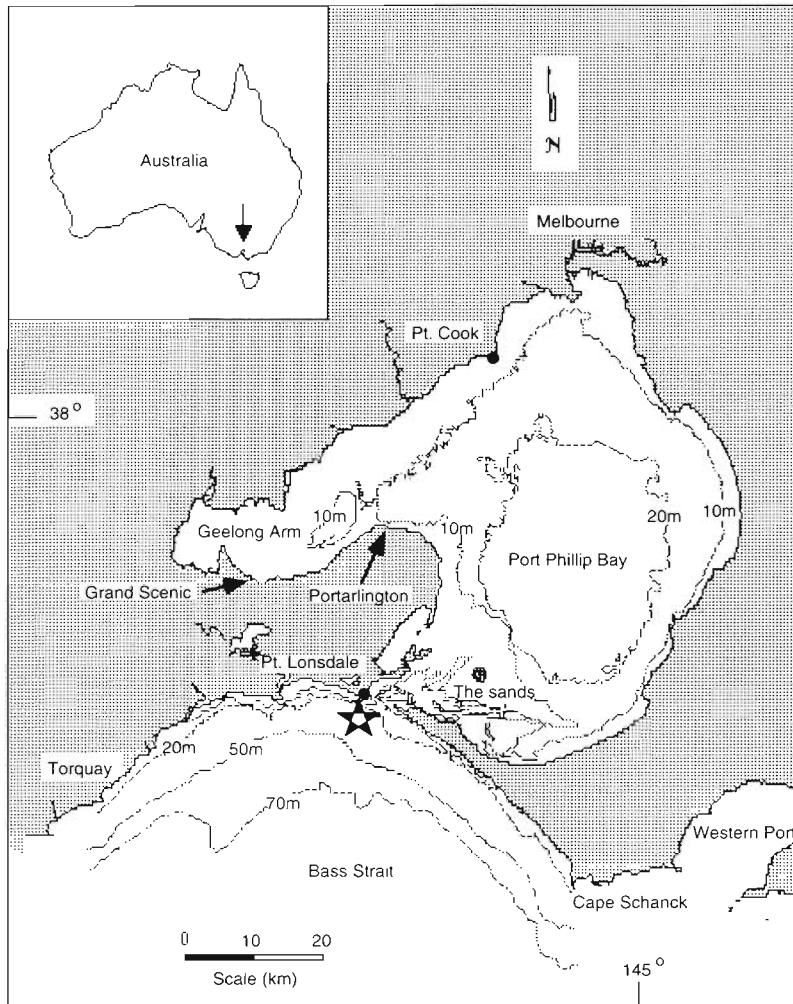


Fig. 1. Port Phillip Bay. Inset: location of Port Phillip Bay on the Australian coast. Star designates the particle release point for numerical modelling

durations determined from otoliths, together with hydrodynamic model simulations of currents in southern Australia, suggest that spawning is most likely to occur along the coast to the west of Port Phillip Bay over 100s of km (G. P. Jenkins unpubl.). Post-larval *S. punctata* recruit to shallow sub-tidal seagrass or reef/algae rather than unvegetated sand (Jenkins & Wheatley 1998). Studies using artificial seagrass indicate that characteristics of plant structure are much less important to recruitment than is the position of the seagrass bed within the bay (Jenkins et al. 1998a).

Entry of post-larvae to Port Phillip Bay tends to occur in pulses, and these events are associated with strong westerly winds and low barometric pressure, leading to coastal water level set-up and net water movement into the bay (Jenkins & Black 1994, Jenkins et al. 1997). Temporal variation in recruitment to individual seagrass beds in the southern area of Port Phillip Bay was highly positively correlated with arrival of passive

particles in models and negatively correlated with modelled wave height (Jenkins et al. 1997). Together, these factors explained $2/3$ of the temporal variation in recruitment (Jenkins et al. 1997). Studies of *Sillaginodes punctata* recruitment in Port Phillip Bay are facilitated by the fact that a transition in increment width occurs on otoliths at about the time of arrival in the bay (Jenkins & Black 1994, Jenkins & May 1994).

In the southern part of Port Phillip Bay, post-larval *Sillaginodes punctata* in the plankton showed a strong diel migration, moving towards the surface during daylight in contrast to a more random distribution ('nocturnal diffusion') at night (Jenkins et al. 1998b). There was also a slight but statistically significant trend for post-larvae to be higher in the water column on flood compared with ebb tides (Jenkins et al. 1998b). Daytime sampling at other sites confirmed that post-larvae were near the surface in daylight (Jenkins et al. 1998b).

The problem

We consider that recruitment of King George whiting into Port Phillip Bay provides an ideal opportunity to study the contribution of active and passive processes to larval transport.

The narrow entrance to Port Phillip Bay provides a point source for modelling of larval inputs. We have previously shown correlation between passive transport and recruitment of post-larval *Sillaginodes punctata* to seagrass beds, but our field data suggests strong vertical migratory behaviour. Does behaviour have a strong influence on dispersal of *S. punctata*? Our approach to this problem involves 2 major questions: (1) is there a strong correlation between predicted and actual post-larval abundances based on passive transport in Port Phillip Bay, and (2) is our ability to predict post-larval abundances enhanced significantly by the addition of behavioural attributes into the model?

