Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctata* in relation to feeding and vertical distribution of prey in a temperate bay

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ABSTRACT: Vertically stratified sampling was undertaken for pre-settlement King George whiting *Sillaginodes punctata* at 1 site in 1995 and 4 sites in 1996, in Port Phillip Bay, Australia. In 1995, 3 depth strata were sampled: surface, 2.5–3.0 m, and 5.0–5.5 m, in a total water depth of 7 to 8 m. Sampling was conducted on 17 dates and encompassed all combinations of day and night, and ebb and flood tide. A total of 3, or in one case 4, replicate samples were taken at each depth. On 4 occasions a smaller zooplankton net was deployed at the same time as the ichthyoplankton net. Pre-settlement *S. punctata* showed 'reverse' diurnal vertical migration, with concentration near the surface during the day and diffusion through the water column at night. A much weaker tidal migration was also detected, with larvae slightly higher in the water column on flood tides. Pre-settlement *S. punctata* only fed in daylight and zooplankton taxa that were eaten did not show vertical stratification during daytime. In 1996, 4 sites were sampled at a minimum of 10 m depth, and an additional depth stratum, 7.5–8.0 m, was sampled. Smaller numbers of larvae were collected in 1996 compared with 1995. All larvae collected in daytime were in the surface stratum, whilst at night larvae were spread through the water column. Although diurnal vertical migration was not a response to prey migrations, daytime ascent of larvae may have occurred to find adequate light levels for visual predation. The generality of tidal migration is unclear, and may have been a result of local factors. Both diurnal and tidal migration would be expected to strongly influence transport of pre-settlement *S. punctata* to seagrass beds in Port Phillip Bay.

KEY WORDS: Vertical distribution · Diurnal vertical migration · Pre-settlement fish · Selective tidal transport · *Sillaginodes punctata*

INTRODUCTION

Many marine organisms have a bipartite life-cycle where a dispersive larval stage separates benthic adults in space and time. Variability in dispersal due to variation in planktonic processes such as larval duration, mortality, regional hydrodynamics, and larval behaviour may lead to spatio-temporal patchiness in recruitment. Thus, understanding the dynamics operating on larvae may, in turn, lead to a greater understanding of the causes of variability seen in, and enhance predictive models of, marine populations.

At the simplest level, dispersal may be considered to be a function of the hydrodynamic regime under which larvae exist, and the time the larva spends in the plankton (Scheltema 1986). This approach may be reasonable in some cases, such as in small, slow swimming, neutrally buoyant larvae of molluscs (McShane et al. 1988) and starfish (Black & Moran 1991). However, for groups with actively swimming, behaviourally complex larvae such as decapods and fish, behaviour
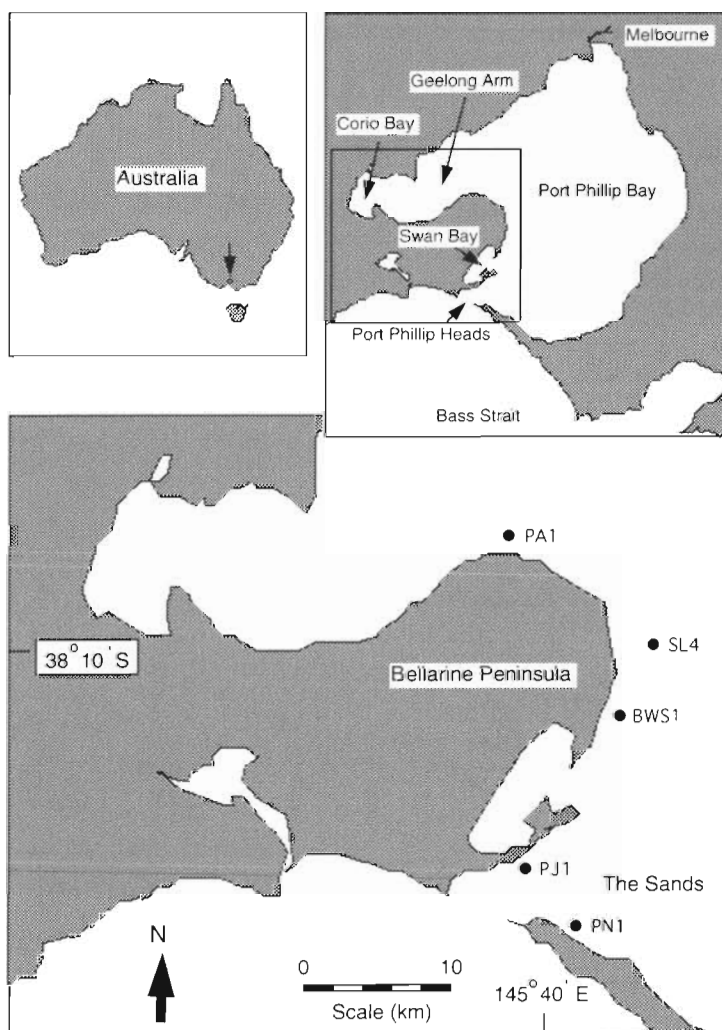
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Fig. 1 Sampling sites in the Bellarine Peninsula region of Port Phillip Bay, Victoria, Australia. Insets: location of the Bellarine Peninsula in Port Phillip Bay and location of Port Phillip Bay on the Australian coast

dispersal-time relationship (Keough & Black 1996).

