

Larval supply, settlement and survival of barnacles in a temperate mangrove forest

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ABSTRACT: Cyprids of the barnacles *Elminius covertus* and *Hexaminius popeiana* were sampled in the water column at differing distances from the seaward edge within a mangrove forest and at different tidal elevations at the seaward edge of a mangrove forest in Sydney, Australia. At differing distances from the seaward edge of the forest, the density of settlers of *E. covertus* and *H. popeiana* was correlated with the density and availability of cyprids in the water column. The density of recruits was correlated with the density of settlers and the density of adults with the density of recruits. Cyprids of each species were most abundant in the water column during high tides that occurred during the night. Since most settlement of *E. covertus* occurs in winter, when nighttime tides are of greater amplitude than at other times of the year, this species has more frequent access to the landward parts of the forest than *H. popeiana*, which mainly settles in spring and summer. At different tidal elevations at the seaward edge of the mangrove forest, the density of settlers, recruits and adults of *E. covertus* was correlated with the density and availability of cyprids. In contrast, the density of settlers of *H. popeiana* among tidal levels was not in concordance with density or availability of cyprids. This is the first example of detailed sampling of cyprids and their survival in a mangrove habitat with calm wave action and a less harsh physical environment than found on rocky shores. In mangrove habitats, the density and availability of cyprids at differing distances from the seaward edge and in the vertical range for 1 species (*E. covertus*) constituted a good predictor of patterns of settlement.

KEY WORDS: Barnacles · Cyprid supply · Settlement · Post-settlement mortality · Recruitment · Mangrove forests · Cirripeds · Larval behaviour

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INTRODUCTION

Since the early 1980s, patterns of distribution and abundance in the arrival of propagules or larvae in the habitat of the adult have been emphasised as important in determining the patterns of adult organisms, particularly in open systems such as aquatic environments (Underwood & Denley 1984, Connell 1985, Lewin 1986, Underwood & Fairweather 1989). Initially, the relationship between settlers, recruits and adults was emphasised (Denley & Underwood 1979, Hawkins & Hartnoll

1982, Caffey 1985, Connell 1985) and later the relationship between these stages and larval supply was quantified in a variety of habitats, including intertidal rocky shores (barnacles: Gaines & Roughgarden 1985, Gaines et al. 1985, Raimondi 1988a,b, 1990, 1991, Minchinton & Scheibling 1991, Bertness et al. 1992, 1996), subtidal rocky reefs (barnacles in kelp forests: Gaines & Roughgarden 1987; ascidians: Davis 1988, Hurlburt 1991, 1992), coral reefs (fishes: Sweatman 1985, 1988, Milicich et al. 1992, Caley et al. 1996), estuarine environments (barnacles: Grosberg 1982; crabs: Eggleston & Armstrong 1995) and mangrove forests (a variety of epifaunal organisms: Bingham 1992). A positive relationship has been found between supply and settlement (Grosberg 1982, Gaines & Roughgarden 1985, 1987, Gaines et al. 1985, Minchinton & Scheibling 1991, Bert-

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ness et al. 1992, 1996, Gaines & Bertness 1992, Milicich et al. 1992, Eggleston & Armstrong 1995) and supply and recruitment for some species (Bingham 1992). Whether the relationship between larval supply and other life-history stages remains, however, is dependent on post-settlement mortality which may uncouple the relationship in parts of the organisms' range (density-dependent mortality: Connell 1985; predation: Minchinton & Scheibling 1991, Eggleston & Armstrong 1995; reviews by Gosselin & Qian 1997, and Hunt & Scheibling 1997).

Interest in determining the mechanisms causing the spatial patterns of larvae has developed alongside quantifying the spatial patterns themselves. Larvae have been shown to act like passive particles entrained by hydrodynamic factors (Shanks 1983, 1985, 1986, Butman 1987, Pineda 1991, 1999, Bertness et al. 1996), relatively unable to influence their distribution and abundance on the shore at a large spatial scale. Thus, at large spatial scales, the mechanisms of physical transport are good predictors of the spatial patterns of larvae and settlers on a shore (Hawkins & Hartnoll 1982, Gaines et al. 1985, Roughgarden et al. 1987, Gaines & Bertness 1992, Bertness et al. 1996). At smaller spatial scales, however, larval behaviour may play more of a role in determining patterns of settlers (Meadows & Campbell 1972, Strathman & Branscomb 1979, Strathman et al. 1981, Raimondi 1991). In habitats such as mangroves and estuarine environments, where waters are calm and swell and splash are greatly reduced, larvae may not act like passive particles and be more able to determine their position in the water column by swimming or vertical migration (de Wolf 1973, Mileikovsky 1973, Grosberg 1982, Woodin 1986, Hui & Moyses 1987, Forward 1988) and thus influence the pattern of settlement.

In mangrove forests around Sydney, Australia, the barnacles *Elminius covertus* and *Hexaminius popeiana* are abundant on the bark and leaves of the grey mangrove tree *Avicennia marina* (Egan & Anderson 1985, Ross 1996, Ross & Underwood 1997). Spatially, these intertidal forests are complex 3-dimensional habitats with trees forming a hard substratum in an area otherwise dominated by soft-sediment. Larvae have access to trees which are close to the seaward and landward edge of the forest. Within each area, the trunks span different tidal heights (Berry 1963, Por 1984). *E. covertus* are most abundant on trunks of trees at the seaward edge of the forest and at mid-tide levels (Ross & Underwood 1997). In contrast, *H. popeiana* are only found as adults on the trunks of trees in the seaward areas of the forest, where they are most abundant at low- to mid-tide levels (Ross & Underwood 1997).

The aim of this study was to quantify the relationship between the distribution and abundance of cyprids, settlers, recruits and adults at different spatial scales in

a mangrove forest and evaluate how larval behaviour may influence any non-differential larval supply into these habitats. The purpose of this was to test the hypothesis that the patterns of the distribution and abundance of adults are determined by the patterns of distribution and abundance of cyprids (or cyprid supply, Ross & Underwood 1997). If cyprid supply is a good predictor of spatial patterns of settlers, then patterns of larval supply will be correlated with patterns of settlers. This should occur at 2 spatial scales, between the seaward and landward areas of the forest and among tidal heights on trees. If settlement is a good predictor of recruitment, then patterns at settlement will be maintained to form patterns of recruits. The mechanisms determining larval supply in these habitats are potentially different from those of an exposed rocky shore, because in this environment of calm wave-action, tidal amplitude may be important in delivering larvae into the upper reaches of the forest and onto the high tidal levels on the trees and larvae may be able to determine their position in the water column. Mangrove forests and the barnacles within them thus provide a potential testing-ground for ideas on cyprid supply derived mostly from exposed habitats.