MATERIAL AND METHODS

Sampling sites. Sampling was conducted approximately fortnightly from September to November in

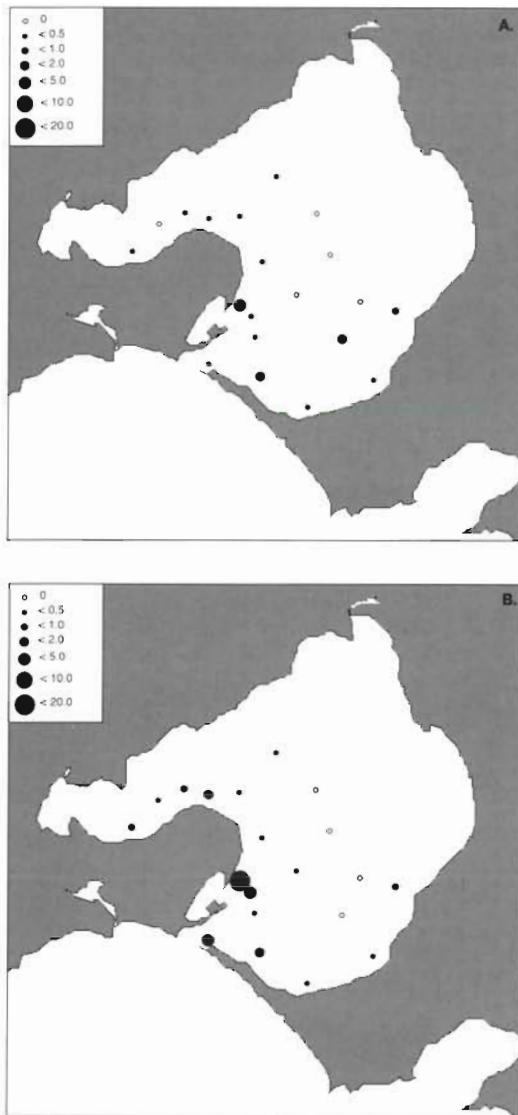


Fig. 2. *Sillaginodes punctata*. Average density (no. 1000 m⁻³) of post-larvae at 20 sampling stations in Port Phillip Bay. (A) 1994 and (B) 1995

1994 and 1995. In total, 20 sites were sampled in the central to southern region of Port Phillip Bay (Fig. 2). Sites were haphazardly placed in depths greater than 5 m but placed over an area expected to encompass a wide range of post-larval abundances. Sampling was conducted using 1 vessel in 1994 with western and eastern sites generally sampled on consecutive days. In 1995, 2 vessels sampled concurrently so that all sites were completed in a single day. Details of sites sampled are provided in Table 1

Sampling methods 1994. Post-larval *Sillaginodes punctata* were sampled with a plankton net of 1 mm² mesh and 4 m length, attached to a 0.8 × 0.8 m square frame. The towing cable was attached to a chain bridle attached to the top corners of the frame. A 16 kg depressor was attached to a chain bridle at the bottom of the frame. This configuration meant that the towing cable and bridles did not impinge on the mouth of the net. The towing speed was approximately 1 m s⁻¹, producing an angle of attack of the net of approximately 30° and an effective mouth area of 0.55 m². Estimates of volumes filtered were based on an Ocean Instruments mechanical flow-meter, calibrated before sampling and suspended in the mouth of the net.

A double-oblique tow of 20 min duration was made at each site. After fishing the top of the net at the surface for 1 min, 1 m of warp was let out per minute up to 9 m, and then the procedure was reversed. The wire angle of the warp to the vertical while towing was approximately 55° so that the maximum depth of the bottom of the net would have been approximately 6 m. When the net was on the surface, a combination of the davit arm extending from the side of the vessel and a circular tow path kept the net from being influenced by propeller turbulence and the vessel wake.

Sampling methods 1995. Some changes were made to the sampling protocol in 1995 based on the results from 1994. The size of the net frame was increased to 1 × 1 m so that the effective mouth area while fishing was approximately 0.9 m². Based on results of a study of the vertical distribution of post-larvae (Jenkins et al. 1998b), all samples after the first sampling date were surface samples.

Treatment of samples. Upon retrieval, the net was washed down with seawater, and the contents of the cod end emptied onto a 1 mm mesh sieve. The sieved material was immediately preserved in 95% ethanol. Ethanol was replaced within 6 h after the haul was made, and thereafter every 10 to 14 d until sorted.

Table 1. *Sillaginodes punctata*. Details of dates and sites for sampling in 1994 and 1995. Forward slashes separate sites sampled on individual dates

Sampling period	1994	Sites	1995	Sites sampled
1	15 Sep	1-10	7 Sep	1-20
2	21/22/23 Sep	11-20/1/2-10	27 Sep	1-20
3	28/29 Sep	1-10/11-20	4 Oct	1-20
4	5 Oct	1-10, 12	11 Oct	1-20
5	12/13 Oct	1-10/11-20	16 Oct	1-20
6	21 Oct	1-10	24 Oct	1-20
7	26/27 Oct	1-10/11-13, 17-20	31 Oct	1-2, 5-20
8	2/4 Nov	1-10/11-20	12 Nov	1-20
9	9 Nov	1-10	27 Nov	1-20
10	16 Nov	1-10		

Ichthyoplankton samples were sorted in a plastic tray under an illuminated magnifier (5× magnification). All *Sillaginodes punctata* post-larvae were separated out and counted. In 1995 we also collected and quantified the biomass (wet weight) of drifting seagrass/algae and scyphomedusae collected in the net.