The most commonly recognised form of vertical migration is 'diurnal vertical' or 'nocturnal' migration where plankters distribute at the surface at night and migrate deeper during the day (Hutchinson 1967, Haney 1988); however, 'reverse' diurnal migration where animals move downward at night and upwards during the day is also common (Haney 1988, Chae & Nishida 1995). A range of vertical migratory behaviours has been recorded between these extremes (Haney 1988) and a full range of migratory behaviour can be expressed in the same population (Ohman 1990). Fish larvae also show a range of vertical migratory behaviour (Neilson & Perry 1990), from nocturnal ascent (Smith et al. 1978, Kendall & Naplin 1981, Boehlert et al. 1985) to nocturnal descent (Boehlert et al. 1985, Yamashita et al. 1985, Sogard et al. 1987, Davis et al. 1990, Heath et al. 1991, Lyczkowski-Shultz & Steen 1991). In fish larvae, diel differences often tend to result from distinct depth preference during the day in comparison with random distribution at night or 'nocturnal diffusion' (Brewer & Kleppel 1986, Davis et al. 1990, Leis 1991, Haldorson et al. 1993).

One form of vertical migration that has great potential to influence dispersal, and particularly recruitment to nearshore habitats, is a form of tidal vertical migration — selective tidal transport (Boehlert & Mundy 1988, Neilson & Perry 1990). Migration to nearshore habitats may be facilitated by orientation near or on the bottom during ebb tides and rising into the water column on flood tides (Creutzberg 1961, Holt et al. 1989, Rowe & Epifanio 1994). There is also commonly an interaction with diurnal changes; for example, larvae may be found higher in the water column on nighttime, flood tides (Weinstein et al. 1980, Rijnsdorp et al. 1985).

The King George whiting Sillaginodes punctata (Perciformes: Sillaginidae) is an important commercial and recreational fish species in southern Australia (Kailola et al. 1993). Adult fish live in coastal waters, spawning offshore in autumn and early winter (Jenkins & May 1994). The duration of the larval stage is long and variable, ranging from 80 to 170 d, and larvae reach a size of 15 to 20 mm (Jenkins & May 1994, Fowler & Short 1996). In spring, late-stage larvae enter shallow bays and inlets containing their juvenile habitat, shallow macrophyte beds (Jenkins et al. 1996).

would be expected to modify the pattern predicted for the 'passive' case.

The most obvious and well studied form of larval behaviour that might influence dispersal is vertical migration (Hutchinson 1967, Haney 1988). Vertical migration has great potential to influence horizontal dispersal because horizontal current profiles vary with depth and, within a moderate horizontal current, residual vertical advection may be as little as 0.01 cm s^{-1} (Mileikovsky 1973). This may be compared with typical horizontal currents of a few cm s^{-1} up to extremes of several m s^{-1} as encountered in tidal jets (Kingsford 1990, Black et al. 1993). Thus, even weak swimming larvae may be capable of vertical movement between strata of different horizontal current speeds and possibly direction, and therefore may generate noise in any

Some success has been achieved in modelling the temporal variability in transport of whiting larvae to Port Phillip Bay (Jenkins & Black 1994), and their supply to juvenile habitats within the bay (Jenkins et al. 1996, Jenkins et al. 1997). The modelling includes passive horizontal advection and random vertical movement of particles (Black et al. 1993). In order to develop a more realistic model of larval dispersal, incorporation of any significant behavioural attributes is required. In the present study, we investigate the patterns of vertical distribution of late-stage larvae of *S. punctata* in relation to time of day and tidal phase in Port Phillip Bay. For 1 site, we compared vertical distributions of larvae between night and day and tidal phases, and then sampled additional sites to test whether vertical migration was consistent spatially. We also investigate the vertical distribution of potential food organisms to test whether vertical stratification of prey might influence any patterns observed.

MATERIAL AND METHODS

Study area. Port Phillip Bay is a large, semi-enclosed, predominantly tidal embayment linked to the oceanic waters 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} at about the entrance to the Geelong Arm. Tides are semidiurnal and the range inside the bay is less than 1 m.

The sampling site in 1995 (BWS1) was in the Sands region of Port Phillip Bay close to the western shoreline (Fig. 1). The site was located in a minor channel (Coles Channel) of approximately 7 to 8 m depth, depending on tide, and with an average width of approximately 200 m. The site was chosen because it had consistently yielded high abundances of pre-settlement *Sillaginodes punctata* over 3 yr of sampling (G. Jenkins unpubl. data). In 1996, sampling was conducted at 4 sites that were at least 10 m in depth (Fig. 1), to test the consistency of vertical distribution patterns in space.

