Consistent spatial patterns of arrival of larvae of the honeycomb barnacle *Chamaesipho tasmanica* Foster and Anderson in New South Wales

C.J. Jeffery*, A.J. Underwood

Centre for Research on Ecological Impacts of Coastal Cities and Institute of Marine Ecology, Marine Ecology Laboratories, A11, University of Sydney, Sydney, NSW 2006, Australia

Received 9 December 1999; received in revised form 6 June 2000; accepted 13 June 2000

Abstract

The small honeycomb barnacle *Chamaesipho tasmanica* occurs in patches at high levels on exposed rocky shores, but often carpets the substratum at mid-shore levels of sheltered shores in south-eastern Australia. Studies of larval supply from 1990 to 1993 and concurrent monitoring of settlement from 1991 to 1993 revealed that larval arrival and settlement were typified by trickles of larvae from late July to December (although some were observed in January and February). Major pulses of arriving cyprids were also recorded once or twice each year. While local patterns of water-flow had no impact on numbers of larvae arriving, major peaks of larval arrival were always associated with strong southerly winds during new and full moons. There was a consistent spatial pattern of larval supply; more larvae were always caught in one area low on the shore. Numbers of larvae caught were, however, very sporadic within a given year and very variable from one year to the next. While the different numbers of cyprids in different places cannot be explained by cyprids arriving first on lower parts of the shore, longer periods of submersion nor aggregations of larvae in the plankton, recurrent patterns of arrival of larvae suggest that local site-specific characteristics have an influence on the demography of populations of this species. Variations in numbers of larvae arriving were responsible for the variations in distributions of juveniles on the substratum.

Keywords: Australia; Barnacle; *Chamaesipho*; Cyprid; Larvae; Larval supply; Plankton traps; Water-flow

*Corresponding author. Present address: Centre for Marine and Coastal Studies, School of Biological Sciences, University of New South Wales, Sydney, NSW 2052, Australia. Tel.: +61-2-9385-1825; fax: +61-2-9662-7995.

E-mail address: c.jeffery@unsw.edu.au (C.J. Jeffery).

0022-0981/00/$ - see front matter Crown copyright © 2000 Published by Elsevier Science B.V. All rights reserved.

PII: S0022-0981(00)00241-0
1. Introduction

Many demographic models in ecology are based on closed populations (Roughgarden and Iwasa, 1986) but many marine species such as barnacles have open populations with sessile adults and long-lived dispersive larval stages. Early models to explain settlement of sessile marine invertebrates, especially barnacles, were based on populations which had large numbers of larvae arriving to settle (Southward and Crisp, 1954, 1956; Barnes, 1956; Connell, 1961a,b; Paine, 1974; Kendall et al., 1985). Because larval supply was considered to be unlimited, these early models emphasised that competition, predation and physical disturbance in the adult stage determined the abundances of intertidal organisms (Connell, 1961a,b, 1970; Dayton, 1971; Paine, 1974, 1984; Menge, 1976; Menge and Sutherland, 1976; Lubchenco and Menge, 1978; Menge and Lubchenco, 1981). More recent studies have linked barnacle populations with larval supply (Grosberg, 1982; Hawkins and Hartnoll, 1982; Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Kendall et al., 1985).

Where larval settlement is small, however, very different patterns emerge than from areas where larval settlement is large (Underwood et al., 1983; Underwood and Denley, 1984), so patterns of distribution could also be due to processes of settlement or recruitment. Other studies support the relationship between larval settlement and assemblages of species (Denley and Underwood, 1979; Grosberg, 1982; Keough, 1983; Caffey, 1985; Connell, 1985; Gaines and Roughgarden, 1985, 1987; Roughgarden et al., 1985; Roughgarden and Iwasa, 1986; Raimondi, 1988a,b, 1990, 1991; Minchinton and Scheibling, 1991; Bertness et al., 1992; Hurlbut, 1992; Gaines and Bertness, 1993; Pineda, 1994; Carroll, 1996; Robles, 1997).