Otolith analysis. Otoliths from post-larvae collected in 1995 were dissected from fish and examined under a compound microscope with attached video system using the techniques described by Jenkins & May (1994). Where necessary, grinding and polishing techniques were used to increase the resolution of increments. In many recruits, otoliths contained a transition in microstructure, signified by a rapid increase in increment width, that occurs at approximately the time of entry to the bay or inlet (Jenkins & Black 1994, Jenkins & May 1994, Hamer & Jenkins 1996). The number of increments counted outside the transition was subtracted from the date of capture to give the approximate arrival date of an individual to the bay, thus providing an estimate of the time period since the post-larvae entered the bay. Increment counts were done twice, the second reading blind with respect to the result of the first. If there was a discrepancy of more than 2 increments, a third reading was done. If all 3 readings differed as described, the otolith was rejected; if 2 of the counts were within the specified range, then the average of those 2 counts was used.

Numerical modelling. The circulation was depicted using a numerical, hydrodynamic model of Port Phillip Bay and the adjacent ocean of Bass Strait (Black et al. 1993, Black 1995). The model incorporated the important processes identified by analysis of current and sea level measurements. The 3-dimensional model incorporated full specification of the currents through the water column, with depth layer thicknesses from the surface set at 1, 3, 3, 3, and 50 m (maximum depth of Port Phillip: 25 m). The deep layer was set at 50 m to include the depth range outside Port Phillip Bay within the model grid. The model adjusts the deepest layer thickness in each model cell so that the measured depths are accurately reproduced. A high level of calibration against 3 yr of field data has been achieved (Black et al. 1993).

In the present study, a 400 m grid resolution was adopted with an open boundary placed 8 km south of the entrance in Bass Strait (Fig. 1). Tidal oscillations were obtained from records based on previous measurements at the model boundary in Bass Strait (Black et al. 1993). Low frequency (non-tidal) oscillations due to factors such as wind, barometric pressure and coastal-trapped waves were represented by using sea levels recorded at Point Lonsdale (Fig. 1) during the settlement period. Tidal analyses (Foreman 1977) were applied to remove the tidal component of sea level

oscillations at Point Lonsdale. Wind measurements from Point Cook (Fig. 1), recorded at 6 min intervals over the settlement period, were incorporated. Because the model uses actual rather than average conditions, it is capable of simulating the effect of high frequency events such as rapid changes in wind direction.

Dispersal of particles was simulated in a Lagrangian advection/diffusion particle model (Black et al. 1990, Black 1996). The hydrodynamic model solved the fluid flow equations to produce a grid of currents for calculation of the advection in the dispersal model, while diffusion was modelled as a Monte Carlo random walk (Black et al. 1990, Black 1996). Horizontal eddy diffusivity was set at 0.0015. Sensitivity testing of the horizontal eddy diffusivity showed that the general conclusions were not strongly affected by the choice of the eddy diffusivity coefficient; the advection of particles moving with the currents was more important.

The release point for particles was approximately 2 km south of the entrance to Port Phillip Bay, along a line extending 1.6 km east to west (Fig. 1). In total, 32 particles were released every 1 h from the start of the model run. Continuous release was chosen because spawning has been shown to be relatively continuous (Jenkins & May 1994), and previous simulations using continuous release have shown a good correlation with recruitment at sites in Port Phillip Bay (Jenkins & Black 1994, Jenkins et al. 1997). Simulations began at 00:00 h on 1 September, in both 1994 and 1995, and were run until November 30 of each year. Results were recorded spatially as the number of particles in cells over the model grid, and temporally, particles were recorded in 'boxes' superimposed on the model grid. One 'box' was located at the location of each sampling site. The number of particles in boxes was recorded at 30 min intervals, and the data are presented as the average number per 30 min recorded for a 2 d period centred at midday on the date corresponding to a field sampling day.

Particles were modelled to be randomly mixed through the water column, or alternatively, conforming to the average vertical distribution for each combination of day/night, ebb/flood found in our 1995 field study (Jenkins et al. 1998b). The field study showed strong 'reverse' diel migration with a weak tidal vertical migration, with post-larvae higher in the water column on flood tides, superimposed (Jenkins et al. 1998b). This vertical migration field data was obtained at a site of 8 m depth. Because sampling at deeper sites also showed post-larvae to be near the surface (Jenkins et al. 1998b), we kept the daytime depth distribution of post-larvae constant irrespective of water depth (that is, all particles in the model were confined to the upper 7 m of the water column and most were in the top metre). Conversely, because post-larvae at night were found to be dispersed through the water column

irrespective of depth (Jenkins et al. 1998b), we randomly mixed particles throughout the water column at night.

In a second series of simulations, a release point inside the bay at Portarlinton (Fig. 1) was adopted to test the influence of nearshore post-larval abundance on further penetration of passively dispersed post-larvae to the Grand Scenic site (Fig. 1) in the Geelong Arm. The 3-dimensional, 1.5 km square-grid model, modelling methods, field sampling and data analysis methods are described by Jenkins et al. (1997). These simulations were an attempt to explain the recruitment of post-larval *Sillaginodes punctata* in an area not predicted by the main model of Jenkins et al. (1997).

Data analysis. Post-larval abundances were converted to densities 1000 m^{-3} based on flowmeter readings. Linear regression was used to compare particle numbers with post-larval densities; both variables were $\log(x+1)$ transformed to normalise the residuals. A further variable, distance from the nearest point of the coast, was included in a stepwise multiple regression model. Cross-correlation was used to compare the temporal pattern of particle arrival with abundance of recruits at the Grand Scenic site in 1993. An adjusted sample size (n^*) based on the modified Chelton method (Pyper & Peterman 1997) was used in cross-correlation to adjust for the effect of autocorrelation in the time-series on significance levels. For modelling dispersal, it was necessary to specify a mortality coefficient for particles entering the bay. This was achieved by fitting an exponential curve to the frequency distribution of post-transition increment numbers on otoliths.