All sites were in the 'exchange' zone where there is considerable exchange of water with Bass Strait (Anonymous 1973). Thus, the salinity was essentially marine, water temperature was similar to Bass Strait (12 to 16°C over the sampling period), and turbidity was relatively low but increased episodically due to runoff or strong winds. No strong stratification occurs in this zone in the spring period (Black et al. 1993).

Ichthyoplankton sampling methods. In 1995, sampling for *Sillaginodes punctata* larvae was conducted on 17 dates between 12 September and 16 November. Sampling excursions were chosen to encompass all combinations of day and night, and ebb and flood tides (Table 1). On each sampling date, 3 hauls were made at each of 3 depths: surface (top of net just under surface), mid (top of net 2.5 to 3.0 m below surface) and bottom (top of net 5.0 to 5.5 m below surface). Three

Table 1. *Sillaginodes punctata*. Total number and mean density with respect to depth for sampling in 1995. N: number of replicate hauls per depth. S: surface; M: mid; B: bottom

Date	Diurnal-tidal state	N	Number			Mean density per haul (no. 1000 m^{-3})		
			S	M	B	S	M	B
12 Sep	Day-flood	3	17	2	0	11.85	1.39	0
15 Sep	Day-flood	3	28	1	0	18.05	0.67	0
19 Sep	Day-ebb	3	4	1	0	2.75	0.63	0
22 Sep	Day-ebb	3	4	5	0	2.80	3.33	0
26 Sep	Day-flood	3	18	0	0	13.0	0	0
27 Sep	Night-ebb	3	32	43	27	21.64	28.62	18.01
2 Oct	Day-ebb	3	1	0	0	0.66	0	0
4 Oct	Night-ebb	3	23	23	44	14.76	14.94	28.31
6 Oct	Night-flood	3	69	26	32	31.84	19.52	21.62
8 Oct	Night-flood	3	14	6	2	10.40	4.27	1.33
15 Oct	Night-ebb	3	45	45	213	34.35	32.13	150.17
18 Oct	Day-ebb	3	19	5	1	13.33	3.35	0.63
24 Oct	Night-flood	4	42	25	33	21.54	13.50	16.12
26 Oct	Day-flood	3	74	1	0	62.37	0.69	0
3 Nov	Day-ebb	3	55	5	1	39.40	3.42	0.71
8 Nov	Day-flood	3	9	1	0	8.13	0.97	0
16 Nov	Day-ebb	3	28	0	0	21.40	0	0

replicate hauls were made at each depth, except on 24 October when 4 hauls were made. Replicates alternated amongst the 3 depths, with the order of alternation chosen haphazardly on each separate sampling excursion. Sampling began within 0 to 3 h of the beginning of the respective tidal phase. When sampling at night, sampling began within 0 to 3 h of the onset of darkness. The total sampling period was approximately 4.5 h.

In 1996, sampling was conducted on 11 dates between 17 September and 12 November, spread across 4 additional sites (Table 2). The sampling protocol was the same as in 1995 but with an additional depth stratum sampled (top of net 7.5 to 8.0 m below surface). Sampling was conducted during daylight with the exception of 2 night sampling trips at site PJ1 (Table 2). Unlike 1995, sampling was random with respect to tidal flow.

For ichthyoplankton sampling, a plankton net of 1 mm^2 mesh and 4 m length was attached to a 1 × 1 m square frame. The towing cable was attached to a chain bridle attached to the top corners of the net frame. A 16 kg depressor was attached to a chain bridle on the bottom of the net. 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 0.9 m^2. Estimates of volumes filtered were based on a General Dynamics mechanical flow-meter, calibrated before sampling and suspended in the mouth of the net.

Each of the replicate samples involved fishing the net for 15 min at the chosen depth. The depth of the net was estimated from the length of towing cable and the angle of the cable (approximately 55° to the horizontal). The depth of the net was checked a number of times during each tow by sending a messenger weight down to the net with a mechanical depth gauge attached that measured maximum depth. The length of cable deployed was adjusted to achieve the correct depth where necessary. Methods for deploying the net were designed to minimise cross-contamination amongst sampling strata. For mid and bottom tows the net was lowered to the required depth with the vessel stationary, and then further cable was let out while the boat accelerated to towing speed and the predetermined length of cable was deployed. The timing of the tow began when the vessel started accelerating. The boat was stopped for net retrieval. Net deployment and retrieval took no more than 1 min for the deepest hauls. For surface hauls, 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.

