

Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles

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Summary

1. Two common species of acorn barnacle, *Chthamalus montagui* and *C. stellatus*, with similar resource needs, occur together on rocky shores of NW Europe but differ in their adult distribution over two environmental gradients, wave exposure and vertical height on the shore.
2. A sampling programme was undertaken over 2 years to determine the causal mechanisms of this differential distribution. Three alternative, although not mutually exclusive, models were tested: first, adult distribution is determined at settlement as a direct result of differential larval supply; secondly, adult distribution is determined at settlement as a result of larval choice rather than differential larval supply; and thirdly, settlement occurs homogeneously over the two gradients and the adult pattern is set by differential post-settlement mortality.
3. Near-shore larval abundance in the water column over the gradient of wave exposure was determined at eight dates during the main settlement period in 2003. Larval production was assessed by quantifying early-stage larvae, while the supply of competent settlers to the adult habitat was determined by quantifying late-stage cyprid larvae.
4. The pattern of settlement of the two species was determined over both environmental gradients by daily sampling of the proportional abundance of *C. stellatus* and *C. montagui* settled cyprids at three tidal heights at exposed and sheltered shores. Differential post-settlement mortality was determined by quantifying day-old, week-old and up to 3 months-old metamorphosed individuals.
5. Larval production reflected the distribution of adults, with early-stage larvae of *C. montagui* predominating in shelter and *C. stellatus* in exposure. However, the supply of late-stage cyprid larvae to the near-shore area showed no difference in the proportion of each species over the wave-exposure gradient; differential larval supply was not responsible for dictating adult distribution.
6. Despite no differential supply of larvae, the pattern of settlement of the two species differed over both environmental gradients, with *C. stellatus* settling in greater proportions low on the shore and in exposure and *C. montagui* settlement predominating higher on the shore and in shelter. This pattern directly matched the distribution of adults. Post-settlement mortality accentuated, but did not change, the pattern set at settlement.
7. The implications of the results, and the usefulness of the technique employed, to understanding the degree of ‘openness’ in populations of marine benthic invertebrates are discussed.

Key-words: benthic invertebrate, *Chthamalus*, larval behaviour, larval dispersal, open populations, recruitment.

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Introduction

Invertebrates with complex life cycles, in which different life stages occupy different habitats, are common in terrestrial, marine and freshwater environments. Transition between life stages can be crucial to the population dynamics of species and this is especially true in the marine realm, where separate planktonic and benthic life stages are common in most benthic invertebrates (Thorson 1950). The planktonic larval phase of benthic invertebrates may last from minutes to months, during which time larvae face high levels of mortality, due to predation and advection away from the adult habitat. The larval phase must culminate in locating suitable adult habitat, settling and adopting the adult morphology. Variation in the level of supply, settlement and subsequent recruitment has been documented for a wide range of benthic species (e.g. Morgan *et al.* 1996; Jenkins *et al.* 2000; Navarrete *et al.* 2002), but our understanding is still limited as to how such variation is generated and the consequences of this for the adult population.

A number of studies over the last 20 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 both small (1–10 m, e.g. Gaines, Brown & Roughgarden 1985), medium (100–1000 m, e.g. Eggleston & Armstrong 1995) and large (100–1000 km Connolly & Roughgarden 1998) scales. Studies of larval supply in benthic invertebrates have generally concentrated on the quantitative relationship between supply and settlement or recruitment. However, variation in larval supply may also set distributional limits of adults (Grosberg 1982; Eggleston & Armstrong 1995; Carlon 2002). Study of complex larval behaviour in response to biological, physical and chemical cues has shown that larvae can under some circumstances maintain themselves within the limits of suitable adult habitat. For example, by orientating in a stratified flow, through vertical migration, larvae may control the direction of transport toward suitable settlement habitat (see Kingsford *et al.* 2002 for review). Such behaviour may have a high probability of success on extended coastlines of similar oceanography and orientation (e.g. Pineda 1999) or at a smaller scale in partially enclosed water masses such as estuaries (e.g. Cronin 1982). However, the extent to which such behaviour contributes toward general patterns of larval distribution and consequently towards patterns of settlement is not clear.

