



Barnacle larval supply to sheltered rocky shores: a limiting factor?

S.R. Jenkins & S.J. Hawkins

Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, U.K.

E-mail: sjen@mba.ac.uk

Key words: larval dispersal, *Semibalanus balanoides*, settlement, supply, wave exposure

Abstract

In northwest Europe, sheltered rocky shores are dominated by furoid canopy algae and barnacles are rare, although the latter are extremely abundant on exposed shores. The supply of the intertidal barnacle *Semibalanus balanoides* (L.) to sheltered, furoid dominated rocky shores was investigated to determine the importance of larval supply in limiting the abundance of adults in shelter. Larval supply was measured at two spatial scales, at the scale of shore (100s of metres), by comparing larval concentrations at exposed and sheltered sites, and at a smaller spatial scale (m), by examining the role of furoid canopies in limiting supply to the substratum. Replicate plankton trawls were carried out above the intertidal zone at high water at two sheltered sites and nearby exposed headlands. The concentration of *S. balanoides* cyprid larvae was significantly higher at the sheltered sites on two out of three sampling occasions with up to 14 times greater larvae on one occasion than the nearby exposed site. The effect of the macroalgal canopy on supply to the substratum was assessed in two ways: directly, by pumping water from the substratum in areas with and without *Ascophyllum nodosum* (L.) Le Jolis, and indirectly by measuring cyprid settlement in a canopy-manipulation experiment. Pumped plankton samples from mid tide level showed that the *A. nodosum* canopy did not form a barrier to larval supply and may have had a positive effect on larval concentrations at the substratum. Cyprid settlement was assessed in the mid shore *A. nodosum* and low shore *Fucus serratus* L. zones to areas with canopy algae (but protected from the sweeping effects of macroalgal fronds) and without canopy. Settlement over three consecutive 24-h periods showed a consistent pattern; settlement was consistently lower beneath the *F. serratus* canopy than in cleared areas, suggesting that this algal species forms a barrier, limiting supply of cyprid larvae to the substratum.

Introduction

The majority of marine benthic invertebrates exhibit a complex life cycle, that includes separate planktonic and bottom dwelling phases, linked by a settlement event (Thorson, 1950). Planktonic larvae undergo varying degrees of dispersal depending on the length of larval life, larval behaviour and the hydrographic regime which they encounter. Larval dispersal, or advection away from the spawning site, tends to limit competition between adults and offspring, prevents consumption of larvae by their parents and removes larvae from benthic predators. An obvious consequence of larval dispersal is that individuals are advected away from the habitat they will occupy as adults and return to this habitat will be dictated largely or wholly by physical transport processes. Several lar-

val transport mechanisms have been studied including tidally forced internal waves (Shanks, 1986; Shanks & Wright, 1987), upwelling events (Roughgarden et al., 1988; Fairweather, 1991) and wind forcing (Hawkins & Hartnoll, 1982; McConnaughey et al., 1992; McQuaid & Phillips, 2000). However, we still know relatively little about patterns of dispersal and transport in benthic invertebrate larvae.

Variability in the level of dispersal of larvae from the spawning site and transport to an appropriate adult habitat will have a major effect on the level of larval supply. Studies over the last 15 years have shown convincingly that settlement rates can be dictated by the level of supply of larvae reaching a settlement site. This relationship operates over small (1–10 m, e.g. Gaines et al., 1985; Minchinton & Scheibling, 1991; Miron et al., 1995) and medium (100–1000

m, e.g. Eggleston & Armstrong, 1995; Bertness et al., 1996) scales. The level of larval settlement can have a major impact on adult population dynamics, although the way in which variability in settlement interacts with post-settlement processes to determine adult abundance is the subject of debate.

Acorn barnacles have been used extensively as a model organism to examine physical transport processes and the relationship between larval supply, settlement and adult population dynamics. They are extremely common world wide on hard substrata, and both planktonic and newly-settled larvae are easily identified and enumerated. In northwest Europe, acorn barnacles are major space occupiers at exposed intertidal sites and in the absence of mussels can dominate the entire mid shore area. Barnacle abundance declines markedly and furoid canopy cover increases with a decline in wave exposure. At sheltered sites, barnacles often only occur in any numbers on the high shore, and on vertical surfaces and steep seaward facing slopes (Lewis, 1964). Lewis (1964) suggested a number of causative factors for the decline of barnacles in shelter including low larval supply, destruction of settling larvae and metamorphosed spat by the sweeping action of large algal fronds, the grazing activities of patellid limpets, and the lack of a suitable substratum. Interactions between settling barnacles and large canopy algae are clearly a major factor in limiting barnacle abundance on sheltered shores of northwest Europe (Jenkins et al., 1999a). It is not clear, however, to what extent supply of larvae to the substratum on sheltered shores is a contributory factor. The settlement rates of barnacles at shores with identical biota but differing in the degree of exposure have suggested that supply of larvae may be low in sheltered positions (Caffey, 1985; Bertness et al., 1992). On the other hand, there is evidence to suggest that shallow inlets and bays can be areas of larval retention through the formation of tidally driven eddy systems (e.g. Archambault et al., 1998).