Larval delivery or supply (Raimondi, 1991) may therefore influence the abundance and distribution of these open populations, so processes influencing the numbers of larvae arriving in different places will be important. For example, Roughgarden et al. (1991, 1994) have demonstrated that recruitment pulses of barnacles on the Californian coast are associated with the accumulation of larvae in fronts which are driven shorewards and deposited on the coast when winds relax. Other studies at large spatial scales have shown a positive relationship with onshore winds (Hawkins and Hartnoll, 1982; Bertness et al., 1996) or no relationship (Shanks, 1986; Wethey, 1986). Hydrodynamics at small spatial scales, such as direction of flow, turbulence and shear stress, have also been shown to have roles in determining arrival and settlement of cyprids (Mullineaux and Butman, 1991; Mullineaux and Garland, 1993).

In Botany Bay (New South Wales, Australia), there are great spatial variations in densities of the honeycomb barnacle *Chamaesipho tasmanica*. In 1989, early in this study, larger numbers of juveniles and adults were recorded on lower than on upper mid-littoral shores. If larval supply is responsible for these variations in abundances it can be predicted that numbers of larvae settling on the shore should be directly related to the numbers arriving in the plankton. Moreover, if traps were set to catch cyprids at different levels on the shore at one site, there would be more larvae caught in traps low on the shore than further up the shore. Barnacle cyprids were also observed to arrive in major pulses in September and October, 1989 close to full moons when strong southerly winds and waves more than 1 m prevailed. If such meteorological patterns are closely
associated with pulses of arrival of barnacles, these conditions should also coincide with future peaks of larval supply.

Further, the densities of *Chamaesipho* differ from those of another species *Tetraclitella purpurascens* (Wood). Again, if differences in larval supply are responsible, there should be consistent differences in numbers of larvae of the two species arriving, and these numbers should be consistent with the subsequent numbers of barnacles of the two species.

More *Chamaesipho* inhabit lower mid-littoral shores whereas *Tetraclitella* are evenly distributed across the mid-littoral shore in more shaded areas (Denley and Underwood, 1979). These different spatial distributions suggest that different processes are operating. For example, some studies have demonstrated that more larvae may arrive on lower areas of a shore because they settle here first and settle later on upper areas (Roughgarden et al., 1988). Different positions of larvae in the water column (Grosberg, 1982; Gaines et al., 1985) may also explain different spatial patterns. Variations in amount of water flowing over different areas may also be responsible for spatial distributions of these barnacles so that there should be close correlations between patterns of water-flow and numbers of cyprids arriving.

From the initial field observations of differences in distributions of the barnacles, it was predicted that physical processes at large spatial scales (lunar cycles, wind direction, wind speed and wave height) and at small spatial scales (water-flow) would affect larval supply, hence spatial distributions of juveniles on the substratum. These hypotheses were tested on a shore in New South Wales.

2. Materials and methods

2.1. Study area

*Chamaesipho tasmanica* were studied in the mid-shore regions of the Cape Banks Scientific Marine Research Area, Botany Bay, New South Wales (34°00′ S, 150°15′ E). The study area faces south and is prone to the influence of south-east swells which can produce waves larger than 3 m during the winter months (Short and Trenaman, 1992). Tides are semi-diurnal and range over 2 m.

Settlement was defined as the period of attachment and metamorphosis of cyprid larvae (Underwood, 1979; Underwood and Denley, 1984; Connell, 1985). Settlement in *C. tasmanica* is considered to include the cyprid stage which lasts for less than 1 day, the 2–3-day six-plate metamorph stage and the less than 4-day four-plate juvenile stage (Jeffery, 1997).

2.2. Field experiments

2.2.1. Larval supply of *Chamaesipho tasmanica*

Plankton traps (Otaiza, 1989) were used to estimate the numbers of larvae arriving at one site and two heights on the shore (low and mid/upper) within the distribution of *Chamaesipho*. Each trap consisted of a top made from a 90% PVC elbow, 90 mm in
diameter, secured by a bracket and two screws into rawl plugs in the substratum. The bottom half of the trap, containing a modified PVC filter funnel to prevent backflow of water, was a PVC cup, 90 mm in diameter and 100 mm high, inserted underneath the elbow and secured by three rubber bands. The sides of the PVC cup had eight 2.5 cm circular holes covered with 100 µm plankton mesh to allow water to drain. The top part of the trap faced the incoming waves and traps were placed so that the bottom edge of the opening of the upper part was flush with the substratum. This was done by putting traps on the edge of crevices, so that the PVC cup extended below the substratum (for further details, see Otaiza, 1989).