Far more is known regarding the consequences of larval behaviour at the point of settlement. Numerous studies have demonstrated active substratum selection by benthic invertebrate larvae in the field, generally to biogenic substrata. The cues mediating such settlement specificity are generally believed to be chemical in nature. Pawlik (1992) reviews two types of settlement specificity: gregarious, where larvae settle in response to the presence of adult or larval conspecifics and asso-

ciative settlement, where larvae settle in response to other species, generally on the basis of some nutritional relationship. Gregarious settlement allows larvae to select a habitat that is likely to support post-settlement growth and survival as well as increasing the chance of future reproductive success (see Hui & Moyses 1987 for review).

Despite recent emphasis on supply and recruitment in controlling adult population structure, the importance of post-recruitment factors in the benthic environment remains. The balance between recruitment and post-recruitment factors has been debated at length in considering whether populations are 'recruitment limited' (see Caley *et al.* 1996; Chesson 1998; for reviews). This concept (*sensu* Doherty 1981) recognizes two extreme situations where local adult abundance is either determined solely by the input of recruits, or solely by interactions after recruitment. However, it is now generally recognized that neither of these extremes is likely to apply to many populations (Chesson 1998). It is more likely that fluctuating levels of recruitment interact with density-dependent processes to control adult abundance, i.e. both non-equilibrium and equilibrium concepts apply to most populations.

Two species of *Chthamalus* barnacle, *Chthamalus stellatus* and *C. montagui*, exist on the western coasts of Europe, occurring together along Atlantic coastlines from N. Scotland to N. Africa and throughout the Mediterranean Sea (Crisp, Southward & Southward 1981). *Chthamalus montagui* was formerly regarded as a variety of *C. stellatus* until it was separated on the basis of shell morphology and cirral setation (Southward 1976). In NW Europe the two species differ in their distribution with wave exposure and vertical height on the shore. *C. montagui* is more common in sheltered localities while *C. stellatus* predominates on wave beaten coasts. Where they occur together *C. montagui* dominates at higher tidal levels, while *C. stellatus* is more common lower on the shore (Southward 1976; Crisp *et al.* 1981), although there is a large degree of spatial overlap.

A number of alternative models can be used to explain the differential distribution of adults. First, adult distribution, both vertically (from low to high shore) and horizontally (across the wave-exposure gradient) may be determined at settlement as a direct result of differential larval supply. Secondly, settlement may have a direct effect on adult patterns, but as a result of larval choice rather than differential larval supply. Thirdly, the two species may settle homogeneously over the two gradients and the adult pattern set by differential post-settlement mortality occurring at any time from days to weeks to months after initial settlement. A number of predictions may be made from the three outlined models. Model 1 predicts that cyprids of *C. montagui* should dominate in the water column adjacent to sheltered sites and have a shallow depth distribution while cyprids of *C. stellatus* should dominate at exposed sites and occur at greater depth. Model 2 predicts that cyprids of the two species will show little

or no difference in vertical or horizontal distribution in the water column, but will do so when sampled as settlers on the rock surface. Model 3 predicts that neither cyprid distribution in the water nor in the adult habitat will match adult patterns, but that differential mortality at some stage, whether soon after settlement or in the weeks and months following, will determine the adult distribution patterns. Clearly, these models are not mutually exclusive and patterns may be set by a combination of factors. I aimed to discriminate between these explanations by carrying out field surveys over a 2-year period of planktonic cyprids, newly settled cyprids, early metamorphs and juveniles in exposed and sheltered locations over the vertical gradient of the shore.

In attempting to ascertain the relative importance of larval supply and larval selection at settlement in setting adult distribution patterns compared to post-settlement mortality, it is important to use clear and precise definitions of settlement and recruitment. Settlement may be defined as the point at which a planktonic larva attaches irreversibly to the substratum (Keough & Downes 1982); as such it is very difficult, if not impossible, to determine the magnitude of settlement in the field. However, counts of settlers (in this case settled cyprids) made at short time intervals give a close approximation to true settlement by minimizing the period available for post-settlement mortality. Recruitment of sessile marine invertebrates can be defined as the number of individuals that have survived an arbitrary length of time after settlement. Its magnitude therefore relies on the level of settlement combined with the degree of post-settlement mortality.