MATERIALS AND METHODS

Location. This study was carried out from July 1989 to October 1991 in a mangrove forest on the eastern side of Woolooware Bay in Botany Bay, south of Sydney (Latitude 34° 01' 05", Longitude 151° 09' 02"). The mangrove trees form a fringing stand along the shore, approx. 75 m in width. Two study sites (approx. 300 m apart) were chosen, Sites B and C (to distinguish them from other sites described by Ross & Underwood 1997). Tides in Sydney are semi-diurnal, and range from 0.0 to 2.0 m with a mid-tide level of 1.4 to 1.5 m.

Sampling on trees and in the water column. To determine whether the spatial patterns of cyprid larvae were related to the distribution and abundance of settlers and recruits into the adult population, the bark of trees on which cyprids settle needed to be sampled. With the increase in absolute height of the forest floor from seaward to landward, the absolute height of tidal levels on trees differed in the seaward compared to the landward zone. This meant that while a mid-high tide (1.4 m) rose 50 cm up the tree in the seaward zone, it only rose 10 cm on trees in the landward zone. Any comparisons of tidal heights between different zones thus need to consider the vertical height the tide rises above the forest floor. To determine absolute vertical heights within different zones, tidal heights on tree trunks were measured by surveying and recording the height reached by known predicted tides on 2 m

wooden stakes placed every 10 to 15 m from the seaward to landward zones of the forest at each of the 2 sites. In the seaward zone, low- to high-tide level ranged from 0 to 1.2 m in absolute height up the trunk of the tree or 0.8 to 2.0 m in tidal range (low level, 0 to 50 cm above the forest floor; mid level 50 to 80 cm above the forest floor, high level 80 cm to 1.2 m above the forest floor). In the landward zone, at a distance of 55 m from the seaward edge, low- to high-tide level ranged from 0 to 70 cm in absolute height up the trunk of the tree or 1.3 to 2.0 m tidal range (low level 0 to 10 cm above the forest floor, mid level 10 to 40 cm above the forest floor, high level 40 to 70 cm above the forest floor).

Sampling cyprid distribution and abundance.

Plankton samples were collected at each site on spring high tides at night from July 1989 to October 1991 (Ross 1993). Preliminary sampling in July 1989 over a range of lunar periods revealed that few or no cyprids per cubic metre of water or other zooplankton were present in samples taken on high tides during the day (*Elminius covertus*: 81.17 ± 22.95 night and 3.25 ± 0.97 day $n = 2$, $F = 230.54$, $p < 0.05$, $df = 1 \times 1$, Student-Newman-Keuls [SNK] test, night > day; *Hexaminus popeiana*: 132.79 ± 56.31 night and 1.95 ± 0.62 day, $n = 2$, $F = 743.39$, $p < 0.05$, $df = 1 \times 1$, SNK test, night > day). Only incoming rising tides were sampled because there were significantly fewer cyprids on falling than rising tides (*E. covertus*: 29.20 ± 10.79 ascending and 0.48 ± 0.13 descending $n = 2$, $F = 12.65$, $p < 0.01$, $df = 1 \times 3$, period \times site interaction, SNK test, ascending > descending tide; *H. popeiana*: 9.64 ± 3.11 ascending and 0.16 ± 0.08 descending, $n = 2$, $F = 3.40$ $p < 0.05$, $df = 1 \times 3$, period \times site \times height interaction SNK test, ascending > descending tide, except for 1 site and 1 height).

The frequency of sampling differed according to the abundance of cyprids. Cyprids of *Elminius covertus* are abundant in the water column in July to October and those of *Hexaminus popeiana* from October to March (Ross 1993). Therefore, the results of samples collected from July to October each year have been included here. Plankton samples were collected using a conical plankton net towed from a boat or by hand for a given period of time. A flowmeter (General Oceanics, Model 2030 R, Miami, FL, USA) placed in the mouth of the net estimated the volume of the water that flowed through the net.

Towing the net by hand was necessary in the seaward zone when the water level was too low for access by boat and in the landward zone where many small trees made manoeuvring the boat difficult. In a pilot study, there was no difference in the number of cyprids per cubic metre of water collected walking or using a boat (*Elminius covertus*: 53.06 ± 1.06 boat, and 65.16 ± 16.09 walking $n = 3$, $F = 0.66$, $df = 1 \times 2$, non-significant;

Hexaminus popeiana: 10.65 ± 1.29 , boat and 6.35 ± 1.87 walking, $n = 3$, $F = 1.23$, $df = 1 \times 2$, non-significant).

To quantify the distribution and abundance of cyprids at different distances from the seaward edge of the forest, 2 samples (5 min in duration) were taken 5 times during July 1989 to September 1990 at each of 2 sites in the seaward and landward zones. The samples were taken when the tide reached mid-tide level. To quantify the distribution and abundance of cyprids among different levels in the water column, the seaward zone was sampled on an incoming rising tide at night when the tide was at low-, mid- and high-tide levels. Two samples (3 min in duration) were taken on 8 September and 7 October 1991 at each of 2 sites. Each stage of the incoming, rising tide was sampled: the low-tide level during low-tide L(L), mid-tide L(M) and high-tide L(H); the mid-tide level during mid-tide M(M), and high-tide M(H); the high-tide level during high-tide H (H).

Samples were washed into plastic containers and preserved immediately in 4% formalin/seawater. Cyprids were separated into 2 species (see Ross 1996), *Elminius covertus* and *Hexaminus popeiana*. Except for 2 samples which were subsampled, all cyprids were counted. The number of cyprids available for settlement at each tidal level on a tree trunk is a function of the density of cyprids in the water column and the time each tidal level on the trunk is immersed. Therefore, in addition to expressing the results in density of cyprids per cubic metre of water, the number of cyprids available at each zone and tidal level was calculated (cyprid availability). This was done by multiplying the densities of cyprids by the time each tidal level or zone was immersed. Time of immersion for each tidal level was calculated from tidal curves supplied by the Sydney Ports Authority. The method used was similar to that of Minchinton & Scheibling (1991), but the immersion times were calculated on the ascending tide only, as descending tides have few cyprids.

Cyprids will only have access to mid-tide levels of trees in the landward zones of the forest when tides with an amplitude of ≥ 1.4 to 1.5 m occur in the night. To calculate how many times cyprids would have access in the water column to the mid-tide level of trees in the landward zones of the forest, the number of tides with a tidal amplitude ≥ 1.5 m which occurred in the night were totalled during 1988 to 1991. The proportion of the high tides occurring in the night were then expressed as a percentage of the total number of tides ≥ 1.5 m occurring in the day and night. This was then used to determine how many tides are available to carry cyprids to at least the mid-tide level (1.5 m) in the landward zone of the forest.