RESULTS

Although sample sizes in 1994 were smaller, the distribution of post-larvae was similar in the 2 years 1994 and 1995 ($r = 0.702$, $p < 0.001$). Highest post-larval abundances occurred close to the shore on the south-western coast, and significant numbers occurred at sites within the Geelong Arm, in both years (Fig. 2). There was a significant negative correlation with distance from shore in both years (1994: $r = -0.505$, $p = 0.023$; 1995: $r = -0.767$, $p < 0.001$). Winds over the sampling period in 1994 were predominantly westerly, but in 1995 were more variable, with significant periods of easterly winds (Fig. 3). Floating seagrass and algae were predominantly found at stations close to the western coast of the bay (Fig. 4A), and were significantly correlated with the abundance of *Sillaginodes punctata* post-larvae ($r = 0.629$, $p = 0.003$). Large concentrations of schyphomedusae, mainly *Cyanea capillata*, were collected, particularly in the Geelong Arm

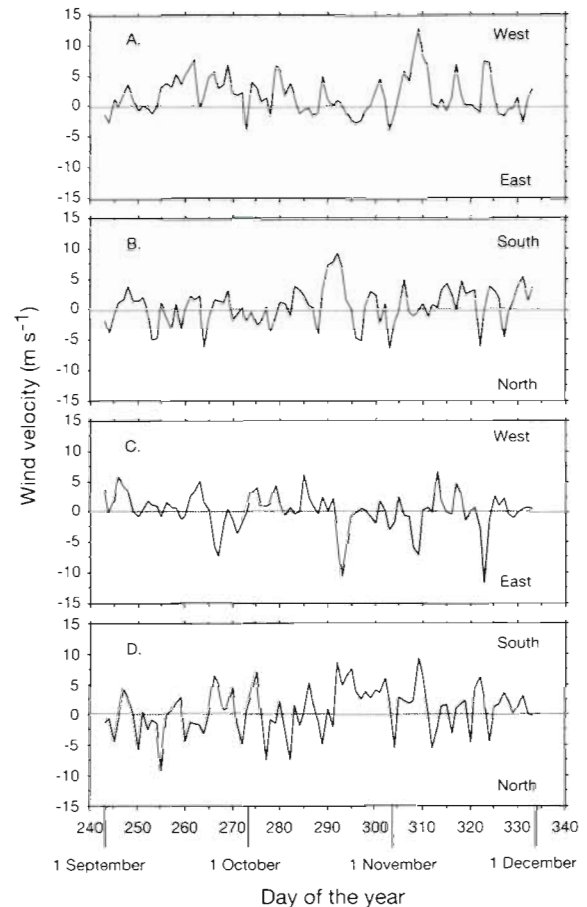


Fig. 3. Mean daily wind vectors over the sampling period. (A) East-west wind vectors, 1994, (B) north-south wind vectors, 1994, (C) east-west wind vectors, 1995 and (D) north-south wind vectors, 1995

(Fig. 4B) but there was no significant correlation between schyphomedusae and *S. punctata* post-larvae ($r = 0.442$, $p = 0.051$).

The frequency distribution of post-transition increment numbers on otoliths showed a large number of post-larvae with 0 increments, and a second peak at around 16 increments. The large number of post-larvae with 0 increments may partly have been due to an inability to distinguish low numbers of post-transition increments at the otolith edge from zero. To offset this problem, increment numbers were pooled into groups of 3 (Fig. 5). A second possibility was that the increment transition in some otoliths was not visible, even though the post-larva had been in the bay for a significant period. This error would tend to bias the mortality rate upwards. The uneven frequency distribution probably reflects the pulsed rather than continuous entry of post-larvae into the bay. The model parameter, T90, the time taken for 90% of the particles to die off, was set at 28 d in accordance with the measured exponential decay in ages. This seemed reason-

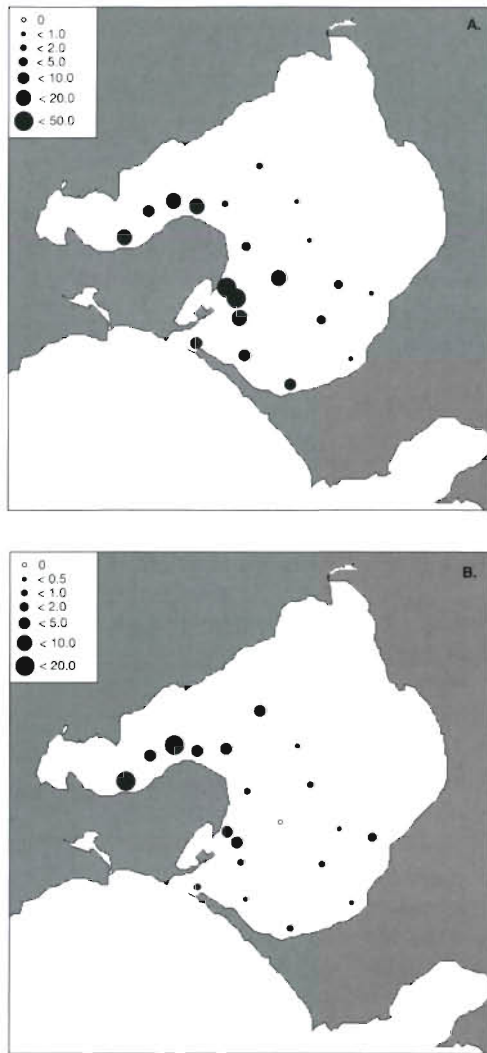


Fig. 4. Biomass (gm) of (A) seagrass/algae and (B) schyphomedusae at 20 stations in Port Phillip Bay sampled in 1995

able given that the maximum number of post-transition increments was approximately 40. Sensitivity testing showed that overall conclusions were not affected by varying the mortality coefficient.