Materials and methods

ADULT DISTRIBUTION

Four locations were selected within the environs of the Plymouth Sound area, which supported dense populations of chthamalid barnacles (Fig. 1). Two of these locations, Renny Rocks and Queener Point, are exposed to high

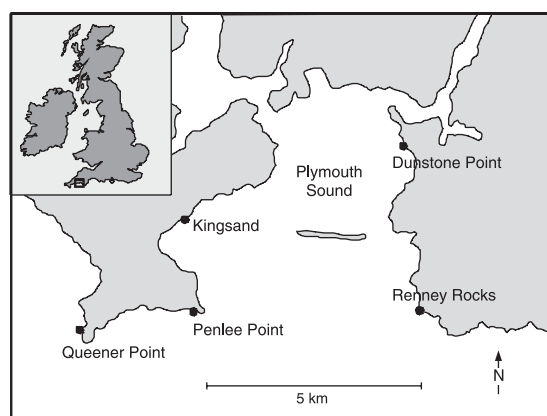


Fig. 1. Map showing the five sampling locations in the environs of Plymouth Sound. Inset map shows the area in SW England (marked by a black rectangle) depicted by the main map.

levels of wave action while the other two, Dunstone Point and Kingsand, are relatively sheltered. At each location, two sites were selected between 50 and 100 m apart. At each of these sites two patches were chosen approximately 10 m apart and at each patch three heights within the barnacle zone were selected from low to high. Tidal heights selected approximated to 4.5, 3 and 1.5 m above Chart Datum. At each of the three heights within each patch, six areas of 25 cm² were photographed digitally. The digital photographs were analysed in the laboratory and the density of the four barnacle species, *Chthamalus montagui*, *C. stellatus*, *Semibalanus balanoides* and *Elminius modestus*, was determined.

CYPRID AND SPAT DISTRIBUTION

Settlement (cyprid counts) and recruitment (spat counts) were monitored over the horizontal and vertical gradients on the shore during the summer of 2002 and 2003. Because neither settled cyprids nor metamorphosed spat could be identified to species level in the field, sampling required collection of settlers and identification under a stereomicroscope in the laboratory. In 2002 this was achieved by removing cyprids and metamorphs from the rock surface carefully using a fine scalpel, while in 2003 a different approach was taken by removing chips of rock from the shore.

In July 2002 two exposed (Queener Point and Renny Rocks) and two sheltered (Dunstone Point and Kingsand Bay) shores were selected. At each shore, three tidal heights were selected as described above from low to high within the barnacle zone. At each height, at each shore, six 6 × 6-cm quadrats were cleared of all adult barnacles. All quadrats on each shore were sampled twice, between 15 and 30 August. One week prior to sampling, quadrats were brushed with a stiff brush to remove any settled barnacles; hence each sampling event represented 1 week's accumulation of recruits. Quadrats were sampled by removing a subset of cyprids and metamorphs from within the cleared quadrat and placing in 95% alcohol. In addition to the weekly sampling, six additional quadrats were cleared at each shore height in the second week of August and sampled 1 month later.

In 2003, sampling was restricted to one exposed (Penlee Point) and one sheltered (Kingsand) shore in order to increase the resolution of sampling over the summer period (see Fig. 1). Penlee Point was selected as representing a similar shore to the two previously sampled exposed locations but with improved accessibility. At weekly intervals between 30 July and 26 August, small areas of rock (between 25 and 100 cm²) were cleared of all adult barnacles using a bolster chisel and brushed to remove any newly settled cyprids or recruits. Areas were cleared at three tidal heights within the barnacle zone at Kingsand and Penlee Point and were distributed at each shore over a horizontal distance of approximately 50 m.

At each weekly shore visit the areas of rock cleared the week before were removed using a lump hammer

and sharp chisel. In this way new settlers up to a maximum of 1 week old were collected weekly for three shore levels at one exposed and one sheltered shore for a period of 5 weeks during the main chthamalid settlement season. In order to determine differences in the ratio of settlement of the two species on a daily basis, an intensive sampling programme was undertaken for 6 days (26 August–1 September). The same protocol was followed, except that areas of rock were cleared and collected daily. In this way settlement was monitored with minimal post-settlement mortality.