Sampling settlers, recruits and adults. The most common substratum for barnacles to settle on in a

mangrove forest is the bark of the mangrove tree. Because the trunks bend, they have a lower and upper surface at low-, mid- and high-tide levels in each zone. Densities of barnacles were greater on the lower compared to the upper surfaces of the trunk (Ross & Underwood 1997). Therefore, to estimate the relationship between cyprids with settlers, recruits and adults, settlers recruits and adults were quantified on the lower surface of tree trunks.

Densities of settlers, recruits and adults of *Elminius covertus* were compared between zones by sampling 2 replicate areas of the bark on the lower surface of trunks of 2 trees at mid-tide level at 1 site. For the among tidal level comparison, settlers, recruits and adults were estimated on trees in the seaward zone at 3 vertical elevations (low-, mid- and high-tide levels) on 2 trees at each of 2 sites (Table 1). To do this, quadrats (11 cm diam.) were set up in July 1990 approximately 1 mo before the main period of settlement. On 7 August 1990, during the low tide before an anticipated peak of settlement, all areas were cleared of recruits that had settled within the period after the initial set up. After 2 high tides (8 August 1990) all cyprids and metamorphosed cyprids present within quadrats were quantified. A study prior to this investigation found no differences in the spatial patterns of cyprids and metamorphosed cyprids after the passing of 1 or 2 high tides (Ross 1993). The quantification of cyprids and metamorphosed cyprids was done by mapping the position of individuals on acetate sheets. Mortality of cyprids and recording of new individuals settling was estimated by sampling quadrats 1 d after the first mapping (9 August 1990), and then at new and full

moons during the settlement season, which corresponded to peaks of settlement of barnacles in this habitat (Ross 1993). Virtually no mortality of individuals settling was recorded until 21 September 1990: this date was called the initial settlement census date. The total density of settlers was thus estimated at the initial settlement census date as the cumulative number of barnacles totalled for each quadrat. The density of recruits was estimated as the number of *E. covertus* present in each quadrat at the end of the main settlement period (16 October 1990). The density of adults was estimated as the number of *E. covertus* present in each quadrat at the end of the sampling period (19 June 1991).

Densities of settlers, recruits and adults of *Hexaminus popeiana* were also estimated in 2 replicate areas on the lower surface of the bark of trunks. For the among tidal level comparison, this was done in the seaward zone at low-, mid- and high-tide levels on 2 trees. Because of the amount of time taken to quantify the settlement in this design, it was set up at 1 site only (Table 1) and not between zones (Table 1). Quadrats were initially set up in December 1989. On 19 February 1990 they were cleared of any cyprids and metamorphosed cyprids. After 2 high tides (20 February 1990), all cyprids and metamorphosed cyprids present on the quadrats were mapped onto acetate sheets. Mortality of cyprids and settling of new individuals were estimated by sampling quadrats 1 d after the first mapping and then at new and full moons during the settlement season. Virtually no mortality of individuals settling was recorded until 1 mo after the first settlers had arrived (22 March 1990). This was the initial settlement census date when the density of settlers was

estimated. The density of recruits was estimated as the number of *H. popeiana* present in each quadrat at the end of the main settlement period (24 April 1990). The density of adults was estimated as the number of *H. popeiana* present in each quadrat at the end of the sampling period (19 June 1991). Adult barnacles were defined as being part of the reproductive population (Ross 1996); these methods correspond to procedures used in similar studies (Connell 1985, Minchinton & Scheibling 1991, Bertness et al. 1992).

The between-zone comparison for *Hexaminus popeiana* was done using artificial substrata (hardwood wooden blocks), because *H. popeiana* settle in large densities on wooden blocks (Ross 1993). To secure wooden blocks on a surface which mimicked the flow of water around a tree, cut lengths of

Table 1. *Elminius covertus* and *Hexaminus popeiana*. Sampling design for settlers, recruits and adults used in this study

	<i>E. covertus</i>	<i>H. popeiana</i>	<i>H. popeiana</i>
Substrate	Bark	Bark	Artificial substrate
Orientation	Horizontal component (between zones)		
Zone	Seaward and landward zone		
Design			
Site	1	None	1
Zone	2		2
Tree	2		2 (artificial tree)
Replicate	2		2
Orientation	Vertical component (among tidal levels)		
Zone	Seaward zone		
Design			
Site	2	1	
Tree	2	2	
Tidal heights	3 (low, mid, high)	3 (low, mid, high)	
Replicate	2	2	

PVC pipes (15 cm diam.) were fixed to wooden stakes and hammered into the mud (hereafter referred to as artificial trees) at mid-tide level. Holes were drilled into the PVC and wooden blocks were tied on the lower surface of the pipes with fishing line. Densities of settlers recruits and adults of *H. popeiana* were estimated in the central area (6.25 cm²) of 2 wooden blocks (5 × 5 cm) attached to an artificial tree.

For comparisons between species and substrata, all densities were converted to numbers per 6.25 cm². Densities of barnacles (cyprids, settlers, recruits and adults) were analysed using analyses of variance. Each analysis contained a combination of fixed and random factors (fixed = zones, tidal heights; random = site, tree nested in site and artificial tree nested in zone). Cochran's C-test was used to indicate heterogeneity of variances, and densities were transformed if Cochran's test proved to be significant. SNK tests were used to detect post-hoc differences among means. The analysis was dependent on the experimental design for each species (Table 1).

RESULTS

Supply of cyprids

There was a greater number of high-amplitude tides (≥1.5 m) in the night from May to September (49 to 91%) than in the night from October to February (6 to 35%). The majority of cyprids in the water column during June to October comprise *Elminius covertus* (Ross 1996), and between October and March *Hexaminus popeiana* (Ross 1996, Ross & Underwood 1997). This means that *E. covertus* will have more frequent access to the landward parts of the forest than *H. popeiana* because cyprids of *E. covertus* are in the water column during those times of the year when high tides with a large enough tidal amplitude to submerge trees to at least mid-tide level occur at night.

There were significantly more cyprids of *Elminius covertus* and *Hexaminus popeiana* in the seaward zone than in the landward zone (Fig. 1, Table 2). The greater number of *E. covertus* cyprids in the seaward zone was apparent in the comparison of means from the site × zone interaction (seaward greater than landward zone at each site: Table 2), and on 5 September 1990, zone was significant.