Zooplankton sampling methods. Zooplankton sampling was conducted concurrently with the ichthyoplankton sampling on the final 4 days of sampling in 1995 (Table 1). Samples were collected with a 253 μm plankton net attached to a 30 cm diameter ring. Estimates of volumes filtered were based on an Ocean Instruments mechanical flow-meter, calibrated before sampling and suspended in the mouth of the net. Consecutive zooplankton hauls of 2 min duration were taken at 4 and 11 min after the beginning of the ichthyoplankton tows. The bridle of the zooplankton net was clipped to the tow cable of the ichthyoplankton net. Upon release, it ran down the cable to deploy above the top edge of the ichthyoplankton net. The zooplankton net was deployed and retrieved manually by its tow line. To avoid contamination during deployment and retrieval, a second line was looped around the collar of the net, which closed off the cod end. The loop was released when the net was in position.

Table 2. *Sillaginodes punctata*. Total number and mean density with respect to depth for sampling in 1996. N: number of replicate hauls per depth. S: surface; M: mid; D: deep; B: bottom

Site	Date	Diurnal state	N	Number				Mean density per haul (no. 1000 m^{-3})			
				S	M	D	B	S	M	D	B
PJ1	17 Sep	Day	2	2	0	0	0	1.58	0	0	0
PJ1	2 Oct	Day	2	6	0	0	0	2.51	0	0	0
PJ1	13 Oct	Day	3	7	0	0	0	2.43	0	0	0
PJ1	20 Oct	Night	3	6	8	8	10	2.32	3.07	3.27	4.14
PJ1	21 Oct	Night	3	0	0	2	2	0	0	0.85	0.90
PJ1	12 Nov	Day	3	0	0	0	0	0	0	0	0
SL4	23 Sep	Day	2	0	0	0	0	0	0	0	0
PN1	27 Sep	Day	2	4	0	0	0	4.58	0	0	0
PA1	8 Oct	Day	3	1	0	0	0	0.62	0	0	0
PA1	25 Oct	Day	3	1	0	0	0	0.39	0	0	0
PA1	31 Oct	Day	3	0	0	0	0	0	0	0	0

Treatment of samples. Upon retrieval, the nets were washed down with seawater, and the contents of the cod end emptied onto a sieve (1 mm mesh for ichthyoplankton, 253 µm for zooplankton). The sieved material was immediately preserved in 95% ethanol. Ethanol was replaced within 6 h from when the haul was made, and thence every 10 to 14 d until sorted.

Ichthyoplankton samples were sorted in a plastic tray under an illuminated magnifier (5× magnification). All *Sillaginodes punctata* larvae were separated out and counted. *S. punctata* larvae from ichthyoplankton samples taken concurrently with zooplankton sampling had their gut contents analysed. The guts of specimens from 4 night-time sampling trips (6, 8, 15 and 24 October 1995) were also analysed. Specimens were placed in a drop of glycerol on a microscope slide, and the entire length of the gut was dissected from the specimens using electrolytically sharpened tungsten needles. Prey items were counted and identified to the lowest taxonomic level possible (generally Order or Suborder).

Zooplankton samples were stained with Rose Bengal and then sorted under a binocular dissecting microscope. Plankters were generally identified to Order or Suborder, and to developmental stage for larval forms. When more than approximately 150 of the more common taxa were present in a sample, the sample was halved once or more using a Folsom plankton splitter. The resulting subsample was sorted, and the remainder proportionally assigned to the groups present. The smallest subsample sorted was 1/32.

Data analysis. Abundances of *Sillaginodes punctata* were standardised to number per 1000 m^3 (mean volume sampled was 477 m^3) and plankton abundance data were standardised to number per m^3. Box and probability plots of *S. punctata* and zooplankter abundance data and model residuals were examined to assess normality and homogeneity of variance in the data. These plots showed a need for $\log(x + 1)$ transformation. Proportions of larval densities were also analysed to reduce the influence of day to day variation in abundance; these data were arcsine transformed. To satisfy the assumptions of analysis of variance of *S. punctata* densities in 1995 it was necessary to omit the data from 2 October, because only 1 larva was collected on this date.

Variation in density of *Sillaginodes punctata* was analysed with a partially nested design, with day nested within time of day and tide, and orthogonal with depth. Replicates were averaged to simplify the analysis as they were used to test only the day by time of day by depth by tide interaction, in which we had little interest. For the analysis of proportions, the data for the middle layer were omitted, so the means were not limited to a sum of 1.0 (which would make the data

non-independent). For the zooplankton data, 4 taxa were chosen for analysis: copepods, decapod zoeae, carid myses and euphausiid calyptopes. A similar partially nested analysis was performed on these log-transformed densities, with day nested within tide and orthogonal with depth. Time of day, tide and depth were treated as fixed factors while day was treated as a random factor. Variance components were approximated using the method described by Sokal & Rohlf (1981). Statistical analyses were carried out with the Systat 5.2 computer programs (Wilkinson et al. 1992).