Towards the end of the main settlement period in September, samples of natural unmanipulated rock were taken from the three levels at both shores. These samples were taken from two sites at each location, the site of regular sampling and another site selected between 50 and 100 m away. Samples contained natural unmanipulated adult barnacles and recruits which had accumulated throughout the settlement season.

All samples collected in 2002 and 2003 were examined in the laboratory within 2 days of collection under a stereomicroscope. Cyprids could not be identified initially to species level on the basis of morphology, but previous work by Power *et al.* (1999) suggested they could be separated on the basis of their size. Hence, the length of a subsample of cyprids was measured using image analysis of magnified images. One other barnacle species, *Elminius modestus*, was found to settle at the same time as *Chthamalus* during the sampling periods. The cyprid of this species, although of an overlapping size, could be distinguished clearly from *Chthamalus* species and hence was omitted from any analysis. Metamorphosed spat could be identified to species level using the descriptions provided from SEM analysis by Burrows (1988). Hence the number of *Chthamalus montagui* and *C. stellatus* spat in random subsamples of the rock surface was counted.

LARVAL SUPPLY

In the summer of 2003 a larval sampling programme was initiated to determine the variation in larval production and larval supply of the two chthamalid species between exposed and sheltered locations. A stretch of sheltered coastline at Kingsand and exposed coastline at Penlee Point was selected and plankton samples collected from a 5 m work-boat between 8 July and 7 October. Samples were collected approximately weekly in shallow (8–10 m depth) water during periods of high water, within 30–40 m of the shore line, using plankton nets with a 0.5 m diameter mouth. Two different net mesh sizes (90 μm and 150 μm) were used throughout the study to effectively sample early stage II larvae and the later non-feeding settling cyprid stage. Previous unpublished work by M. T. Burrows in the Plymouth area, followed by work within this study, showed that a mesh size of 150 μm was suitable for collecting late-stage larvae, allowing relatively large volumes of water to be sampled before clogging of the net. However, this

mesh size was inefficient at collecting the much smaller early-stage larvae and particularly so for the smaller species *C. montagui*; for this reason a smaller mesh size of 90 μm was used.

At each of the two locations a transect approximately 300 m long was established close to shore. Plankton trawls were made at a speed of 1.5–2 knots. A weighted net with attached flowmeter was deployed and the towing line gradually lengthened over a 5-min period to obtain an oblique haul covering the whole of the water column. On reaching the maximum line length the net was steadily retrieved and the plankton sample placed immediately in 5% formalin in seawater. Throughout the study a depth logger was attached to the net to verify that samples were taken over the whole water column (within 1–2 m of the sea bed). Flowmeter readings showed the volume of water sampled using the 150 μm net varied between 19 and 59 m^3 (mean volume 43 m^3) for each tow, compared to between 8 and 41 m^3 (mean volume 27 m^3) using the 90 μm net.

Samples were analysed under a Leica MZ8 stereomicroscope. A small subsample (between 1 and 2.5%) of the 90- μm net samples was analysed for stage II larvae, while a much larger subsample (between 12.5 and 100%) of the 150 μm net samples was analysed for cyprids. Small subsamples were taken from a known volume of sample using a 5-mL Hensen–Stempel pipette, while a Fulsom plankton splitter was used to take larger subsamples. Early-stage larvae were identified using the descriptions of Burrows, Hawkins & Southward (1999) and of Ross *et al.* (2003).