A comparison of the mean densities of cyprids indicates that Site C in the seaward zone received more cyprids than Site B. For *H. popeiana* the presence of more cyprids in the seaward zone can also be seen in the interpretation of the site × zone interaction, and on 5 September 1990, zone was significant (Table 2). Comparisons between means showed that on all except 1 occasion at 1 site, the seaward zone had a greater density of cyprids than the landward zone.

The vertical distribution of cyprids in the water column differed significantly among tidal heights and sites for each species (height × site interactions; Table 3) except on 7 October, when height was significant. There was a trend for more cyprids of *Elminius covertus* and *Hexaminus popeiana* at mid- and high-tide levels in the water column (Fig. 2, Table 3; SNK tests, $p < 0.05$). The clearest pattern when comparing means at each site (SNK tests, $p < 0.05$), shows fewer cyprids arriving at low-tide levels when the ascending tide was at low- and mid-tide levels (Fig. 2, Table 3; height × site interactions on 3 out of 4 occasions).

The patterns of relative abundance of the 2 species between zones and levels remained similar after correcting for the time each zone and tidal level were immersed (see third subsection of 'Materials and Methods'). There were more cyprids of each species in the seaward than in the landward zone (Figs. 3a & 4a). Correcting for the time each tidal level was immersed increased the densities of cyprids at low- and mid-tide level and decreased the densities of cyprids at high-tide level on each date sampled (Figs. 3a & 4a). The

Table 2. *Elminius covertus* and *Hexaminus popeiana*. Analysis of densities of cyprids between zones at mid-tide level at Woolooware Bay from 18 August 1989 to 5 September 1990. Data were transformed to $\log_e(x + 1)$, as Cochran's test proved to be significant. Each analysis was a combination of fixed factor (zone) and random (site). * $p < 0.05$; ** $p < 0.01$

Source of variation	df	18 Aug 89		8 Aug 90		5 Sep 90	
		MS	F	MS	F	MS	F
<i>E. covertus</i>							
Site, S	1	0.19	2.43	0.90	40.86**	0.03	0.43
Zone, Z	1	11.64	25.67	6.43	28.63	20.15	80.72*
S × Z	1	0.45	15.79*	0.22	10.15*	0.23	3.21
Residual	8	0.08		0.02		0.07	
<i>H. popeiana</i>							
Site, S	1	3.38	83.10**			0.04	0.69
Zone, Z	1	5.08	1.50			12.96	120.63*
S × Z	1	3.38	83.10**			0.11	2.16
Residual	8	0.04				0.05	
SNK tests (SB: Site B; SC: Site C; SZ: seaward zone; LZ: landward zone)							
<i>E. covertus</i> (18.8.89 and 8.8.90)				<i>H. popeiana</i> (18.8.89)			
S × Z interaction				S × Z interaction			
In the SZ, SC > SB				In the SZ, SC > SB			
In the LZ, SC = SB				In the LZ, SC = SB			
At each site, SZ > LZ				At site C, SZ > LZ			

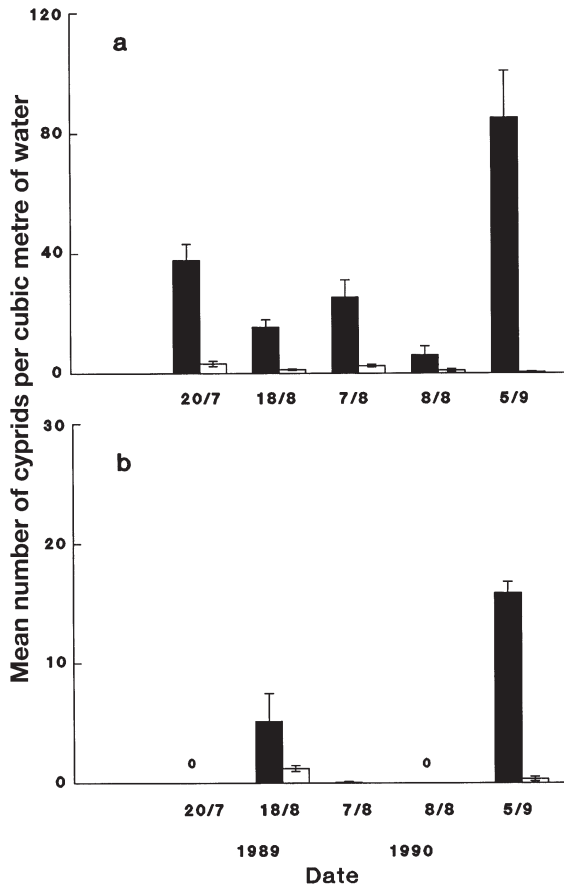


Fig. 1. (a) *Elminius covertus* and (b) *Hexaminus popeiana*. Densities of cyprids in the seaward and landward zones at mid-tide level from 20 July 1989 to the 5 September 1990 (5 sampling dates) at Woolooware Bay. Data are means (\pm SE, $n = 2$) per cubic metre water. Black bars: densities of cyprids in the seaward zone on each date; open bars: densities of cyprids in the landward zone on each date

greatest availability of cyprids was more at mid- and less at low-tide level (Figs. 3a & 4a), although this differs as a function of sampling date.

Settlers, recruits and adults

The densities of settlers of *Elminius covertus* were approximately 3 times greater in the seaward than in the landward zone (Fig. 3b, Table 4a). Among tidal levels in the seaward zone, the densities of settlers of *E. covertus* were greater at the mid-rather than at the low- or high-tide levels (Fig. 3b, Table 4b). The signifi-

cance of these trends was somewhat dependent on the specific tree and sometimes on the site (Tree [(Z)] and H \times T[(S)] interactions respectively, Table 4). There was a similar pattern for the recruits and adults. The densities of recruits and adults of *E. covertus* in the seaward zone were approximately 3 times those in the landward zone (Fig. 3c,d). Among tidal levels, densities of recruits and adults were greatest at mid-tide levels and less at low- and high- tide levels (Fig. 3c,d, Table 4b). The significance again was somewhat dependent on the specific tree and site (height \times tree [site] interaction and SNK test). The reason for such similarity in pattern between settlers and adults was that there was a differential pattern of post-settlement mortality of settlers between zones and among tidal levels at each life history stage.