One aspect of larval supply that is rarely considered is delivery of larvae to the substratum rather than merely to the general area. Hatton (1938) postulated that dense stands of canopy algae may form a barrier to the water-borne movement of plant and animal propagules and thus influence the establishment of benthic communities. For example, the presence of several algal canopy species has been shown to inhibit colonisation of *Sargassum muticum* (Yendo) Fensholt (Deysner & Norton, 1982). It was proposed that the algae formed a physical barrier between settling zy-

gotes and the substratum. This phenomenon has also been suggested to inhibit the establishment of limpets on sheltered shores, although no tests of this hypothesis have been made (Fischer-Piette, 1948; Lewis & Bowman, 1975).

We aimed to examine the supply of cyprid larvae of *Semibalanus balanoides* to sheltered furoid dominated shores to investigate the general model that low larval supply is a causative factor in limiting the abundance of adult *S. balanoides* on sheltered shores. Supply was examined at two spatial scales: firstly, at scales of 100s of metres between exposed and sheltered sites and, secondly, at the scale of metres by examining the role of furoid canopies in limiting supply to the substratum. In so doing, we tested the hypotheses that larval concentration is lower at sheltered compared to exposed sites and that larval concentration at the substratum is negatively affected by the overlying canopy.

Materials and methods

Experimental sites

Sampling and experimental work was carried out at three locations in the south of the Isle of Man (Irish Sea) between 1993 and 2002 (Fig. 1). At all locations, sheltered sites where the intertidal community was dominated by furoid canopy algae were chosen. Typically, these sites supported dense stands of fucoids, with the mid and low shore dominated by *Ascophyllum nodosum* and *Fucus serratus*, respectively. Descriptions of the communities in these furoid assemblages on the Isle of Man are given by Jenkins et al. (1999b,c). At two of these locations (Fleshwick and Port St Mary), exposed shores, dominated by grazing patellid limpets and the acorn barnacle *Semibalanus balanoides*, were chosen in close proximity (200–400 m) to the sheltered bays (Fig. 1).

Supply of larvae to exposed and sheltered shores

The concentration of barnacle larvae in the water column above the intertidal zone at exposed and sheltered shores at Fleshwick and Port St Mary was assessed on two dates during the settlement period of *Semibalanus balanoides* in May 2002. Cyprid larvae were captured using a 0.5 m diameter 250 μ m plankton net with attached flowmeter. This was towed from a small boat approximately 1 m below the sur-