Plankton traps were secured to the substratum on low and mid/upper heights at one site in a nested design from late July generally to late December 1990 to 1993. Duplicate sets, each of three traps, were put at each of low (1.02 m above MLWS) and mid/upper (1.17 m above MLWS) heights of Chamaesipho's distribution within the mid-shore level. These sets of traps will be referred to hereafter as 1 Low, 2 Low, 1 Mid/Upper and 2 Mid/Upper. Sets of traps low on the shore were 5 m apart; sets at the higher level were 3 m apart and were 6 m (vertically) away from lower sets. Traps within each set were approximately 30 cm apart; observations on distributions of adults suggest that these can be considered spatially independent. In 1990, traps were put on the rock platform every fortnight for 5 days leading up to the new and full moons to coincide with anticipated settlement. From 1991 to 1993, traps were also secured on the substratum one day after new and full moons. Plankton cups were collected and replaced daily and their contents examined under a binocular microscope; therefore, the numbers of cyprids captured during two tidal cycles were recorded.

2.2.2. Wind direction, wind speed and wave height

Wind direction was recorded once daily when plankton traps were set. Additional average hourly wind data from July, 1989 to December, 1993 were obtained for La Perouse, close to Cape Banks, from Robert Hyde (School of Earth Sciences at Macquarie University). Data were only used from 1 Low set of traps (n = 3) for 6 peaks of larval arrival during 1990–1993 (see Fig. 2); each peak encompassed 24 h of data from low tide of one day to low tide of the next, thus including two tidal cycles when cyprids would have been arriving. Wind speed was also averaged over this 24-h period. Approximate heights of waves were also recorded daily when plankton traps were set. Data were provided by Bruce Hudson from the Maritime Services Board (Sydney Ports Authority) from offshore waverider buoys anchored in 73 m water depth just south of Cape Banks off Botany Bay (34°02’ S, 151°15’ E). Mean monthly heights from 1990 to 1993 (waverider buoys 1 and 4) and daily averages of the highest third of waves during six peaks of larval arrival from 1990 to 1993 (waverider buoy number 4) were used.

2.2.3. Water-flow

Clod cards were used to measure water-flow; weight lost from each card was proportional to water velocity over a wide range of measurements (Jokiel and Morrissey, 1993). Hemispherical clods of Velmix Dental Stone (7:23 water/powder) were prepared in the laboratory (see Doty, 1971; Jokiel and Morrissey, 1993). The % loss of dry weight from each of these over a 24-h period was a measure of water-flow.
Large clods (4.2 cm in diameter and 2.0 cm high) were attached to 9 × 6 × 0.1 cm aluminium plates with Selley’s silicone RTV marine sealant and the plates were secured to the substratum next to each plankton trap with screws in rawl plugs. To determine the relative amount of water passing through plankton traps, small hemispherical clods of dental cement (1.7 cm in diameter and 1.5 cm high) were each glued to a 2 × 2 × 0.1 cm aluminium plate and then one of these glued to the bottom of each removable filtering cup of the plankton trap. All clods were dried at 60°C for 24 h and reweighed to ascertain the % mass lost from each clod in the field over 24 h (two tides).

The experimental design was the same as that used for testing the hypothesis about larval supply. Clods on the substratum and in plankton traps were emplaced and removed concurrently, except that clods could not be fixed to the substratum on 8th September 1992 (when a major peak of larval arrival occurred). All clod cards were replaced daily for 5 days up to and 1 day after each new and full moon (2 × 72 clod plates per lunar sampling period) from early September (8th September — plankton trap clods; 11th September — substratum clods) until mid December, 1992 and from late July until mid December, 1993.

2.2.4. Settlement on the substratum

In July in each year from 1991 to 1993, a 6-cm diameter patch was cleared within aggregations of barnacles, or in areas where barnacles were sparse, next to each plankton trap (n = 3). Remnants of adults were removed with a hammer and cold chisel. Each replicate was washed after preparation to remove any fine particles of sand. Generally, during the lunar sampling periods from late July to late December, cyprids and settlers were counted and removed daily with a dissecting needle concurrent with the removal of plankton trap samples from the previous two tidal cycles. Settlers could not be counted on 9th September 1992 after a major peak of arrival occurred; plankton samples were, however, collected on that day.