The densities of settlers of *Hexaminus popeiana* on bark were greater at low- and mid- than at high-tide levels in the seaward zone (Fig. 4b, Table 5a), although this was dependent on the tree (height \times tree interaction). Similar to the trend in post-settlement mortality of *Elminius covertus*, post-settlement mortality of settlers of *H. popeiana* was different among tidal levels in the seaward zone. There was greater post-settlement mortality at high-tide levels (100%) and less at low-tide levels (Fig. 4c,d). The densities of recruits and adults were thus similar at low- and mid-tide level and less at high-tide level (Fig. 4d). The significance of these trends is somewhat dependent on the tree, as shown in the height \times tree interaction in each analysis (Table 5a).

The densities of settlers on wooden blocks were approximately 10 times greater in the seaward than in the landward zone (Fig. 4b, Table 5b). Post-settlement mortality acted differentially on this initial pattern of settlers. Post-settlement mortality was greatest in the landward

Table 3. *Elminius covertus* and *Hexaminus popeiana*. Analysis of densities of cyprids among tidal levels in the seaward zone at Woolooware Bay on 8 September 1991 and 7 October 1991. Data were transformed to $\log_e(x + 1)$ because Cochran's test was significant. Each analysis was a combination of fixed factors (tidal height) and random (site). * $p < 0.05$; ** $p < 0.01$

Source of variation	df	8 Sep 91		7 Oct 91	
		MS	F	MS	F
<i>E. covertus</i>					
Height, H	5	0.48	0.31	2.96	2.56
Site, S	1	12.82	23.80**	5.18	37.84**
H \times S	5	1.58	2.93*	1.15	8.44*
Residual	12	0.54		0.13	
<i>H. popeiana</i>					
Height, H	5	2.53	1.46	6.00	7.28*
Site, S	1	9.42	37.62**	11.13	27.46**
H \times S	5	1.73	6.94*	0.76	1.89
Residual	12	0.25		0.40	

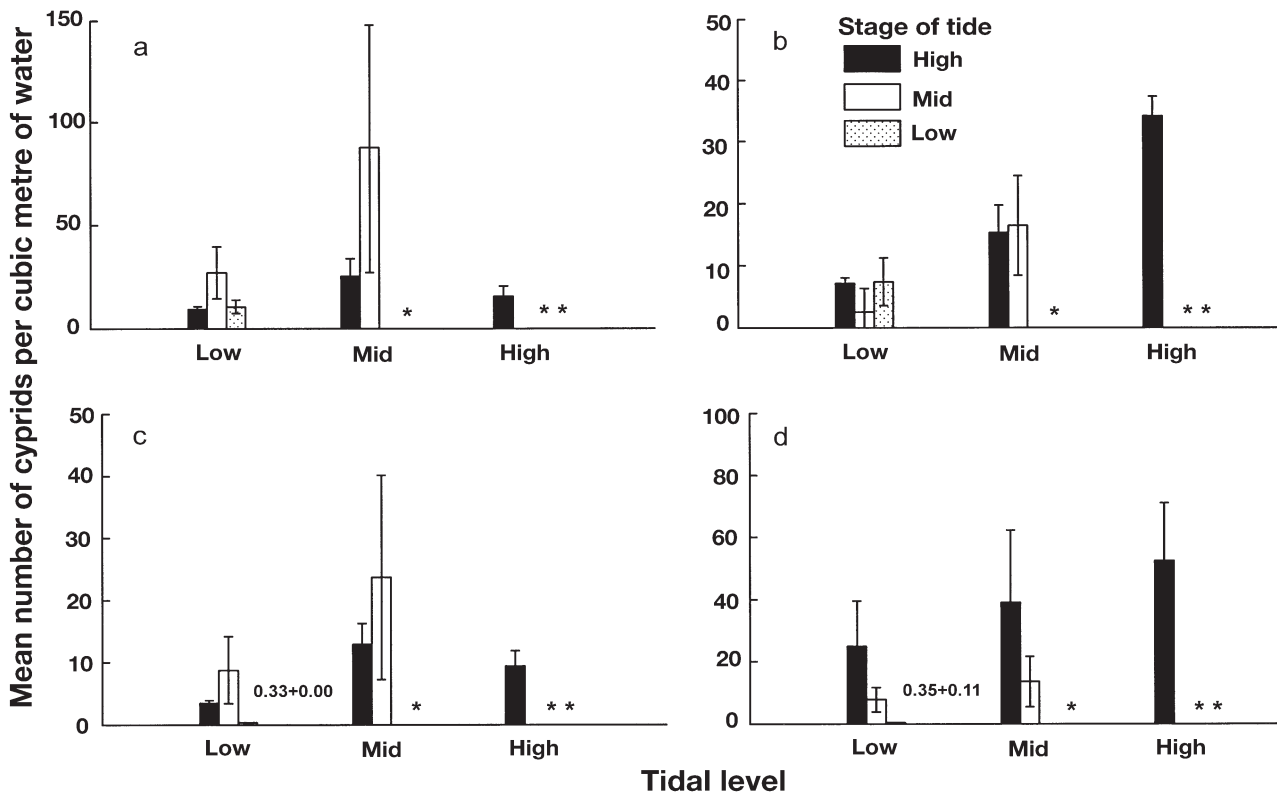


Fig. 2. (a, b) *Elminius covertus* and (c, d) *Hexaminius popeiana*. Densities of cyprids at low- mid- and high-tide levels at differing stages of the tide in the seaward zone on 8 September (a, c) and 7 October (b, d) 1991 (2 sampling dates) at Woollooware Bay. Low tide level was sampled 3 times: during low L(L), mid L(M) and high tide level L(H); mid-tide level was sampled 2 times: during mid M(M), and high tide level M(H); and high tide level was sampled 1 time: during high tide level H. Data are means \pm SE (n = 2) per cubic metre of water. *no sampling was possible because this combination of tidal level and stage of tide did not exist

Table 4. *Elminius covertus*. Analysis of densities of settlers, recruits and adults from the 1990 cohort: (a) between zones at mid-tidal level at Woollooware Bay; data were not transformed because Cochran's test was not significant; each analysis was a combination of fixed factors (zone) and random factor (tree nested in zone); (b) among tidal levels in the seaward zone at Woollooware Bay; data were not transformed because Cochran's test was not significant; each analysis was a combination of fixed factors (tide height) and random (site and tree nested in site). *p < 0.05; **p < 0.01

Source of variation	df	Settlers (1)		Recruits (2)		Adults (3)	
		MS	F	MS	F	MS	F
(a)							
Zone, Z	1	4186.12	14.89 < 0.06	3570.12	36.02*	1104.50	3.32
Tree (Z)	2	281.12	10.18*	99.12	2.21	332.24	3.83
Residual	4	27.62					
(b)							
Site, S	1	253.50	1.55	408.37	83.77**	2.90	0.02
Tree (site), T(S)	2	163.33	5.73**	4.87	0.20	136.31	3.36
Tidal height, H	2	1042.12	0.42	2730.50	4.82	2113.33	2630.80**
S \times H	2	2472.87	8.78*	566.00	7.37*	0.80	0.00
H \times T(S)	4	281.58	9.88**	76.75	3.09*	188.97	4.66**
Residual	12	28.5		24.87		40.51	

SNK test for (b): (1), (2) and (3) settlers, recruits and adults, H \times T(S) interaction; 3 out of 4 trees mid > low = high; Site C, 1 tree mid = low = high

than in the seaward zone (Fig. 4b,c), with 100 % mortality of settlers in the landward zone (Fig. 4b,c). The densities of recruits and adults were thus greater in the seaward than in the landward zone (Fig. 4c,d, Table 5b).