The integrated distribution of particles at the end of each simulation showed a trend for particles in the passive case to stream up the east and west coast and for there to be relatively few particles in the centre of the bay (Figs. 6 & 7). A much greater spread of particles occurred in the simulations using vertical migration in 1994 (Fig. 6), in contrast to only a slightly greater spread in 1995 (Fig. 7). The distribution of particles showed a high correlation with post-larval abundances in 1995 with a similar amount of variation explained in each case (Table 2). In contrast, variation in post-larval abundance explained in 1994 was highest in the passive case, intermediate in the active case and was

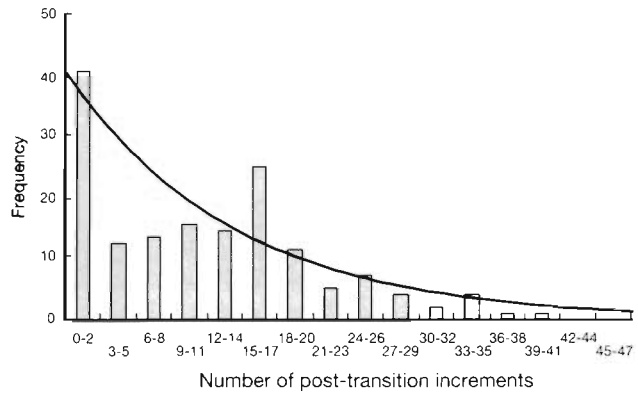


Fig. 5. *Sillaginodes punctata*. Frequency distribution of post-transition increments on otoliths of post-larvae collected from 20 stations in Port Phillip Bay in 1995. Frequencies are averaged over 3 d intervals and the fitted mortality curve is superimposed

lowest for the day/night case (Table 2). The regression in the day/night case for 1994 was not statistically significant (Table 2). Overall, correlations were lower in 1994 compared with 1995 (Table 2).

In general, post-larvae appeared to be distributed closer to shore than predicted by the models, and a combination of the 1995 particle distributions and distance from shore gave an r^2 of approximately 70% (Table 3). This 'near-shore' phenomenon would appear to partly explain our inability to predict the temporal pattern of recruitment at a site deep within the Geelong Arm for recruits collected in 1993. Using the same numerical model, but seeding it close to shore at the entrance to the Geelong Arm (Fig. 8), we find a close

Table 2. *Sillaginodes punctata*. Regression equations comparing numbers of model particles (P) with density of larvae (L) collected from 20 sampling sites in Port Phillip Bay

Comparison	Equation	p	r ²
1994			
Passive	$P = 1.17 \cdot L + 0.64$	0.002	0.43
Tidal/diurnal	$P = 1.13 \cdot L + 0.69$	0.009	0.32
Diurnal	$P = 1.01 \cdot L + 0.89$	0.065	0.18
1995			
Passive	$P = 1.40 \cdot L + 0.65$	<0.001	0.58
Tidal/diurnal	$P = 1.57 \cdot L + 0.49$	<0.001	0.53
Diurnal	$P = 1.75 \cdot L + 0.67$	<0.001	0.58

Table 3. *Sillaginodes punctata*. Stepwise regression equation comparing numbers of model particles (P) and distance from shore (D) with density of larvae (L) collected from 20 sampling sites in Port Phillip Bay in 1995