3. Results

3.1. Larval supply of Chamaesipho tasmanica

Each year from 1990 to 1993, larval supply was characterised by trickles of larvae, punctuated by one or two major pulses, from the end of July to mid-December (Figs. 1 and 2). These major peaks of arrival of larvae occurred 2 days before the full moon of 4th October 1990, on the new moon of 17th November 1990, 1 day before the new moon of 8th September 1991, 1 day after the new moon of 6th November 1991, 4 days before the full moon of 12th September 1992 and on the new moon of 14th November 1993 (Fig. 2).

Despite temporal variation, there were consistent spatial patterns in arrival of cyprid larvae of *Chamaesipho* within shore levels and among sets of traps at these different times (Fig. 2). On lower mid-littoral shores, more *Chamaesipho* were always caught in 1 Low than 2 Low traps. Numbers of larvae arriving were always similar for 2 Low and 1 and 2 Mid/Upper traps (Figs. 1 and 2; Table 1). Thus, larval supply differed from low to
mid/upper heights among sets of traps and most larvae were consistently caught in one 
set of Low shore traps.

3.2. Wind direction, wind speed and wave height

Winds from the south (south, south-east, south-west and south-south-west) prevailed 
during peaks of larval arrival 1990–1993, except on 7th September 1991 when least 
cyprids of the six peaks were caught and north-east and north-west winds predominated: 
north-east winds were two to three times stronger than north-west winds and southerly 
winds blew for 1 h before low tide on 8th September (Fig. 3).

There was a relationship between mean numbers of cyprids arriving at each larval 
peak for 1 Low set of traps and the average wind speed over 24 h for two tidal cycles 
before these pulses of cyprids were recorded \((r = 0.76; P = 0.08; n = 6)\). Although more 
cyprids arrived as wind velocities increased, cyprid numbers were fewer at the two 
highest velocities than at a lower speed within the range recorded: average 24-h wind 
speeds ranged from 3.6 to 6.8 m \(s^{-1}\) during these larval peaks.

Data for mean monthly wave heights (Maritime Services Board, Sydney Ports 
Authority, unpublished data) indicate that, at Cape Banks, highest waves predominated 
in February, March, June and October from 1990 to 1993 although large waves can 
occur at any time. There was a strong correlation between mean numbers of cyprids 
arriving at each larval peak and mean daily height of waves during that peak \((r = 0.85; \)
Fig. 2. Mean numbers of cyprids captured in sets of traps (n = 3) nested in low and mid/upper heights of *Chamaesipho*’s distribution; data are from peaks of arrival on 2nd October 1990, 17th November 1990, 7th September 1991, 7th November 1991, 8th September 1992 and 4th November 1993. SNK results refer to all dates.

More cyprids arrived when waves were high: average wave heights ranged from 1.2 to 1.8 m during these larval peaks.

South-east waves occur in 41% of the year with a predominance from June to August.

### Table 1

Analysis of mean numbers of cyprids in sets of plankton traps (n = 3) nested in low and mid/upper levels of *Chamaesipho*’s distribution on the shore at one site: data are from peaks of arrival on 2nd October 1990, 17th November 1990, 7th September 1991, 7th November 1991, 8th September 1992 and 14th November 1993

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (T)</td>
<td>5</td>
<td>4.94</td>
<td>9.84</td>
<td>**</td>
</tr>
<tr>
<td>Height (H)</td>
<td>1</td>
<td>23.83</td>
<td>1.65</td>
<td>ns</td>
</tr>
<tr>
<td>Set (Height) (S(H))</td>
<td>2</td>
<td>14.44</td>
<td>32.81</td>
<td>***</td>
</tr>
<tr>
<td>T × H</td>
<td>5</td>
<td>0.12</td>
<td>0.23</td>
<td>ns</td>
</tr>
<tr>
<td>T × S(H)</td>
<td>10</td>
<td>0.50</td>
<td>1.14</td>
<td>ns</td>
</tr>
<tr>
<td>Residual</td>
<td>48</td>
<td>0.44</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* ns, not significant at *P*>0.05; *P*<0.05; **P**<0.01; ***P**<0.001. Analysis of variance, data transformed Log(x+1); Cochran’s test, *P*>0.05.
and a gradual decrease from August through summer (Short and Trenaman, 1992). While south-east waves also dominate from August to November, there is an obvious decline in height and frequency in November (Short and Trenaman, 1992). In fact, in this study, when strong south-easterly winds and waves prevailed, larval peaks of *Chamaesipho* occurred.