To determine the relative importance of each prey type in the diet of the larvae dissected, an index was calculated that was the product of F (percent frequency of occurrence in larval guts) and N (percent of total number of items in the diet) (Govoni et al. 1983). This index was compared across the 4 sampling days.

RESULTS

A total of 1024 *Sillaginodes punctata* larvae were collected at BWS1 in 1995 (Table 1). Abundance of *S. punctata* larvae varied significantly with depth and time of day, with larvae concentrated near the surface during daylight but showing a relatively even distribution at night (Table 3, Fig. 2). The interaction of depth and time of day was also significant when proportions of larvae in the surface and bottom samples were analysed (Table 4, Fig. 3). There was no significant interaction between depth and tide when abundance data was analysed (Table 3), but there was a significant interaction when between-day variation in abundance was removed by analysing proportions, with larvae significantly closer to the surface on flood tides (Table 4, Fig. 3). Approximate variance components, however, indicated that the depth by tide interaction only explained 6% of the total variance, compared with 57% for the interaction between time of day and

Table 3. *Sillaginodes punctata*. Partially nested analysis of variance of log-transformed density of pre-settlement individuals with respect to depth, day/night and tide over 16 sampling dates

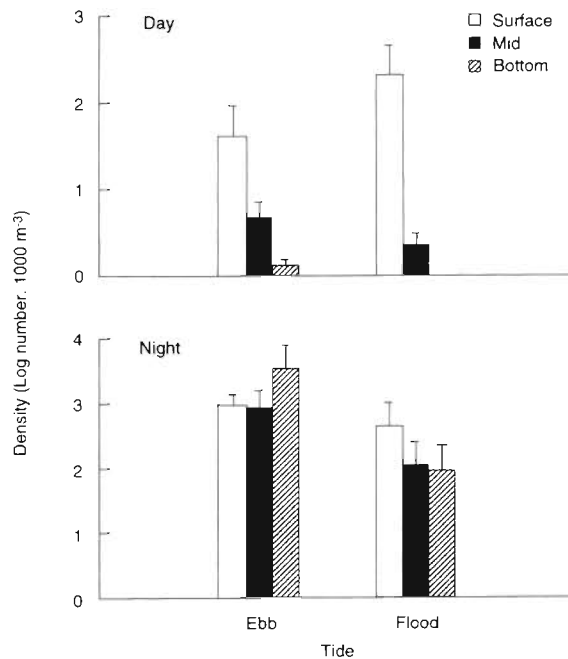| Source	df	MS	F	p
Day/night	1	37.60	40.63	<0.001
Tide	1	2.98	3.22	0.098
Day/night × Tide	1	2.40	2.59	0.133
Day(Day/night × Tide)	12	0.93	2.90	0.013
Depth	2	5.47	17.21	<0.001
Depth × Day/night	2	3.91	12.30	<0.001
Depth × Tide	2	1.01	3.18	0.060
Depth × Tide × Day/night	2	0.29	0.92	0.393
Error	24	0.32		

Fig. 2. *Sillaginodes punctata*. Log-transformed densities of pre-settlement individuals in 1995 at 3 depths with respect to stage of tide and day or night. Error bars are standard error
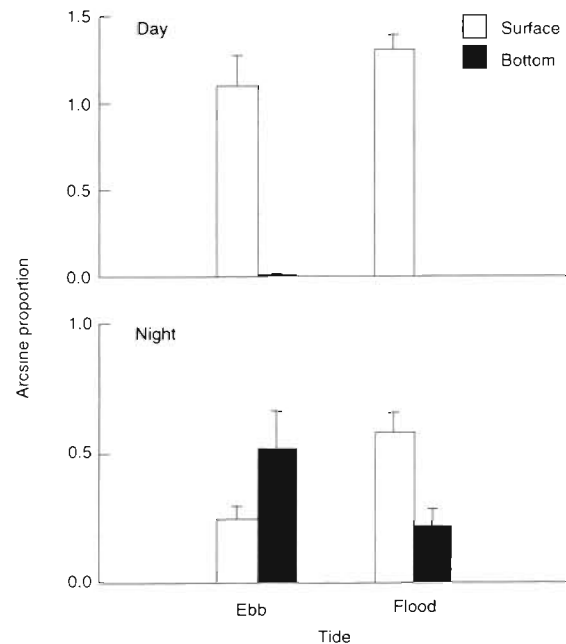

Fig. 3. *Sillaginodes punctata*. Arcsine-transformed proportions of pre-settlement individuals in 1995 in surface and bottom samples with respect to stage of tide and day or night. Error bars are standard error

depth. Overall, significantly greater numbers of larvae were collected at night, and the day/night difference in abundance was the other major source of variation, explaining approximately 30% of the overall variation in larval densities (Tables 3 & 4).

In 1996, a total of 51 *Sillaginodes punctata* larvae were collected at PJ1 whilst few larvae were collected at the other sites (Table 2). All larvae collected during daytime were collected in the surface sample. Significant numbers of larvae were collected at night at PJ1 and these had a relatively even distribution through the water column (Fig. 4).