Quantitative plankton tows of any length were not possible using mesh size lower than 90 μm in the coastal waters sampled owing to rapid clogging of the mesh. The size of *C. montagui* larvae (width 150 μm) meant that there was a possibility of biasing sampling toward *C. stellatus* using a 90- μm net. In July 2004 this possibility was tested by comparing the ratio of stage II *C. montagui* and *C. stellatus* larvae caught using a 90- μm net and using water samples pumped from the same depth and directed through a 50- μm net at the surface. This comparison showed that the 90- μm net did bias sampling toward *C. stellatus*. The proportion of *C. montagui* larvae was 1.68 times greater in pumped samples. This correction factor was used to remove the bias from stage II larval results. Such a correction does not change the overall outcome of the sampling aims, to determine any difference in the proportion of each larval species across the wave-exposure gradient. It merely allows a more accurate reflection of the absolute abundances of the two species at this larval stage.

DATA ANALYSIS

Throughout this study absolute abundance data are not given. Owing to the generally low recruitment levels in *Chthamalus* and difficulties in identification to species level, high settlement/recruitment patches were targeted during sampling, thus biasing any estimates of

absolute abundance. Instead, and consistent with the aims of this work, analyses for both planktonic larvae and recruits use the number of *C. stellatus*, expressed as a percentage of all chthamalids, as the dependent variable. ANOVA is used throughout to determine the effects of wave exposure and vertical height on the shore (both fixed factors). Where multiple spatial scales are used (shore, site, patch) these are treated as random factors. Prior to ANOVA, data were examined for heterogeneity of variance using Cochran's test and heterogeneous data transformed. All transformations were successful in eliminating heterogeneity. Significant factors were analysed further using SNK multiple comparisons.

Results

LARVAL IDENTIFICATION

Over 1500 chthamalid cyprids were collected and measured throughout the summer of 2003. Their size range, between 402 and 647 μm , was distinctly bimodal with modal size classes differing by 120 μm (485 vs. 605 μm) (Fig. 2). There was no evidence of a change in size range or in modal size class throughout the period of collection (7 August–1 September). Cyprid carapace length of *C. montagui* and *C. stellatus* has been verified by molecular techniques as an effective tool to separate these two species (Power *et al.* 1999), which otherwise differ little in morphology. Power *et al.* (1999) found that of 68 cyprids collected in west Ireland and examined using mtDNA-RFLP analysis, those measuring 525 μm and under were *C. montagui* and those of 550 μm and over were *C. stellatus*. Although latitudinal variation in cirripede larval size is well documented, this division of species at 525–550 μm corresponds exactly with the trough in the size frequency distribu-

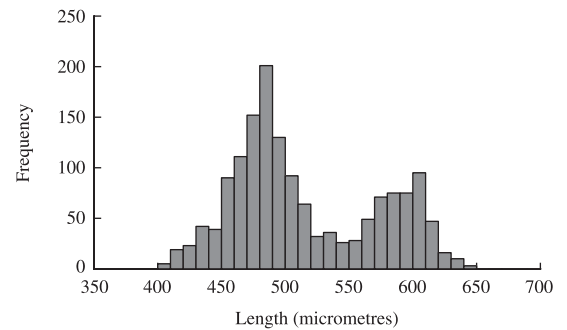


Fig. 2. Size–frequency distribution of settled chthamalid cyprids collected in the Plymouth Sound area during the summer of 2003.

tion of cyprids collected from around Plymouth Sound (Fig. 2). In calculating the ratio of species distribution of cyprids in the present study, those individuals over 540 μm have been classified as *C. stellatus* and those under 540 μm as *C. montagui*. Following analysis of size distributions it was subsequently found that cyprids of the two species could be identified by morphological features. Such identification matched exactly the division of species based on size. To maintain consistency throughout the study, size was continued to be used as a key discriminatory factor.

ADULT DISTRIBUTION

The survey of adult barnacle distribution identified four species of acorn barnacle, *Chthamalus stellatus*, *C. montagui*, *Semibalanus balanoides* and *Elminius modestus* in the mid-shore barnacle zone. Over all shores the two chthamalid species were by far the most abundant barnacle (Fig. 3), but the relative proportions of *C. stellatus* and *C. montagui* varied consistently over the wave exposure and vertical gradients. Considering