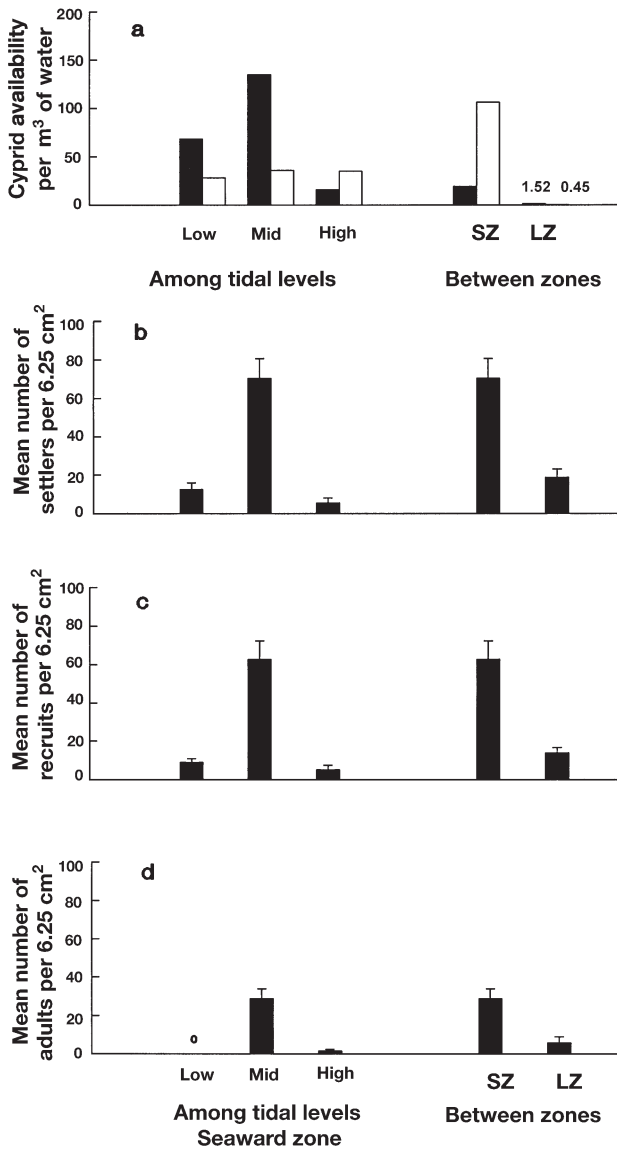


Fig. 3. *Elminius covertus*. Availability of cyprids and densities of settlers, recruits and adults on trees between zones at mid-tide level and among tidal levels in the seaward zone during August 1989 to June 1991 at Woolooware Bay. Data are means per 6.25 cm² ± SE (n = 2). (a) Cyprid availability (see third subsection of 'Materials and methods' for explanation); among tidal levels: black bars = 8 September 1991, open bars = 7 October 1991; between zones: black bar = 18 August 1990, open bar = 5 September 1990. (b) Density of settlers among tidal levels and between zones on the initial settlement census date, 21 September 1990. (c) Density of recruits among tidal levels and between zones on 16 October 1990. (d) Density of adults among tidal levels and between zones on 19 June 1991. SZ: seaward zone; LZ: landward zone

Comparing between species, *Elminius covertus* settled at mid-tide levels in greater densities and had less post-settlement mortality and greater survival than *Hexaminus popeiana* on bark (Figs. 3 & 4b,c,d).

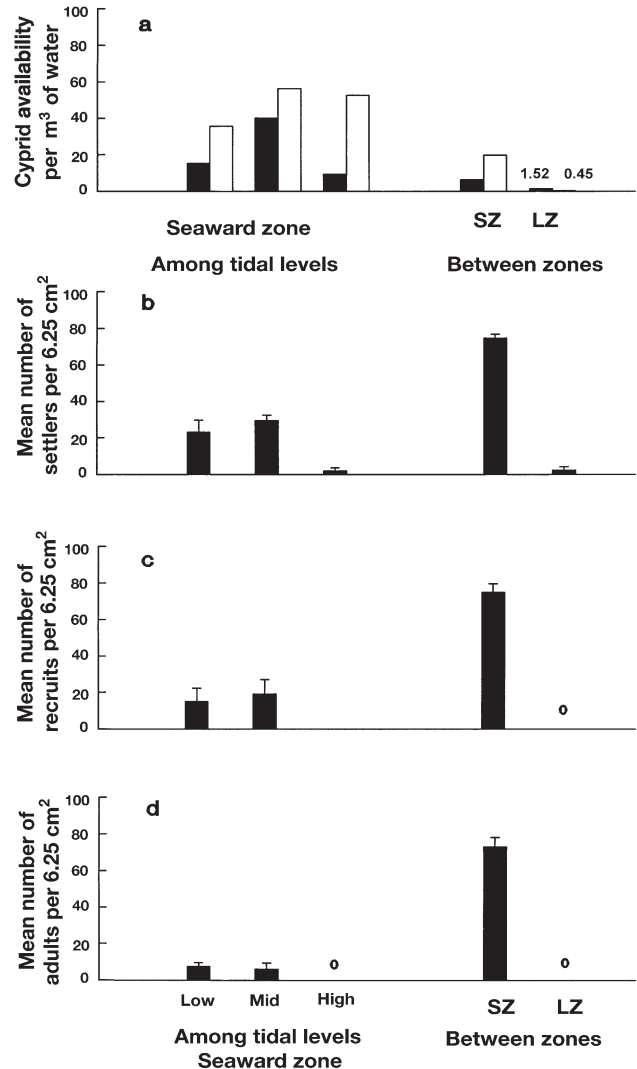


Fig. 4. *Hexaminus popeiana*. Availability of cyprids and densities of settlers, recruits and adults on trees and artificial trees (wooden blocks attached to poles) between zones at mid-tide level and among tidal levels in the seaward zone during March 1989 to December 1990 at Woolooware Bay. Data are means per 6.25 cm² ± SE (n = 2). (a) Cyprid availability (see third subsection of 'Materials and methods' for explanation); among tidal levels: black bars = 8 September 1991, open bars = 7 October 1991; between zones: black bar = 18 August 1990, open bar = 5 September 1990. (b) Density of settlers among tidal levels and between zones on the initial settlement census date, 22 March 1990. (c) Density of recruits among tidal levels and between zones after 1 mo, 24 April 1990. (d) Density of adults among tidal levels and between zones on 4 December 1990. For comparison between zones, (b), (c) and (d) indicate densities of settlers, recruits and adults on wooden blocks attached to poles (artificial trees)