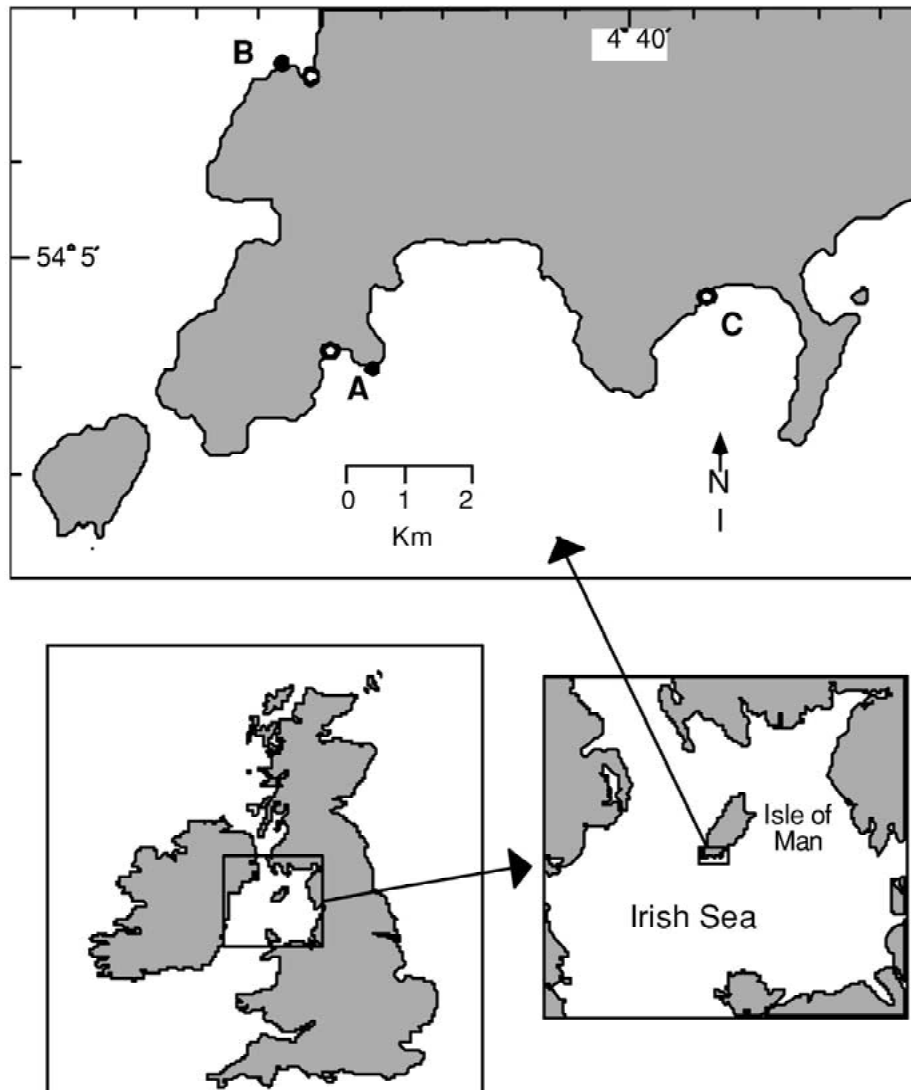


Figure 1. Location of sampling and experimental sites in the south of the Isle of Man, in the Irish Sea, British Isles. (A) Port St Mary location showing sheltered bay and exposed headland; (B) Fleshwick location showing sheltered bay and exposed headland; (C) Castletown Bay experimental site. Open circles represent sheltered sites, closed circles represent exposed headland sites.

face over the intertidal and shallow subtidal zones at a speed of 1–2 knots during the period of high water ($HW \pm 1.5$ h). The water depth varied between 2.5 and 6 m. At each site on each sampling occasion, three tows, each of 10 min were made. The volume of water sampled in each tow ranged from 29 to 93 m^3 , with a mean sampled volume of 56 m^3 . The volume of water sampled varied owing to different flow conditions between exposed and sheltered sites and the varying degrees to which nets were clogged with phytoplankton. Plankton samples were preserved in 5% buffered formalin in seawater and the num-

ber of cyprid larvae of *S. balanoides* counted using a dissecting microscope.

Direct assessment of the effect of the Ascophyllum nodosum canopy on larval supply to the substratum

The concentration of *Semibalanus balanoides* larvae at the substratum in the presence and absence of a canopy of *Ascophyllum nodosum* was determined at a sheltered site in Castletown Bay during May 1993 using a petrol driven water pump (Honda WB10). The pump was located above the high water mark and con-

nected via rigid tubing (internal diameter 25 mm) to two positions at approximately mid shore level (4 m above Lowest Astronomical Tide, L.A.T.). One position was located within a dense stand of *A. nodosum* and the other at the same tidal level but within an area at least 5 m wide, where *A. nodosum* was naturally absent. At each position, the inlet of the tube was fixed 10–20 cm above the substratum. In this way, the pump could be used to draw water from the substratum surface in areas with and without a canopy.

In May 1993, sampling was undertaken on 6 days during the barnacle settlement season, during a period 1 h either side of high water. At each date, three 10 min periods of pumping took place on each of the two tubes and water passed through a 100 μm plankton net. The pump rate for each of the two tubes on each date was calculated by determining the time taken to fill a container of known volume. The average pump rate over all sampling dates was 115 l per min.

Indirect assessment of the effect of the Ascophyllum nodosum and Fucus serratus canopy on larval supply to the substratum

Large macroalgae may affect barnacle settlement negatively through two processes: by forming a physical barrier limiting cyprid access to the substratum, or through a 'whiplash' or scouring effect of algal fronds at settlement. The potential barrier effect was examined in May 1997 by comparing settlement in two treatments, one in which the algal canopy was cleared (no barrier, no whiplash) and one in which the canopy was left intact but the substratum protected from algal whiplash by the use of cages (barrier but no whiplash). A third treatment, cleared areas with cages, was used to assess any artefacts associated with the use of cages. Each treatment was replicated six times at each of two shore levels, which corresponded with the middle of the *Fucus serratus* (2.8 m above L.A.T) and *Ascophyllum nodosum* (4.1 m above L.A.T.) zones.