3.3. Water-flow

During major peaks of arrival of larvae, more *Chamaesipho* cyprids were always caught in 1 Low traps than 2 Low traps or those at mid/upper heights (Figs. 1 and 2; Table 1). On peaks of larval arrival at 8th September 1992 and 14th November 1993, there was no significant difference in percentage loss from clod cards. Therefore,
water-flow through all sets of traps was similar across the substratum at the different places (Figs. 4 and 5). Therefore, water-flow could not account for the differences in larval supply from place to place. Percentage mass lost from plankton trap clods and from substratum clods were positively correlated at each place in 1992 and 1993 (Fig. 6).

3.4. Larval supply of Tetraclitella purpurascens

Very few Tetraclitella cyprids were caught coincidentally with Chamaesipho during this study from 1990 to 1992 and none were caught in 1993. When Tetraclitella larvae were, however, caught with those of Chamaesipho, there were different patterns for major peaks of arrival on the mid-littoral shore. Many more cyprids of Chamaesipho were caught in one set of traps low on the shore (Fig. 2; Table 1). When peaks of arrival for Tetraclitella were recorded, there was, however, no significant difference in numbers of cyprids of Tetraclitella caught among sets of traps (Fig. 7). There was also no relationship between numbers of cyprids of Tetraclitella and Chamaesipho caught when major pulses of arrival of Chamaesipho were recorded on 7th November 1991 ($r = 0.04$; $P > 0.05$; $n = 12$) nor when pulses of Tetraclitella occurred on 5th and 6th November 1991 ($r = 0.02$; $P > 0.05$; $n = 24$).

No difference in percentage mass lost from each set of clods in plankton traps was recorded for the arrival peak of Tetraclitella on 20th November 1992 (Fig. 8), when no
Chamaesipho were caught coincidentally (Jeffery, 1997), nor for peaks of Chamaesipho recorded on 8th September 1992 and 14th November 1993 (Figs. 4 and 5). That is, water-flow through traps was similar within and among shore levels for the peaks of larval arrival despite differences in patterns of larval arrival for the two species. In contrast, patterns of arrival of Tetraclitella mirrored patterns of water-flow (Fig. 8), so that water-flow may be implicated in determining larval supply of Tetraclitella.

3.5. Settlement on the substratum

From late July to late December in each year from 1991 to 1993, the daily mean numbers of cyprids caught in plankton traps were generally positively correlated with daily mean numbers of settlers on the substratum next to these traps at low and mid/upper heights within Chamaesipho’s distribution (Table 2). That is, the numbers of
cyprids arriving were directly related to the numbers of larvae settling (Table 2); therefore, larval supply is implicated in determining the distributions of juvenile *C. tasmanica*.

### 3.6. Total numbers of cyprids and settlers

There were generally more settlers on the substratum than cyprids caught in traps (Fig. 9; Table 3) which could reflect inefficiency of traps rather than true larval availability. Despite this discrepancy, there were strong correlations between daily numbers of cyprids arriving and daily numbers settling on the substratum (Table 2). A decline in total numbers of larvae arriving was recorded from 1990 to 1993 (Fig. 10).

### 4. Discussion

Nearshore transport mechanisms have been shown to be primarily responsible for determining numbers and patterns of cyprid larvae available for settlement (Hawkins and Hartnoll, 1982; Roughgarden et al., 1991, 1994; Bertness et al., 1996). For example, deposition of barnacle larvae on shores can be determined by wind driven currents (Hawkins and Hartnoll, 1982), or may vary with lunar cycles (Wethey, 1986),
Fig. 7. Mean numbers of cyprids of *Tetraclitella* captured in sets of traps (*n* = 3) nested in low and mid/upper heights of *Chamaesipho*’s distribution on the shore at one site during peaks of arrival of *Tetraclitella* from 5th to 7th November 1991 and on 20th November 1992. SNK results refer to all dates.
suggesting that cyprids in offshore fronts use onshore currents to arrive and settle on rocky shores (Shanks, 1986). In this study, major pulses of arrival of *Chamaesipho* cyprids were also associated with physical processes. In fact, because cyprids settle soon after reaching the shore, onshore transport must be implicated (Shanks, 1986). Furthermore, while not tested for in this study, internal waves may also be involved because internal waves can distribute larvae shorewards and in different densities along a shore (Shanks and Wright, 1987; Roughgarden et al., 1991).