Table 5. *Hexaminus popeiana*. Analysis of densities of settlers, recruits and adults: (a) among tidal levels on trees in the seaward zone at Woolooware Bay; data were not transformed because Cochran's test was not significant; each analysis was a combination of fixed factors (tidal height) and random (tree); (b) on artificial trees (Atree) between zones at mid-tidal level at Woolooware Bay. Data were not transformed for settlers or recruits because Cochran's test was not significant; for adults, data were not transformed: Cochran's test ($p < 0.05$) each analysis was a combination of fixed factors (zone) and random (artificial tree nested in zone). * $p < 0.05$; ** $p < 0.01$

Source of variation	df	Settlers (1)		Recruits (2)		Adults (3)	
		MS	F	MS	F	MS	F
(a)							
Tree, T	1	4.08	0.25	0.33	0.01	1.33	0.38
Height, H	2	312.25	4.21	153.25	0.91	25.08	0.82
H × T	2	74.08	4.47*	169.08	6.07*	30.58	8.74**
Residual	6	16.58		27.83		3.50	
(b)							
Zone, Z	1	9591.12	1257.85**	10658.00	519.90**	10585.12	699.84**
Atree (Z)	2	7.62	0.19	20.50	0.34	15.12	0.22
Residual	4	39.62		59.75		67.62	

SNK tests for (a): (1) and (2) settlers and recruits, H × T interaction; Tree 1, mid > low = high tidal level; Tree 2, low = mid > high tidal level; **SNK tests for (3) adults,** H × T interaction; Tree 1, mid > low = high; Tree 2, low > mid = high

DISCUSSION

The densities of cyprids of *Elminius covertus* and *Hexaminus popeiana* sampled in the mangrove forest at different distances from the seaward edge of the forest were correlated with the distribution and abundance of settlers. This pattern was present before and after adjusting the densities of cyprids, and expressing them in terms of immersion at different tidal levels (i.e. cyprid availability). An explanation of differences in cyprid supply between zones may be that the process of settlement itself could act as a significant drain on larval supply (Gaines & Roughgarden 1985). In a similar situation to cyprids passing from seaward sites to more landward sites on a rocky shore in Monterey Bay, California (Gaines et al. 1985), mangrove trees may act as a filter, with relatively few cyprids arriving in the landward zone (Gaines et al. 1985, Gaines & Roughgarden 1985). In addition, predation in the water column may occur throughout the mangrove forest, depleting larval abundance and resulting in few cyprids reaching the landward zone (Gaines & Roughgarden 1987, Young & Gotelli 1988, Young 1990). In contrast, a differential supply of planktotrophic larvae was not found to determine the pattern of *Balanus* spp. recruits in a mangrove forest in Florida (Bingham 1992), or crabs within an estuary in Grays Harbor, Washington, USA (Eggleston & Armstrong 1995). Larval supply in general, however, was considered the main factor structuring populations between intertidal and subtidal barnacles in a well protected harbour (Grosberg 1982) and epifaunal organisms with lecithotrophic larvae in mangrove forests (Bingham 1992). Such explanations consider larvae as passive particles

being transported to the habitat of the adult. The structural features or predators in the forest act as a filter with larvae relying on tidal amplitude to transport them to the upper reaches of the mangrove forest.

Evidence from this study shows, however, that cyprids may not act like passive particles in the water column. Cyprids were found only on high tides occurring during the night. This may indicate that cyprids are selecting when to enter the water column. Thus, an alternative model is that the behaviour of cyprids in the water column may itself determine the initial supply of cyprids. In this habitat, with low wave action and no swell, cyprids may be able to stay in the seaward zone and, by active swimming, prevent themselves from being swept upshore (Mileikovsky 1973, Young & Chia 1987). Other studies have also found larvae of barnacles retained in estuaries by a combination of vertical migration and time of the tide (Bousfield 1955). It has also been shown even in the high-wave-action areas of rocky shores that cyprid larvae can be active in detecting differences on the substratum at settlement, depending on chemical cues from conspecifics and microalgae (Meadows & Campbell 1972, Strathman & Branscomb 1979, Strathman et al. 1981, Raimondi 1988a,b, 1990, 1991). It is thus possible that cyprids of *Hexaminus popeiana* use cues on the trees in the seaward zone and select to settle on the first available tree, while cyprids of *Elminius covertus* move throughout the mangrove forest. This would explain why there are virtually no settlers or recruits of *H. popeiana* in the landward zone. This reasoning would suggest that the number of larvae available in the landward zone is a combination of filtration and larval behaviour in the water column and at settlement.

Among tidal levels at different vertical elevations in the water column, there was a clear pattern of vertical stratification in the water column of larvae of *Elminius covertus* and *Hexaminus popeiana*. The pattern was consistent at each sampling date. In September there were more cyprids available at mid-tide levels, and in October all tide levels were similar. At low-tide levels the presence of few settlers of *E. covertus* can be explained by the reduced supply of cyprids on only 1 date. It is possible that cyprids which do arrive there may also select not to settle because of the oysters (*Saccostrea commercialis*) present at this tidal level (Minchinton & Ross 1999): oysters may set up currents during feeding which larvae of barnacles avoid (Bushek 1988). Cyprids may also avoid settling at low-tide levels because of the adjacent muddy floor of the mangrove forest (Bayliss 1993). Mid-tide levels on each date sampled had an abundant supply of cyprids of *E. covertus*. These areas are where they settled most abundantly.