Settlement tiles bearing adult conspecifics were used in all treatments to provide a cue to enhance settlement. Tiles were made from natural rock and had a minimum settling area of 12 \times 12 cm with a patchy adult barnacle cover of between 33 and 50%. Where appropriate, tiles were caged. Cages were made from plastic-coated chicken wire (mesh size 13 \times 13 mm) and were designed to form a complete cover over the whole tile with a 'roof' 3–4 cm above the settlement surface.

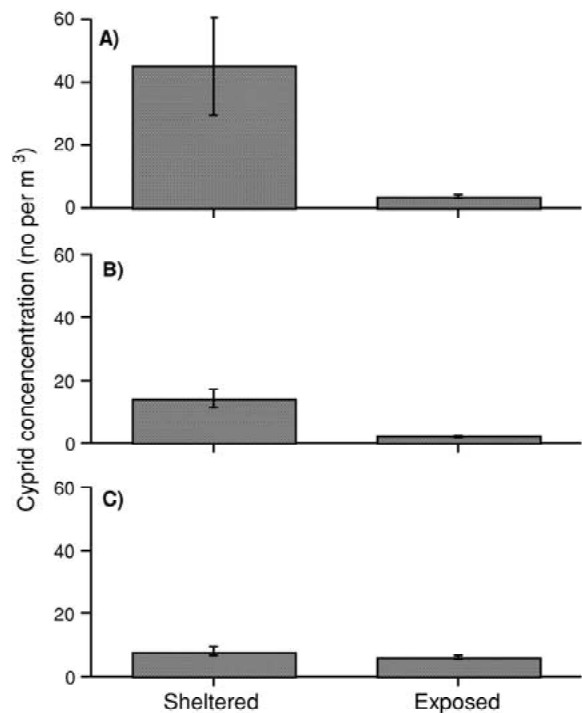


Figure 2. Mean concentration (\pm SE) of *Semibalanus balanoides* cyprid larvae above the intertidal zone at exposed and sheltered locations during May 2002. (A) Fleshwick - 27th May; (B) Port St Mary - 27th May; (C) Port St Mary - 31st May.

A stretch of shore approximately 100 m long was chosen at Castletown Bay. At each of the two shore levels, 18 plots were selected and experimental treatments were assigned at random to them. Canopy algae were completely cleared from a 2 \times 2 m area in the appropriate plots. A single settlement tile was fixed in position using rapid setting cement at each plot. Settlement to experimental tiles was assessed over 24 h on three separate dates. At each date, all settled barnacles were cleared from the tile surfaces and the number of settled cyprids determined after 24 h. No examination of recruitment over longer time scales was made.

Statistical analysis

Analysis of variance (ANOVA) was used throughout to test for treatment effects. Cochran's test (Winer, 1971) was used to test for heterogeneity of variance and, where necessary, data were square root or log transformed. Multiple comparisons of levels within significant factors were made using Student Newman Keuls (SNK) tests.

Table 1. Two way mixed model ANOVA of *Semibalanus balanoides* cyprid concentration at the substratum with and without a canopy of *Ascophyllum nodosum*. Data Sqrt transformed. Cochran's test for homogeneity of variance: $C=0.285$, $P > 0.05$

| Source | df | MS | F | P | F versus |
|-------------|----|------|------|--------|----------|
| Canopy | 1 | 6.4 | 1.1 | >0.3 | Ca×Da |
| Date | 5 | 25.9 | 12.4 | <0.001 | Residual |
| Canopy×Date | 5 | 5.9 | 2.8 | <0.05 | Residual |
| Residual | 24 | 2.1 | | | |

SNK test on Canopy×Date Interaction:

Date 4: Canopy present>Canopy absent ($P < 0.05$).

Results

Supply of larvae to exposed and sheltered shores

The concentration of *Semibalanus balanoides* cyprid larvae above the intertidal zone at exposed and sheltered sites showed a similar trend on all three sampling occasions with higher larval numbers per unit volume of water in shelter (Fig. 2). This was very marked at Fleshwick Bay on 27th May where, on average, there were over 14 times higher numbers of cyprids in the sheltered bay compared to the exposed headland. There was, however, a high degree of variability among replicate hauls, indicating patchiness at a scale of 10s to 100s of metres. One way ANOVA showed a significantly higher concentration of larvae in shelter at only one of the three sampling occasions at a P value of 5%, but at two occasions with a P value of 10% (Fleshwick, 27th May – df 1,4, F 6.72, $P < 0.07$; Port St Mary 27th May – df 1,4, F 16.17, $P < 0.05$; Port St Mary 31st May – df 1,4, F 1.24, $P > 0.3$).