Table 4. *Sillaginodes punctata*. Partially nested analysis of variance of arcsine-transformed mean proportion of pre-settlement individuals in surface and bottom depths, with respect to day/night and tide over 16 dates

Source	df	MS	F	p
Day/night	1	0.30	8.57	0.013
Tide	1	0.03	0.75	0.404
Day/night × Tide	1	0.04	1.19	0.298
Day(Day/night × Tide)	12	0.04	0.74	0.691
Depth	1	2.70	57.07	<0.001
Depth × Day/night	1	2.22	46.93	<0.001
Depth × Tide	1	0.37	7.92	0.016
Depth × Tide × Day/night	1	0.05	1.00	0.337
Error	12	0.05		

A total of 137 *Sillaginodes punctata* larvae collected in 1995 were dissected for gut analysis, 99 from daytime and 38 from night-time sampling. For daytime samples, only 7 larvae from depths other than the surface were available, so these individuals were omitted from the analysis. For night-time samples, specimens from all depths were selected. Of the larvae collected at night only 4 had prey items in the gut. These larvae came from 2 hauls that started within 30 min after the onset of darkness. By contrast, only 2 larvae from daytime samples had no prey in their guts.

The diet of larvae collected in daytime, in terms of frequency of occurrence and percentage of prey number, was dominated by copepods (predominantly calanoids), and to a lesser extent carid myses, on 3 of the 4 dates. However, on 8 November, the diet was dominated by calyptopes, with copepods also important (Table 5). Mean prey number per gut on 3 and 8 November was approximately double that on 26 October and 16 November (Table 5).

Analysis of variance indicated that there was little variation in the depth distribution of the major zooplankton taxa found in *Sillaginodes punctata* guts (Table 6, Fig. 5). Only zoeae showed significant variation with depth, with generally lower concentrations near the surface (Table 6, Fig. 5), while calyptopes showed a significant interaction between depth and tide, with individuals near the surface during ebb tide
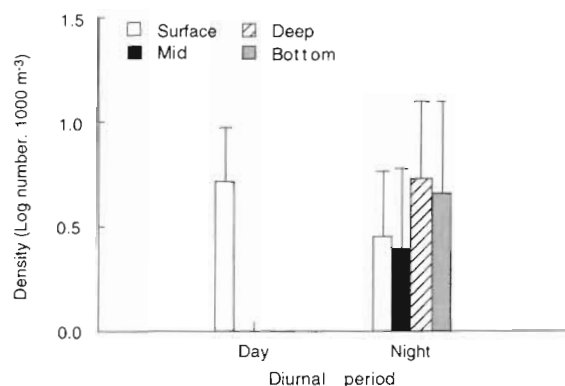
Fig. 4. *Sillaginodes punctata*. Log-transformed densities of pre-settlement individuals in 1996 at 4 depths with respect to day or night. Error bars are standard error

on 3 and 16 November (Table 6, Fig. 5). Variation in the diet of *S. punctata* was reflected to a large extent by the composition of the zooplankton. Copepods dominated the zooplankton with the exception of samples taken on 8 November, when calyptopes occurred in very high concentrations (Fig. 5). This was reflected in the significant variation between days within tides for calyptopes (Table 6). The other taxon to show a significant variation amongst days was zoeae, which decreased in abundance over time (Table 6, Fig. 5).

Zoeae in the plankton were under-represented in the diet (Table 5).

DISCUSSION

Sillaginodes punctata larvae showed pronounced vertical migration in relation to the day/night cycle. Larval whiting, like larvae of many fish species, show a form of 'reverse' diurnal migration (Boehlert et al. 1985, Yamashita et al. 1985, Sogard et al. 1987, Neilson & Perry 1990, Heath et al. 1991, Lyczkowski-Shultz & Steen 1991), specifically, stratification near the surface during the day, and random distribution or 'nocturnal diffusion' at night (Brewer & Kleppel 1986, Davis et al. 1990, Leis 1991, Haldorson et al. 1993). All larvae collected in Port Phillip Bay were relatively large (15 to 20 mm) and competent to settle (Jenkins & May 1994). Vertical migratory behaviour generally becomes stronger with development (Neilson & Perry 1990, Heath et al. 1991, Champalbert & Koutsikopoulos 1995); therefore, migration in younger larvae may be less pronounced than in the late-larval stage we investigated.

The reverse diurnal migration seemed even more pronounced at deeper stations in 1996, although the sample size was much smaller compared with 1995.