In contrast to *Elminius covertus*, there was no correlation between the densities of cyprids and settlers of *Hexaminus popeiana*. The availability of cyprids of *H. popeiana* at each sampling date were least at low-tide levels, while the density of settlers on bark were greatest at low- and mid-tide levels. Cyprid supply can, however, be considered a combination of the density of cyprids, how long they have access to the substratum, and integration over many tidal cycles. Cyprids of each species were present only on high tides occurring at night. The majority of high tides occurring during the night in the settlement season of *E. covertus* are of great amplitude. These 2 factors combined (behaviour of larvae and availability of larvae) provides this species with the opportunity for transport to the high-tide levels of the trunks in the seaward zone and into the landward zones of the forest. In contrast, the settlement season of *H. popeiana* coincides with a small percentage of high-amplitude tides occurring at night. This means that the cyprids of *H. popeiana* will have less opportunity for transport to the high-tide levels, and more to the low- to mid-tide levels on the trunks of trees. To determine the significance of the vertical stratification of cyprids in the seaward zone requires integration over many tidal cycles (Gaines & Bertness 1992).

This is not the first study to find a vertical stratification of cyprid larvae in the water column. In a protected harbour area, Grosberg (1982) found clear patterns of vertical stratification for an intertidal and a subtidal barnacle. Within the vertical range of the intertidal species *Balanus glandula*, however, there was no clear pattern between cyprids and settlers. On an exposed rocky intertidal shore, the vertical distribution of cyprids of *Semibalanus balanoides* has been shown to reflect the vertical distribution of settlers,

with more cyprids and settlers at low-tide levels and fewer at mid- and high-tide levels (Minchinton & Scheibling 1991). This pattern was only apparent after correcting for the period each level was immersed (Minchinton & Scheibling 1991). The vertical stratification of larvae of *Elminius covertus* in this study, however, can explain the more abundant pattern of settlers at mid-tide level, is within the vertical range of the organism, and occurred before and after correcting for the period of time each shore level was immersed.

Patterns of settlement on tree bark for each species were strongly correlated with patterns of recruitment and density of adults. The amount of post-settlement mortality differed, depending on the tidal level and species, but did not change the differential distribution established at settlement. Densities of settlers, recruits and adults of *Elminius covertus* were greater in the seaward than in the landward zone, and in the seaward zone were greater at mid- than at low- and high-tide levels on trunks of trees. There was 100% mortality at low-tide levels. Survival was greatest in areas of greatest settlement (mid-tide levels). Similar to this study, Bayliss (1993) found that the density patterns of settlers of *E. adelaidae* matched the density patterns of adults. There were more settlers and adults in the mid area of pneumatophores and greater settlement of cyprids with adult conspecifics. Bayliss's (1993) study suggested that adults of *E. adelaidae* may act as a cue for cyprids at settlement, as has been found for other species of barnacles (e.g. Raimondi 1988a,b). Thus, the presence of more adults of *E. covertus* at mid-tide levels may act as an attractant to cyprids, causing more settlement in these areas.

For *Hexaminus popeiana*, mortality did not follow the same pattern as for *Elminius covertus*. Mortality of *H. popeiana* on tree bark increased with increasing tidal level. This has been found in other studies with barnacles on rocky shores (Wethey 1984, Bertness et al. 1992). The densities of settlers, recruits and adults were greater at low- and mid-tide levels and less at high-tide level, as has been found in other studies (Coates & McKillup 1995, Ross & Underwood 1997). There was 100% mortality at high-tide levels, with survival greatest in areas of greatest settlement (low- and mid-tide levels).

The factors causing the mortality of each species on tree bark is unknown. At high-tide levels, increased desiccation may be responsible for the mortality of *Elminius covertus*, as the timing of the greatest mortality coincided with summer (Ross 1993, Ross & Underwood 1997). Recent reviews on mortality of juvenile benthic invertebrates have suggested that desiccation and predation are widespread and may often be the most important causes of early juvenile mortality (Gosselin & Qian 1997, Hunt & Scheibling 1997). On the

trunks of trees there are no predatory gastropods. The gastropod *Bembicium auratum*, which feeds on microalgae, is probably not a significant cause of mortality because it is more often associated with the shells of oysters rather than the bark of trunks (Underwood & Barrett 1990, Anderson 1999, Minchinton & Ross 1999). Other studies have found that predation by whelks changed the pattern of settlement at low-tide levels (Minchinton & Scheibling 1991), whereas predation by fishes and cannibalism uncoupled the relationship between settlement and recruitment of crabs in an estuary (Eggleston & Armstrong 1995; for and reviews on mortality of other invertebrates in differing habitats see Gosselin & Qian 1997 and Hunt & Scheibling 1997).

Between zones, temporal and spatial patterns of cyprids are the main determinants of spatial and temporal patterns of settlers, recruits and adult barnacles in this mangrove forest. In mangrove forests, many organisms with planktonic larvae (including the barnacles) live in the upper reaches of the forest and the saltmarsh. For the saltmarsh to be covered in water requires a tidal amplitude of >1.7 m (spring tides). Larvae need to first access the habitat of the adult to be able to select where in the habitat of the adult they will settle. In the absence of wave action and swell, which would increase the absolute tidal range in habitats with strong wave action such as rocky shores, organisms in mangroves may be more dependent on the amplitude of the tide for transport into the habitat of the adult. Transport of later-stage pre-settlement larvae on nocturnal spring-flood tides has been found for crabs (Brookins & Epifanio 1985, Epifanio et al. 1989, Dittel & Epifanio 1990, van Montfrans et al. 1990), molluscs in saltmarshes (Russell-Hunter et al. 1972) and polychaetes in mud flats (Levin 1986). The differences in densities of settlers between zones correlates with the survival of the barnacles. *Hexaminus popeiana* as an adult is rarely found in the landward zone (Ross & Underwood 1997); those larvae choosing to settle in these areas suffer great mortality, remain small in aperture length due to slow growth (Coates & McKillup 1995), and do not reach reproductive maturity (Ross 1993). In contrast, survival of *Elminius covertus* settlers in each zone is similar, and reproductive maturity occurs the following year (Ross 1993).

Previous studies from rocky shores on cyprid supply attribute some of the differences in spatial and temporal abundance of settlers to variation in the supply of cyprids acting as passive particles in the water column. These studies have not attributed the variation to larval behaviour, which may influence the number of the cyprids in the water column. Differential larval supply has been predicted as an important factor in structuring the populations in other environments with calm wave action (Grosberg 1982, Bingham 1992). This

study, however, has shown a differential supply of cyprids coupled with variation in the supply of cyprids (perhaps because of larval behaviour) between day and night high tides. This has not been found by other studies. In comparison to habitats such as rock platforms with great waveaction, mangrove forests are areas of calm waveaction with no major predatory gastropods. Generalisations about the importance of cyprid supply to the structure of a population need to be done in a variety of habitats with different conditions of exposure and availability of predators before generalisations regarding their role and importance can be made.

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