Direct assessment of the effect of the Ascophyllum nodosum canopy on larval supply to the substratum

The concentration of *Semibalanus balanoides* cyprid larvae at the substratum at the sheltered site in Castletown Bay was relatively high, but varied considerably among dates and among individual pumping periods within a date. Over all dates, the average cyprid concentration was 34 cyprids per m^3 in the presence of the canopy and 22 cyprids per m^3 in the absence of the canopy (Fig. 3). Data were analysed using a mixed model two way ANOVA with date considered a random factor. The effect of the *Ascophyllum nodosum* canopy on the concentration of cyprids differed according to the date as indicated by the sig-

nificant Canopy×Date interaction (Table 1). Student Newman Keuls multiple comparison test on this interaction revealed only one date (May 27th) when there was a significant effect of the canopy. On this date, cyprid concentration was significantly greater in the presence of the canopy.

Indirect assessment of the effect of the Ascophyllum nodosum and Fucus serratus canopy on larval supply to the substratum

On all three sampling dates, the effect of the different treatments showed a similar trend. The effect of the three canopy treatments differed clearly between the *Fucus serratus* and *Ascophyllum nodosum* zones on all three dates, with highly significant interactions between treatment and shore height (Table 2, Fig. 4). In the *F. serratus* zone, settlement in the two cleared treatments was consistently higher than in the canopy treatment. Thus, despite being protected from the sweeping effects of *F. serratus* fronds, settlement beneath the canopy was apparently limited. Clearly, this was not an artefact of the cages since settlement in cleared areas was the same irrespective of the presence/absence of a cage. SNK tests confirmed these conclusions; tiles beneath the canopy showed significantly lower settlement than those in cleared areas on all three dates (Table 2, Fig. 4). In contrast, settlement in the *A. nodosum* zone was consistently highest in the canopy treatment. SNK tests showed settlement in this treatment was significantly higher than one or both canopy cleared treatments over the three dates (Table 2, Fig. 4).

Discussion

Assessment of larval supply to exposed and sheltered sites showed clearly that high larval concentrations of *Semibalanus balanoides* do occur at sheltered sites. Larval concentrations were, on average, greater in shelter than in exposed positions and, on one occasion, over 14 times higher. It is important to consider the relevance of measuring larval concentrations in the water column as an indicator of larval supply in areas of differing tidal flow. Larval concentrations such as are given by plankton tows or pumped water samples give a snapshot of larval supply, but do not integrate over time. Use of larval traps, which provide a time averaged signal of larval supply (e.g. Yund et al., 1991) or estimates of 'larval flux', which

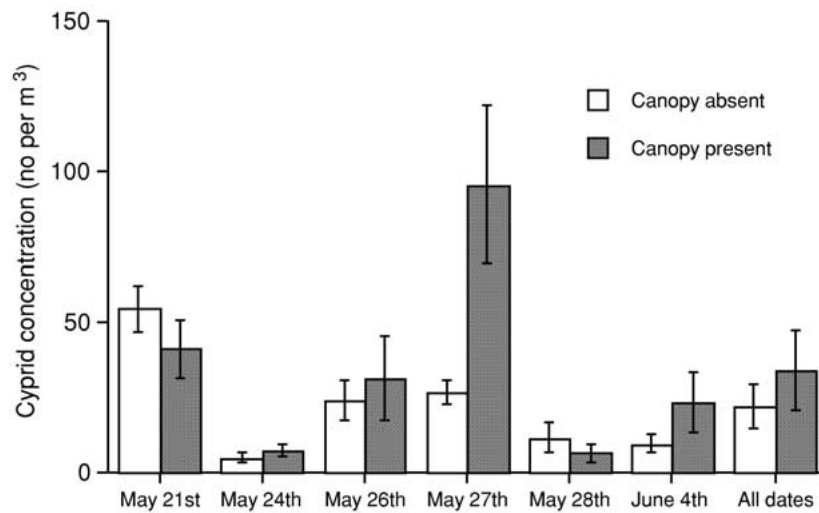


Figure 3. Mean concentration (\pm SE) of *Semibalanus balanoides* cyprid larvae at the substratum in two adjacent areas, one with a dense *Ascophyllum nodosum* canopy and one where canopy algae were naturally absent.