Table 5. *Sillaginodes punctata*. Diet of pre-settlement individuals in 1995 expressed as percent frequency of occurrence (F) and percent of total number (N) of prey in the diet, and the product ($F \times N$) that was taken as an index of relative importance

Taxon	26 October (n = 35)			3 November (n = 29)			8 November (n = 10)			16 November (n = 25)		
	F	N	$F \times N$	F	N	$F \times N$	F	N	$F \times N$	F	N	$F \times N$
Copepods	77	62	4774	52	46	2392	40	19	760	88	67	5896
Nauplii	6	2	12	31	20	620	10	1	10	40	15	600
Carid myses	37	28	1036	69	24	1656	20	3	60	36	13	468
Calyptopes	0	0	0	7	1	7	90	77	6930	4	1	4
Zoeae	9	3	27	7	2	14	0	0	0	12	3	36
Other	3	1	3	14	7	98	0	0	0	0	0	0
Mean prey number per larva		3.3			7.1			7.7			3.7	

Table 6. Partially nested analysis of variance of log-transformed zooplankton density with respect to tide and depth for the different taxa. $^{ns}p > 0.05$, $^*p < 0.05$, $^{**}p < 0.001$

Source	df	Copepods		Calyptopes		Myses		Zoeae		Total	
		MS	F	MS	F	MS	F	MS	F	MS	F
Tide	1	4.84	4.35^{ns}	77.15	1.35^{ns}	1.60	0.38^{ns}	0.45	0.08^{ns}	5.54	2.83^{ns}
Day(Tide)	2	1.11	6.94^{ns}	57.13	317.39^{**}	4.22	2.08^{ns}	5.84	20.13^*	1.96	9.8^{ns}
Depth	2	0.27	1.72^{ns}	0.03	0.17^{ns}	0.67	0.33^{ns}	3.78	13.15^*	0.67	3.31^{ns}
Depth × Tide	2	0.54	0.55^{ns}	1.53	8.55^*	1.77	0.87^{ns}	0.48	1.65^{ns}	0.09	0.47^{ns}
Error	4	0.16		0.18		2.03		0.29		0.20	

Although reasonable numbers of larvae were collected at 1 deeper site near Port Phillip Heads, at other sites they were very rare. The difference in catch between years probably reflected spatial variability. Plankton sampling at 20 sites in the southern half of Port Phillip Bay over 2 yr has shown that larvae are more concentrated in shallow, nearshore waters of the bay, and site BWS1 had by far the greatest abundance of larvae (G. Jenkins unpubl. data).

The strong diurnal variation in gut contents, indicating that feeding only occurs in daylight, may suggest that diurnal migration observed in *Sillaginodes punctata* larvae is an adaptive response to maximise feeding. In some studies, vertical migratory behaviour has been linked to the vertical distribution of prey (Fortier & Leggett 1983, Munk et al. 1989, Neilson & Perry 1990, Haldorson et al. 1993); however, in a number of species, including *S. punctata* in this study, no relationship could be found between diurnal ascent/nocturnal diffusion and prey distribution (Yamashita et al. 1985, Brewer & Kleppel 1986, Lyczkowski-Shultz & Steen 1991). Because fish larvae are visual feeders (Blaxter 1986), the migratory behaviour observed in many species might simply be a response to finding optimum light levels for detection of prey. The threshold of light intensity that initiates vertical migration in fish larvae may be similar to that required for feeding (Blaxter 1986).