Equation	p	r ²
$P = 0.98 \cdot L - 0.06 \cdot D + 1.52$	<0.001	0.68

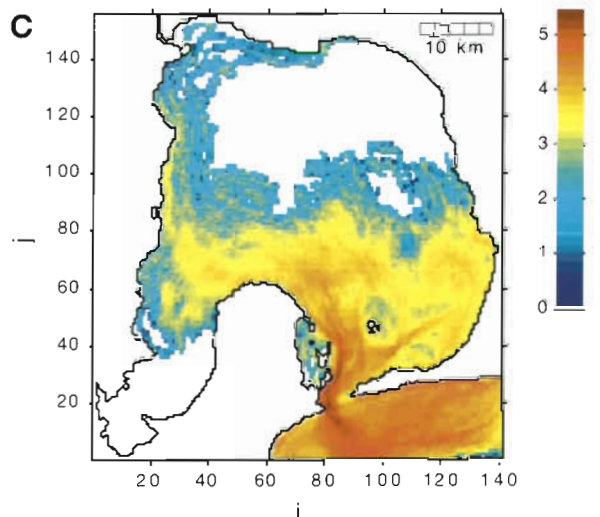
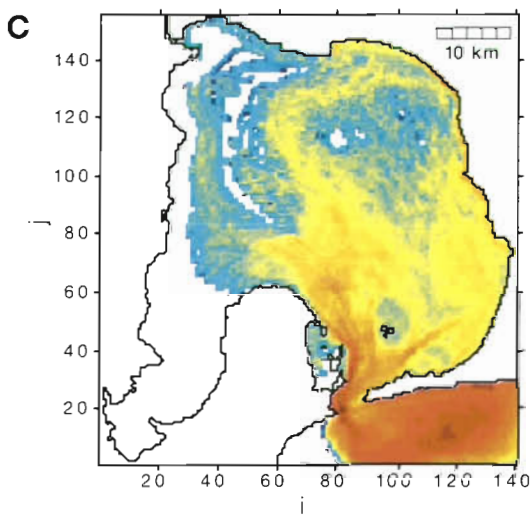
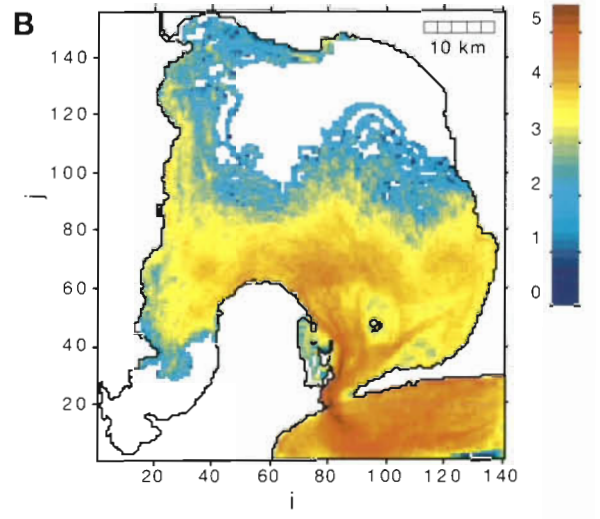
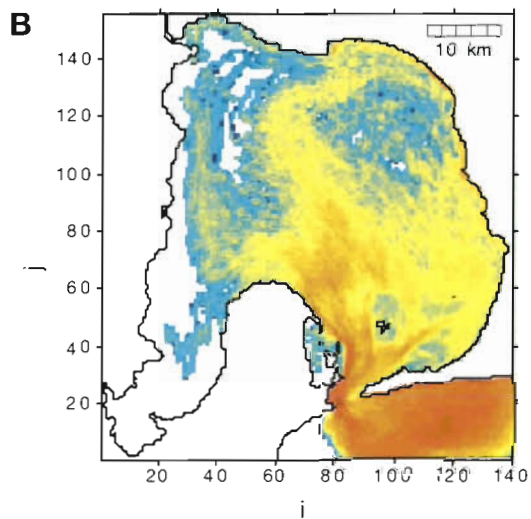
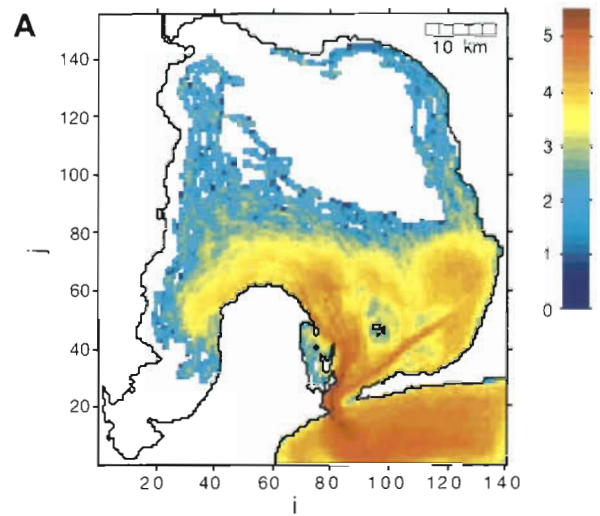
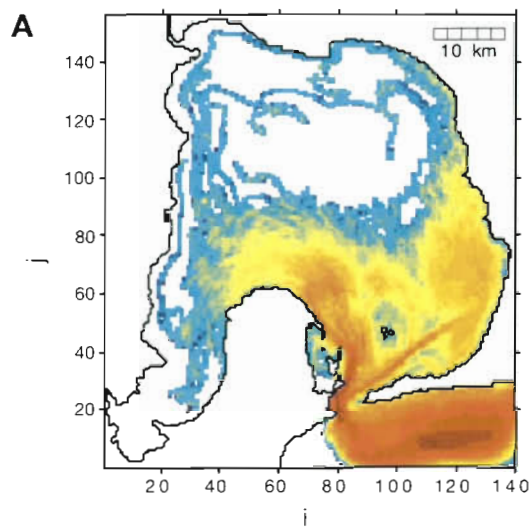


Fig. 6. Integrated log particle number at the completion of (A) passive, (B) tidal/diurnal, and (C) diurnal simulations for 1994

Fig. 7. Integrated log particle number at the completion of (A) passive, (B) tidal/diurnal, and (C) diurnal simulations for 1995

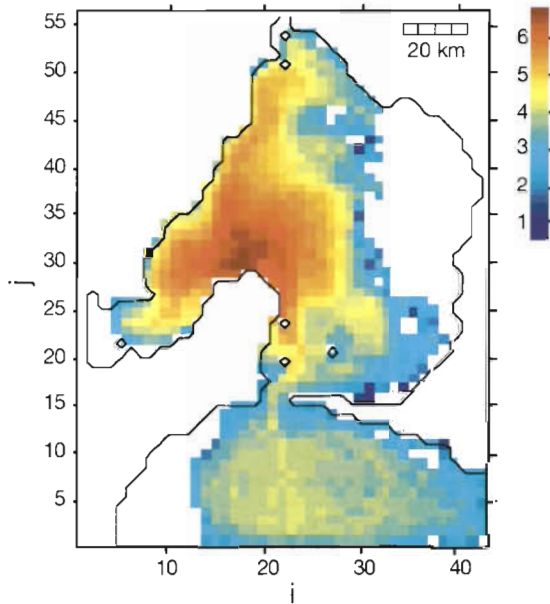


Fig. 8. Integrated log particle number at the completion of a passive dispersal model simulation with particles released at Portarlington

match between predicted particle arrival at Grand Scenic and the actual recruitment pattern using passive dispersal (Fig. 9), with a significant cross correlation ($n^* = 9$, $r = 0.81$, $p < 0.05$).