Table 2. Two way ANOVA of log transformed data testing for the effect of shore height and canopy treatments on the settlement of *Semibalanus balanoides* cyprids on three consecutive dates. C values give results of Cochran's test for homogeneity of variance

| Source | df | Date 1 (C=0.59, $P < 0.01$) | | | Date 2 (C=0.27, $P > 0.05$) | | | Date 3 (C=0.28, $P > 0.05$) | | |
|-----------------|----|------------------------------|-------|--------|------------------------------|------|--------|------------------------------|------|---------|
| | | MS | F | P | MS | F | P | MS | F | P |
| Treatment | 2 | 2.1 | 8.6 | <0.01 | 0.3 | 1.0 | >0.3 | 0.6 | 2.4 | >0.1 |
| Height | 1 | 66.2 | 274.5 | <0.001 | 27.0 | 85.6 | <0.001 | 0.2 | 0.9 | >0.3 |
| Tmt \times Ht | 2 | 5.8 | 24.1 | <0.001 | 5.2 | 16.4 | <0.001 | 4.5 | 17.0 | <0.0001 |
| Residual | 30 | 0.2 | | | 0.3 | | | 0.3 | | |

| | Date 1 | | Date 2 | | Date 3 | |
|-------------------------------------|--------|-----|--------|-----|--------|-----|
| | Mid | Low | Mid | Low | Mid | Low |
| Cleared (caged) v cleared (no cage) | S | NS | NS | NS | NS | NS |
| Cleared (caged) v canopy intact | NS | S | S | S | NS | S |
| Cleared (no cage) v canopy intact | S | S | S | S | S | S |

SNK multiple comparisons of interaction. Comparisons between shore heights not shown (NS= $P > 0.05$; S= $P < 0.05$).

combine estimates of larval concentrations with measures of flow rates (Archambault & Bourget, 1999), may be more reliable indicators of true larval supply. Simple estimates of current velocity combined with larval concentration data have been used in previous studies to provide a better predictor of benthic recruitment than concentration alone (e.g. Archambault & Bourget, 1999). Although estimates of tidal flow are available for the exposed sites sampled, tidal flow inside the small sheltered bays was very low and data are unavailable. An alternative approach would be to use subtidal (Yund et al., 1991) or intertidal (Castilla & Varas, 1998) larval traps to estimate larval flux. Such traps, however, are likely to operate with vary-

ing efficiency in areas of differing tidal flow or wave exposure and, therefore, are probably not suitable for any comparison of sheltered and exposed sites.

Although it is likely, given the much higher tidal flow at exposed sites, that the number of larvae 'supplied' to exposed shores over the period of settlement is higher than to sheltered shores, we showed that the larval concentration at a point in time, and therefore the number of larvae available to settle can be high in shelter. Indeed, where conditions were suitable for settlement, with suitable settlement surfaces and without the sweeping or barrier effects of macroalgae, settlement was high. Jenkins (1995) showed that using identical settlement surfaces, recruitment

of *S. balanoides* was higher on a fucoid dominated sheltered shore when the canopy was cleared than to an adjacent exposed site. It is clear, therefore, that patterns of larval dispersal do allow supply of larvae to sheltered shores. How accumulation of high larval concentrations in sheltered bays occurs is not clear, but retention of larvae in eddy systems generated by tidal flow is one candidate mechanism (Archambault & Bourget, 1999). An alternative is that local production of larvae by adult populations within sheltered bays undergoes limited dispersal. The pelagic larvae of benthic invertebrates are generally assumed to undergo extensive dispersal and large-scale export from the site of production. Hence populations are considered open, with the level of recruitment independent of local production. Recent work, however, has questioned this widely held view and stressed that local retention of pelagic larvae may be more prevalent than previously thought (e.g. Sponaugle et al., 2002; Swearer et al., 2002; Warner & Cowen, 2002). Sheltered embayments are undoubtedly areas where retention may be likely. This has obvious implications for local population dynamics and gene flow. Gaines & Bertness (1992) demonstrated high levels of barnacle recruitment (and hence probably larval retention) in a large bay when flushing times were long. The extent to which larval retention occurs in embayed areas on a much smaller scale, as in the present study, is not clear. Here retention will be related to the interaction of long shore currents with coastal geography and further work integrating measures of larval concentration and hydrography is required.

We examined supply of larvae not only at the scale of shore but also at a much smaller scale—supply to the substratum. Studies investigating larval ‘supply’ have examined larval concentration or larval flux at differing distances from the adult habitat from measures within centimetres (e.g. Minchinton & Scheibling, 1991) to measures over 50 m away (e.g. Bertness et al., 1996). Differential delivery of larvae from larval pools offshore of the adult habitat may disrupt any relationship between larval supply, measured 10s or 100s of metres from the shore, and settlement. On canopy-dominated sheltered shores, supply measured at the scale of shore may bear little relevance to supply to the substratum, owing to the potential of canopy algae to block larval movement to the substratum. Canopy algae may reduce supply of larvae to the substratum by forming a physical barrier to larval movement or reducing water circulation and mixing. For example, subtidal kelp forests have a significant impact on fluid