*Chamaesipho* larvae arrived at Cape Banks from late July to early December, with

![Figure 8](image.png)

**Fig. 8.** Mean number of cyprids of *Tetraclitella* and mean % loss of plankton trap clods per set of traps (*n* = 3) during peak of arrival on 20th November 1992.

Table 2

Summary of analyses of relationship between daily mean numbers of cyprids caught in plankton traps and daily mean numbers of new settlers (lagged by 1 day) at two heights (low and mid/upper) and one site on the shore within *Chamaesipho*’s distribution (data are generally from late July to late December 1991 to 1993)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>41</td>
<td>0.57</td>
<td>&lt;0.001</td>
<td>31</td>
<td>0.41</td>
<td>&lt;0.05</td>
<td>47</td>
<td>0.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>41</td>
<td>0.44</td>
<td>&lt;0.01</td>
<td>31</td>
<td>0.17</td>
<td>ns</td>
<td>47</td>
<td>0.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>MU</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>41</td>
<td>0.46</td>
<td>&lt;0.01</td>
<td>31</td>
<td>0.90</td>
<td>&lt;0.001</td>
<td>47</td>
<td>0.97</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>41</td>
<td>0.44</td>
<td>&lt;0.01</td>
<td>31</td>
<td>0.89</td>
<td>&lt;0.001</td>
<td>47</td>
<td>0.08</td>
<td>ns</td>
</tr>
</tbody>
</table>
main peaks once or twice each year, generally in September, October and November, 1989 to 1993. These major pulses of larval arrival were always close to, or on, new and full moons in association with high velocity onshore southerly winds (3.6–6.8 m s\(^{-1}\)) when wave heights near Cape Banks ranged from 1.2 to 1.8 m. Wind direction, wind

Table 3
Analysis of total numbers of cyprids caught in sets of plankton traps and total numbers of settlers in sets of cleared patches on the substratum (n = 3) at two heights (low and mid/upper) and one site on the shore within Chamaesipho’s distribution\(^*\)

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (T)</td>
<td>1</td>
<td>273.87</td>
<td>38.7</td>
<td>*</td>
</tr>
<tr>
<td>Height (H)</td>
<td>1</td>
<td>79.98</td>
<td>21.49</td>
<td>*</td>
</tr>
<tr>
<td>Set(Height) (S(H))</td>
<td>2</td>
<td>3.72</td>
<td>1.40</td>
<td></td>
</tr>
<tr>
<td>Cyprids vs. settlers (CSe)</td>
<td>1</td>
<td>181.11</td>
<td>15.79</td>
<td>0.058</td>
</tr>
<tr>
<td>T × H</td>
<td>2</td>
<td>7.08</td>
<td>2.65</td>
<td></td>
</tr>
<tr>
<td>T × S(H)</td>
<td>2</td>
<td>34.84</td>
<td>20.40</td>
<td>*</td>
</tr>
<tr>
<td>H × CSe</td>
<td>1</td>
<td>0.08</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>CSe × S(H)</td>
<td>2</td>
<td>11.47</td>
<td>4.30</td>
<td>*</td>
</tr>
<tr>
<td>T × H × CSe</td>
<td>1</td>
<td>1.82</td>
<td>1.07</td>
<td></td>
</tr>
<tr>
<td>CSe × T × S(H)</td>
<td>2</td>
<td>1.71</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>32</td>
<td>2.67</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^*\) Experiments were renewed each year and data are totals from December in 1991 and 1993. ns, not significant at P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001. Analysis of variance, data transformed (x + 1)^{\frac{1}{2}}; Cochran’s test, P > 0.05.
speed and wave height are therefore implicated in mechanisms determining larval supply of *Chamaesipho*. No cyprids, however, arrived and settled when very strong winds and seas predominated.