DISCUSSION

Numerical models of current patterns and dispersal were capable of predicting the spatial distribution of post-larval King George whiting with a high degree of accuracy. This is the first time we have tested the capacity of the hydrodynamic model to predict spatial distribution of young stages of *Sillaginodes punctata*. Previously we have found a similar level of correlation

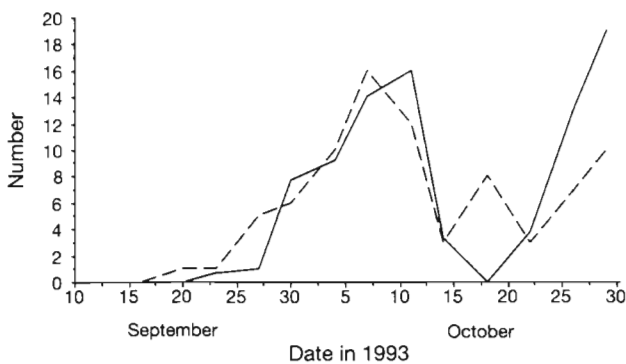


Fig. 9. Number of model particles recorded (solid line) and the total number of *Sillaginodes punctata* collected in 4 seine hauls (dashed line) over 3 or 4 d intervals at the Grand Scenic site in Spring 1993

for temporal variation in the predicted arrival of passive particles compared with recruitment of post-larval *S. punctata* to seagrass beds on the western side of Port Phillip Bay (Jenkins & Black 1994, Jenkins et al. 1997). Our studies of temporal variability in recruitment involved only 3 sites and did not allow a strong assessment of our ability to predict spatial distribution (Jenkins et al. 1997). The ability to predict spatial variation is very important as it may allow important areas of habitat to be identified on the basis of the hydrodynamic model. Importantly, in this study we have shown a strong correlation between the hydrodynamic model prediction and the distribution of post-larvae in the plankton. In previous studies we have concentrated on post-larvae that had recruited to seagrass (Jenkins & Black 1994, Jenkins et al. 1997), and had to make the assumption that the particle-dispersal model results were a reflection of the planktonic distribution of post-larvae prior to arrival at seagrass beds.

The overall level of correlation between the hydrodynamic model and the field results was lower in 1994 compared with 1995. Results of vertical migration studies in 1995 (Jenkins et al. 1998b) led to a change in sampling strategy from oblique tows in 1994 to surface tows in 1995. The lower proportion of variation in post-larval distribution explained in 1994 may be partly related to the lower sampling efficiency and smaller sample size of post-larvae due to oblique tows and the smaller net opening, and also the lower intensity of sampling for some stations on the eastern side of the bay.

The addition of vertical migratory behaviour (Jenkins et al. 1998b) to modelling did not improve predictions of dispersal in 1995 and led to a decrease in predictive capacity in 1994. The greater relative difference in predictions between the passive and behaviour simulations in 1994 compared with 1995 would not easily be explained by the change in sampling strategy. The changes in correlation relate to the spread of particles in the surface boundary layer which is responsive to prevailing wind conditions. The surface boundary layer was represented by the 1 m thick surface layer in the model, equivalent to the layer sampled by the net when at the surface. In 1995, the prevailing winds did not lead to strong net movements of the surface boundary layer compared to the overall water column, and particle distributions for the active and passive cases were similar, both cases showing a similar correlation with post-larval spatial distribution. However, in 1994, dominant westerlies had a stronger influence on particles in the surface boundary layer compared to the passive case, but this was not reflected in the sampled distribution of post-larvae. The results suggest that post-larvae are less influenced by the surface boundary layer than is suggested by the

simulations including behaviour, and behave more like particles randomly mixed through the water column, not predominantly subjected to the higher wind-driven currents near the surface. This result contradicts that of Bertness et al. (1996) showing a strong influence of wind-driven currents on barnacle dispersal in a temperate bay.

One explanation for this lack of influence of behaviour would be that our vertical migration study was carried out largely at 2 sites near the entrance to the bay and cannot be extrapolated to Port Phillip Bay in general. Larval behaviour can change markedly from the oceanic to the bay or estuarine environment (Forward et al. 1996, 1997) and can also vary between sites within an estuary (Forward et al. 1998). Behaviour can change in response to chemical cues in estuarine versus offshore waters (Forward et al. 1996). Hence, it is possible that behaviour of *Sillaginodes punctata* post-larvae changes deeper into the bay. Another possibility is that behaviour may vary with wave conditions, because sampling was generally done in relatively calm conditions. Strong winds and associated rough conditions could lead to larvae being passively mixed deeper or actively avoiding the surface, as has been demonstrated for herring larvae (Heath et al. 1988). Thus, in strong wind conditions post-larvae would act more like 'passive' particles. Finally, behaviour was only measured in 1995, and therefore interannual differences in behaviour might explain why the greatest discrepancy between model predictions incorporating behaviour and actual distribution was in 1994. It is possible that differences in prevailing weather conditions between years meant that behaviour in 1994 was different from 1995.