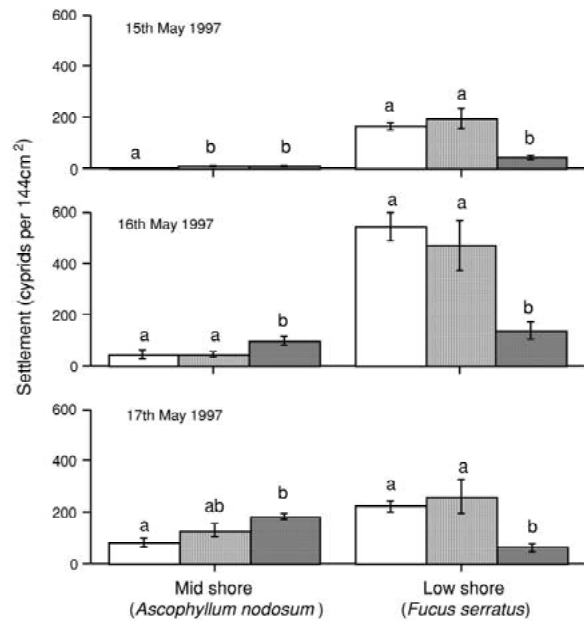


Figure 4. Mean level (\pm SE) of *Semibalanus balanoides* cyprid settlement over a 24-h period at three consecutive dates to experimental treatments in the mid and low shore of a sheltered site in Castletown Bay. For each shore level treatments sharing the same letter are not significantly different (from SNK multiple comparisons of the significant treatment \times shore height interaction).

and particulate transport and can inhibit transport of suspended particles from the overlying water column to the bottom (Eckman et al., 1989). Alternatively, canopy algae may create a ‘behavioural barrier’. Given the complex behaviour patterns and discriminatory processes seen in many planktonic larvae it is feasible that chemical or physical cues from canopy algae may discourage larvae from seeking the substratum.

A combination of direct and indirect measures of larval supply to the substratum in the mid shore *Ascophyllum nodosum* zone showed clearly that this canopy alga does not prevent cyprid access to the rock surface. In fact, evidence from both pumping and canopy manipulation suggests that supply may be higher where the canopy is present. This result is in agreement with observations of Leonard (1999) who found that the *A. nodosum* canopy in the northwest Atlantic created a depositional environment where larvae of *Semibalanus balanoides* accumulated. In contrast, indirect assessment of supply in the low shore *Fucus serratus* zone showed that this alga may form a barrier to larval supply. Settlement was considerably reduced where the canopy was left in place compared to cleared areas, even when settlers were protected from algal sweeping or whiplash. Clearly, measurement of

settlement is not the same as measuring larval concentration or supply. However, given identical settlement surfaces, and the results showing no artefact of using cages, it seems likely that differences in settlement can be accepted as indicating differences in supply. The difference in result between the two shore zones may occur because of differences in the physical characteristics of the two dominant canopy algae. *Ascophyllum nodosum* stands erect in the water column, buoyed by numerous bladders, in contrast to the more bushy nature of *F. serratus*. When viewed from above during high water, *F. serratus* appears to present far more of a physical barrier to cyprids accessing the substratum.

In conclusion, we showed that larval concentrations on sheltered shores, where adult barnacles are scarce, can be very high. A more extensive sampling regime, incorporating estimates of larval flux over a number of years, is required to build on these preliminary observations to improve our understanding of how supply varies along indented coastlines. At a smaller scale, we found differing effects of two species of canopy algae on larval supply to the substratum. Larvae were not impeded by the mid-shore species *Ascophyllum nodosum* but, in the low-shore *Fucus serratus* zone, observations of settlement indicate that this fucoid species can limit larval access to settlement sites. Thus, at mid-shore level, biological interactions between settling larvae and macroalgae (both canopy and turf forming) are probably the main factors limiting barnacle abundance on sheltered shores, while in the low shore, supply to the substratum may be an additional limiting factor.

Acknowledgements

This work was supported by a PhD studentship from the Natural Environment Research Council to SRJ, the EUROROCK project (MAS3-CT95-0012) and fellowships funded by NERC grant in aid from the Marine Biological Association, UK to SRJ and SJH. Thanks to Trevor Norton and Richard Nash for providing facilities at Port Erin Marine Laboratory and Anna Markula for help with fieldwork. The manuscript was improved through the comments of two anonymous referees.