Another form of vertical migratory behaviour that was apparent for late-larval *Sillaginodes punctata* was in response to tide, although this effect was very minor and was only detectable when variation in abundance amongst days was removed. Such tidal migration, often termed selective tidal transport (Boehlert & Mundy 1988), has been detected in a number of species, and is suggested to assist with transport of larvae to nearshore habitats, or retention in habitats such as estuaries (Weinstein et al. 1980, Fortier & Leggett 1983, Rijnsdorp et al. 1985, Holt et al. 1989). Such behaviour might assist *S. punctata* larvae to reach habitats deep within bays and inlets. However, in most cases, this behaviour is strongly developed (Boehlert & Mundy 1988), in contrast to the situation with larval *S. punctata*. Tidal migration in *S. punctata* larvae may not be an adaptation for transport, but rather a consequence of other factors, and may be a localised phenomenon at the site examined. For example, changes in the physical characteristics of the water column, such as water chemistry, temperature, salinity, hydrostatic pressure and turbulence, can influence vertical position (Heath et al. 1988, Heath et al. 1991, De Vries et al. 1995a, b). Such factors might vary between ebb and flood tide, and therefore influence vertical position tidally. Any factor leading to larvae occurring closer to the surface on a flood tide, whether passive or active, would tend
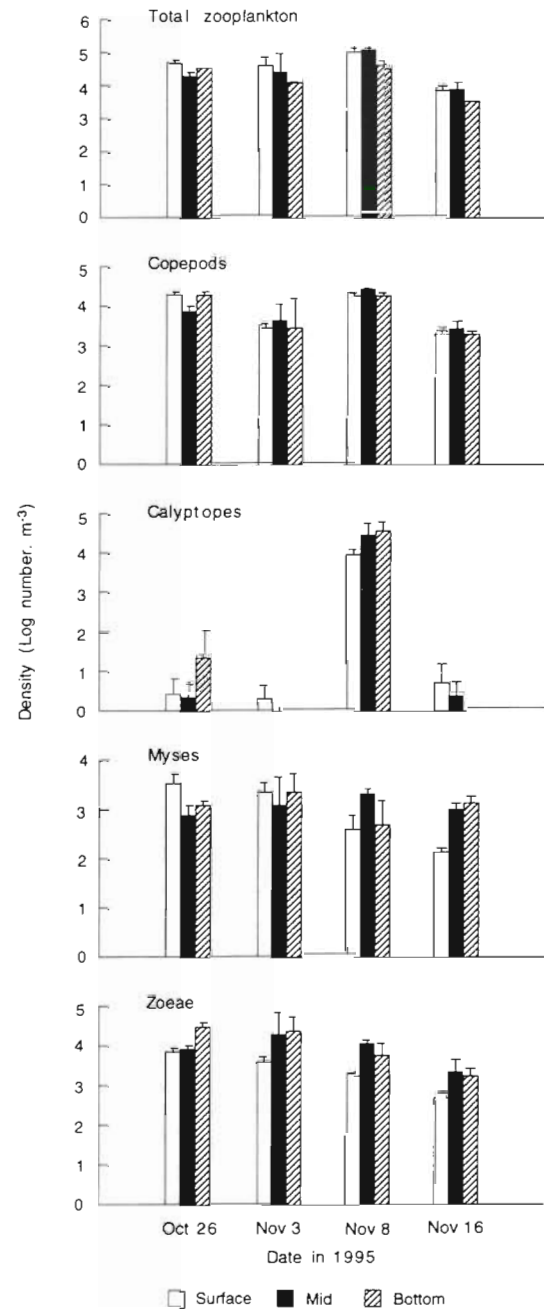

Fig. 5. Log-transformed density of total zooplankton, and common individual taxa, with respect to depth on 4 sampling dates. Error bars are standard error

to facilitate transport into, or retention within, Port Phillip Bay.

Apart from diurnal variation in vertical distribution, the other major source of variation in the analysis related to a greater abundance of larvae collected at night compared to daytime. The collection of greater numbers of fish larvae at night is a common phenomenon and is usually attributed to greater net avoidance

during daytime (Bridger 1956, Brander & Thompson 1989, Davis et al. 1990). Net avoidance during the day is probably more pronounced in larger larvae (Bridger 1956, Brander & Thompson 1989). If net avoidance was significant during the day in our study, then the pattern of stratification we found would be conservative relative to the actual pattern, because net avoidance would be expected to be greater near the surface where more light was available.

The diet of larvae during the day largely reflected the availability of prey in the water column, as was well demonstrated when high abundances of calyptopes occurred both in the plankton and in the diet of larvae on 1 sampling date. An exception, however, was the small proportion of zoeae in the diet relative to their abundance in the water column. This relatively low representation in the diet might relate to the fact that zoeae were more concentrated deeper in the water column, although other factors such as strong spination that might deter predators or strong escape response may also have been important.

The observed vertical migratory behaviour has strong implications for transport of Sillaginodes punctata larvae to seagrass habitats. The southern part of Port Phillip Bay is tidally dominated; however, once north of the 'Sands' region, the circulation is largely wind driven and vertical variation in current strength would be high (Black et al. 1993). In terms of diurnal variation in vertical distribution, larvae concentrated near the surface during the day will be transported much faster than those deeper in the water column, and there is potential for larvae to reach habitats throughout the bay very quickly. If the tidal migration is a general phenomenon, then this may serve to direct movement up the bay, because tidal currents are generally stronger near the surface (Black et al. 1993). However, in the northern part of the bay, wind-driven currents would be expected to overwhelm tidal currents, and therefore the effect of selective tidal transport would be reduced. The potential for vertical tidal migration to influence transport in Port Phillip Bay seems weaker than in systems such as estuaries where countercurrents can exist at depth (Boehlert & Mundy 1988), or in species where individuals can cling to the substrate on ebb tides (Creutzberg 1961, Rowe & Epifanio 1994); however, the effect may be significant in terms of transporting larvae to potential juvenile habitats deep within the bay.

In conclusion, our study shows that in the shallow water of Port Phillip Bay, late larvae of King George whiting are found near the surface in the daytime and dispersed through the water column at night. This pattern is not related to the vertical distribution of prey but may have been a response to light for visual feeding. There is evidence of a change in vertical distribution in relation to tide where larvae are closer to the surface on flood tides; however, any such migration is weak and may be spatially variable. These results may have significant implications for modelling of larval transport and recruitment (Jenkins & Black 1994, Jenkins et al. 1997) whereby movement into the bay may be enhanced by tidal vertical migration and surface, wind-driven currents may lead to rapid transport of larvae within the bay during daytime.

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