The tidal component of behaviour appeared to have little influence compared to diel movements in 1995 but did lead to an improved predictive capacity of the model over averaged 'day/night' behaviour in 1994 (albeit still lower than the passive case). Jenkins et al. (1998b) found that the dominant form of vertical migration was 'reverse' diel, and suggested that this was related to visual feeding near the surface in the daytime. A very small component of the overall variation involved a tidal 'migration' where post-larvae were slightly higher in the water column in flood tides. Jenkins et al. (1998b) suggested that this variation may have been due to local physical or environmental conditions rather than an entrained behaviour. For example, flood-tide currents are stronger than ebb-tide currents at the main sampling site for behavioural studies (Black unpubl. data), and this is likely to influence the vertical distribution of *Sillaginodes punctata* post-larvae. The evidence suggests that behaviourally based 'selective tidal transport' is not occurring in post-larvae of this species.

Apart from spatial and temporal variation in vertical migratory behaviour, there are other possible explanations for the 'passive' pattern of post-larval dispersal in the face of evidence of vertical migration, and also for the fact that post-larvae tend to be closer to shore than predicted by passive dispersal. It is possible that other forms of behaviour, not measured in our studies to date, are negating the effects of surface wind transport. Post-larvae may show horizontal as well as vertical orientation. An example of this would be if post-larvae were actively swimming toward shore. Post-larvae that had recently arrived at seagrass beds, and were at a similar stage of development to those sampled offshore in our study, were capable of maintaining an average swimming speed of 6 cm s^{-1} over a 2 h trial (Welsford 1996). Using directed swimming, post-larvae could reach the shore in a matter of days at considerably lower average speeds than this. Such a mechanism has been invoked to explain the near-reef distributions of reef fish post-larvae (Wolanski et al. 1997) based on the fact that these larvae are powerful swimmers (Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997), and their swimming can be directional (Leis et al. 1996). Beckley (1985) has suggested that post-larval fish may swim towards shallow banks with weak currents once transported into an estuary on the flood tide. Such active horizontal movement might offset the effects of surface water movement offshore. A variation on horizontal swimming behaviour which would influence spatial distribution would be association with floating seagrass and algal debris (Kingsford 1993). Previous studies have shown that pre-settlement larvae of some species preferentially associate with floating plant debris and this may be a mechanism for shoreward transport (Kingsford & Milicich 1987).

Another form of behaviour that might influence the spatial distribution of post-larvae is 'temporary' settlement and resuspension. A number of studies have now shown that post-larval transport can occur when primary settled individuals are resuspended (physically or behaviourally) into the water (Rijnsdorp et al. 1985, Olivier et al. 1996, Thiebaut et al. 1996, Wang & Xu 1997). Evidence from our previous study on temporal variability in recruitment suggests that post-larvae arriving at seagrass beds near the entrance to Port Phillip Bay may remain there during calm periods, but are resuspended and transported away (or alternatively killed) in rough conditions (Jenkins et al. 1997). Such a process might lead to a concentration of 'resuspended' post-larvae near the coast-line because rough periods would coincide with onshore winds. Thus, an alternative explanation for the association with drifting seagrass and algae would be that both were resuspended and transported away from nearshore habitats in rough conditions.

A reason not related to behaviour for the apparent lack of effect of surface transport on post-larval distribution is that the model's 400 m grid resolution may not be high enough to characterise a narrow coastal boundary layer that would tend to trap post-larvae near the shore, and may allow transport in a different direction to the main body of offshore water. Increased model resolution may allow the simulation of additional entrainment into eddies associated with coastal headlands, and entrainment into protected intertidal and shallow sub-tidal environments.

Finally, conclusions of this study depend on the ability of vertically stratified plankton sampling to accurately represent the vertical distribution of post-larval *Sillaginodes punctata*. The observation that some post-larval coral reef fish have an escape response of swimming to the surface (Leis & Carson-Ewart 1998) suggests a mechanism whereby catches could be biased to a surface net due to a behavioural response.

The observed distribution of post-larvae may explain our previous inability to predict recruitment deep within the Geelong Arm (Jenkins et al. 1997). Results of our field study show that post-larvae are closer to shore than the model predicts. When a release point was positioned close to the shore near the entrance to the Geelong Arm, an accurate prediction of recruitment deep within the arm was obtained. We have used this release point as an example of what would happen to further dispersal into the bay if particles in the model are moved closer to shore as indicated by field data. Thus, the process leading to the nearshore distribution of post-larvae may be crucial to understanding recruitment of King George whiting to seagrass in Port Phillip Bay. Once again, a high degree of correlation was obtained when post-larvae were modelled as 'passive' particles.

In conclusion, a numerical hydrodynamic model of passive particle transport gave a high correlation with the actual distribution of post-larvae, suggesting that spatial distribution of post-larvae in Port Phillip Bay reflects passive advection with post-larvae well mixed through the water column. The prediction was almost identical in simulations involving well-mixed (passive) particles, and particles mimicking the vertical migratory behaviour previously observed near the entrance to the bay in 1995, and was higher than 'active' simulations in 1994. Simulated advection of particles in the surface boundary layer in 1994 was not mirrored by post-larval distribution. Post-larvae were slightly closer to shore than predicted by the models. Possible explanations for these discrepancies include: other behaviours, such as directed horizontal swimming or association with floating seagrass or algal debris; temporary settlement and resuspension of post-larvae on shallow seagrass beds leading to a concentration gradient near-

shore; and a need for higher resolution modelling, to better represent the narrow coastal boundary layer. The finding that spatial distribution of post-larvae is best represented by 'passive' dispersal of post-larvae is consistent with our previous studies showing a strong correlation between input of passively predicted particles and temporal variation in recruitment to seagrass beds (Jenkins & Black 1994, Jenkins et al. 1997).

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