References

Archambault, P. & E. Bourget 1999. Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment

- and diversity of benthic subtidal communities. *J. exp. mar. Biol. Ecol.* 238: 161–184.
- Archambault, P., J. C. Roff, E. Bourget, B. Bang & G. R. Ingram, 1998. Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. *J. Plankton Res.* 20: 671–690.
- Bertness, M. D., S. D. Gaines, E. G. Stephens & P. O. Yund, 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J. exp. mar. Biol. Ecol.* 156: 199–215.
- Bertness, M. D., S. D. Gaines & R. A. Wahle, 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 137: 103–110.
- Caffey, H. M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol. Monogr.* 55: 313–332.
- Castilla, J. & M. Varas, 1998. A plankton trap for exposed rocky intertidal shores. *Mar. Ecol. Prog. Ser.* 175: 299–305.
- Deysher, L. & T. A. Norton, 1982. Dispersal and colonisation in *Sargassum muticum* (Yendo) Fensholt. *J. exp. mar. Biol. Ecol.* 56: 179–195.
- Eckman, J. E., D. O. Duggins & A. T. Sewell, 1989. Ecology of understory kelp environments. 1. Effects of kelps on flow and particle transport near the bottom. *J. exp. mar. Biol. Ecol.* 129: 173–187.
- Eggleston, D. & D. Armstrong, 1995. Presettlement and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol. Monogr.* 65: 193–216.
- Fairweather, P. G., 1991. Implications of 'supply-side' ecology for environmental assessment and management. *Trends Ecol. Evol.* 6: 60–63.
- Fischer-Piette, E., 1948. Sur les elements de prosperite des patelles et sur leur specificite. *J. Conchyliologie* 88: 45–96.
- Gaines, S. D., S. Brown & J. Roughgarden, 1985. Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67: 267–272.
- Gaines, S. D. & M. D. Bertness, 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360: 579–580.
- Hatton, H., 1938. Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. *Annales de l'Institut Oceanographique* 17: 241–348.
- Hawkins, S. J. & R. G. Hartnoll. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J. exp. mar. Biol. Ecol.* 62: 271–283.
- Jenkins, S. R., 1995. The ecology of fucoid canopy dominated shores. PhD, Liverpool.
- Jenkins, S. R., T. A. Norton & S. J. Hawkins, 1999a. Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae. *J. exp. mar. Biol. Ecol.* 236: 49–67.
- Jenkins, S. R., S. J. Hawkins & T. A. Norton, 1999b. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Mar. Ecol. Prog. Ser.* 188: 81–92.
- Jenkins, S. R., S. J. Hawkins & T. A. Norton 1999c. Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *J. exp. mar. Biol. Ecol.* 233: 41–63.
- Leonard, G. H., 1999. Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. *Mar. Ecol. Prog. Ser.* 178: 241–249.
- Lewis, J. R., 1964. *The Ecology of Rocky Shores*. English Universities Press, London.

- Lewis, J. R. & R. S. Bowman, 1975. Local habitat induced variations in the population dynamics of *Patella vulgata* (L.). *J. exp. mar. Biol. Ecol.* 17: 165–203.
- McConnaughey, R., D. Armstrong, B. Hickey & D. Gunderson, 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Can. J. Fish. aquat. Sci.* 49: 2028–2044.
- McQuaid, C. D. & T. E. Phillips, 2000. Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Mar. Ecol. Prog. Ser.* 201: 211–220.
- Minchinton, T. E. & R. E. Scheibling, 1991. The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 72: 1867–1879.
- Miron, G., B. Boudreau & E. Bourget, 1995. The use of larval supply in benthic ecology: testing correlations between larval supply and larval settlement. *Mar. Ecol. Prog. Ser.* 124: 301–305.
- Roughgarden, J., S. Gaines & H. Possingham, 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.
- Shanks, A. L., 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesised mechanism for the cross shelf transport of cyprids. *Biol. Bull.* 170: 429–440.
- Shanks, A. L. & W. G. Wright, 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *J. exp. mar. Biol. Ecol.* 114: 1–13.
- Sponaugle, S., R. K. Cowen, A. Shanks, S. G. Morgan, J. M. Leis, J. S. Pineda, G. W. Boehlert, M. J. Kingsford, K. C. Lindeman, C. Grimes & J. L. Munro, 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bull. mar. Sci.* 70: 341–375.
- Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz & R.R. Warner, 2002. Evidence of self-recruitment in demersal marine populations. *Bull. mar. Sci.* 70: 251–271.
- Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25: 1–45.
- Warner, R. R. & R. K. Cowen, 2002. Local retention of production in marine populations: Evidence, mechanisms, and consequences. *Bull. mar. Sci.* 70: 245–249.
- Winer, B. J., 1971. *Statistical Principles in Experimental Design*. McGraw-Hill Kogakusha, Tokyo.
- Yund, P. D., S. D. Gaines & M.D. Bertness, 1991. Cylindrical tube traps for larval sampling. *Limnol. Oceanogr.* 36: 1167–1177.