This study also indicates that, once barnacles arrive, other processes may influence spatial patterns at smaller scales. For example, the consistent spatial patterns of *Chamaesipho* cyprids recorded during major pulses of arrival, with one set of traps low on the shore always capturing more cyprid larvae than all other traps, suggest that site-specific characteristics may have a primary role in influencing numbers that arrive and settle. In fact, patterns of arrival of *T. purpurascens* were similar to patterns of water-flow so that site-specific water-flow may be implicated in determining larval supply of this species. Because numbers of cyprids were not correlated between the two species and because arrival patterns of *Chamaesipho* did not match patterns of water-flow, these different patterns of larval supply are not simply due to water-flow over different places at one site. Other processes must also be operating to determine larval supply of the two species.

It has previously been suggested that the models of more larvae settling first on lower shores (Roughgarden et al., 1988), longer periods of submersion (Denley and Underwood, 1979; Underwood and Denley, 1984), and aggregations of cyprids in the plankton (De Wolf, 1973; Gaines et al., 1985; Roughgarden et al., 1987, 1988) may be responsible to some degree for differences in larval supply. Because spatial patterns of larval supply of *Chamaesipho* differed consistently low on the shore from 1990 to 1993,
the first two models must be discounted as processes determining larval supply. The third model may still be true — such aggregations may change from place to place and from year to year. It is, however, unknown whether the position of larvae in the water column (Grosberg, 1982; Gaines et al., 1985) contributes to the different spatial patterns exhibited by *Chamaesipho* and *Tetraclitella* which were caught coincidentally.

While local patterns of water-flow do not influence larval supply of *Chamaesipho*, water-flow direction and small-scale turbulence, which were not measured in this study, may contribute to the different numbers of larvae recorded in different places. For example, turbulence can transport and concentrate cyprid larvae in their normal habitat (Gaines et al., 1985; Denny and Shibata, 1989). Turbulence can also be modified by topography of the substratum so that an association between roughness of the surface and slow water means that settlement is enhanced (Pawlik and Butman, 1993). In contrast, on exposed shores, wave-action is great and turbulence may prevent attachment of larvae (Crisp, 1955; Bushek, 1988; Pawlik and Butman, 1993) or cause detachment of settled larvae (Eckman et al., 1990). More *Chamaesipho* larvae may therefore arrive on the more turbulent exposed shores at Cape Banks than settlement data (Jeffery, 1997) suggest. Alternatively, exposed sites at Cape Banks are higher than sheltered sites and the upper limits of vertical distribution of intertidal species are also higher here than on sheltered shores (Underwood, 1981; Underwood and Denley, 1984). If position in the water column determines larval distribution of *Chamaesipho*, fewer larvae should be supplied to these areas. Therefore, while it is still uncertain which processes are determining the recurrent patterns of arrival and settlement of larval *Chamaesipho* recorded from 1990 to 1993, we suspect that site-specific small-scale hydrodynamics, as a function of topography of the substratum, interact with the position of larvae in the water column to concentrate larvae in specific patterns in different areas for both species. Future research on sheltered and exposed shores is needed to clarify this issue.

Larval settlement of *Chamaesipho* was also studied concurrently with larval supply on the sheltered shore at Cape Banks when more total settlers on the substratum than total cyprids in traps were recorded each year. This probably reflects inefficiency of traps rather than true larval availability. While larval supply was strongly correlated with settlement, the many relatively small *r* values for the 1991 to 1993 data indicate that, while larval supply plays a primary role, other factors (including behaviour) must also be involved. Further investigation into the influence of larval behaviour (or larval choice) at settlement (Raimondi, 1991) is therefore warranted for this species.

Overall, this study has shown that a combination of physical processes operates to transport *Chamaesipho* cyprids to different areas at Cape Banks. Peaks of arrival of larvae were always associated with new and full moons in stormy conditions in spring and consistent patterns of larval supply were recorded each year. It was also found that the numbers that arrive and settle play a major role in determining distributions of juvenile *Chamaesipho*.

**Acknowledgements**

This research was part of Carolyn Jeffery’s PhD thesis at the University of Sydney
and was supported by an Australian Research Council Grant (to AJU), an Australian Museum Postgraduate Grant (to CJJ) and funds from the Institute of Marine Ecology at the University of Sydney. Greg Skillreter provided helpful comments and criticisms on a previous draft. We also wish to thank Graham Housefield for technical assistance. [RW]

References