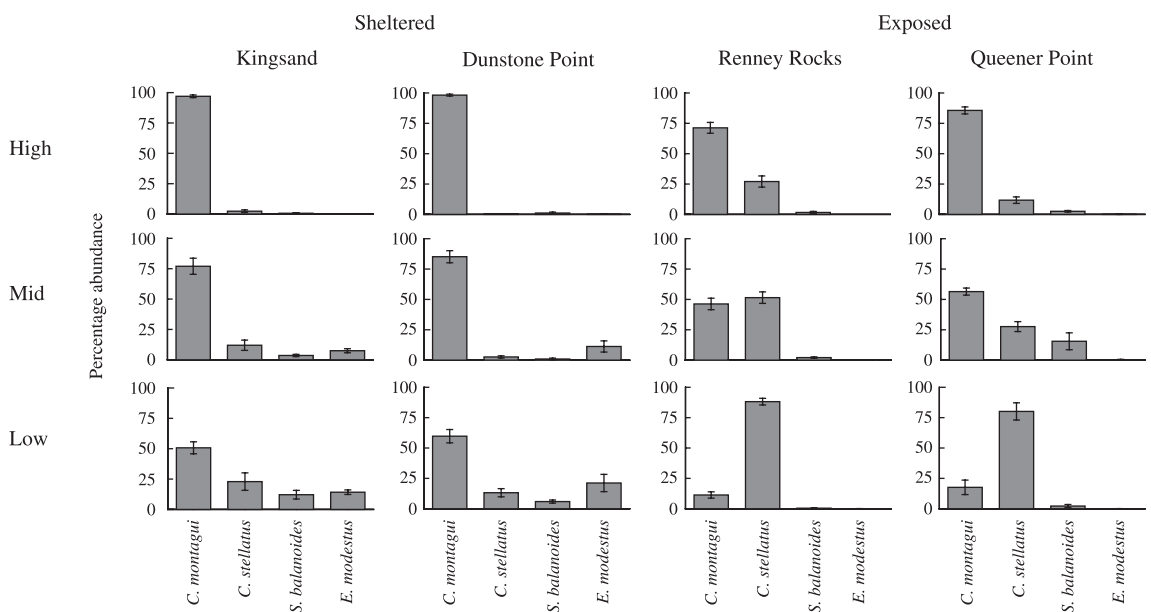


Fig. 3. Percentage abundance of adults of the four common intertidal barnacle species in the Plymouth area at three tidal heights within the barnacle zone at two sheltered and two exposed shores. Error bars ± 1 SE.

Table 1. ANOVA of abundance of adult *Chthamalus montagui* (as a percentage of both chthamalid species) at three shore heights at exposed and sheltered shores in the environs of Plymouth Sound in June 2002. Data are arc-sin transformed. Cochran's C = 0.08; not significant. The factors exposure and height are fixed, shore, site and patch are random

Source	d.f.	MS	F	P	F ratio vs.
Exposure	1	63721	19.47	< 0.05	Sh(Ex)
Shore (exposure)	2	3272	5.63	> 0.05	Si(Sh(Ex))
Height	2	27820	138.00	< 0.001	He × Sh(Ex)
Site (shore (exposure))	4	581	3.64	> 0.05	Pa(Si(Sh(Ex)))
Patch (site (shore (exposure)))	8	159	2.80	< 0.01	Residual
Height × exposure	2	2576	12.78	< 0.05	He × Sh(Ex)
Height × shore (exposure)	4	201	0.35	> 0.8	He × Si(Sh(Ex))
Height × site (sh(ex))	8	580	3.72	< 0.05	He × Pa(Si(Sh(Ex)))
Height × patch (si(sh(ex)))	16	156	2.74	< 0.001	Residual
Residual	240	57			

chthamalid barnacles alone, *C. stellatus* was far more abundant at exposed sites than shelter, making up 50% of all individuals compared to only 11% in shelter, pooled across all three shore levels (Fig. 3). ANOVA of the percentage abundance of *C. montagui* showed the difference across the exposure gradient was consistent over all three tidal heights (SNK of significant exposure–height interaction; Table 1). There was a clear pattern in the relative abundance of the two chthamalid species over the vertical gradient of the shore with a trend of increasing dominance by *C. montagui* with increasing vertical height on both exposed and sheltered shores (SNK of significant height–patch interaction). On exposed shores the dominance of the two species switched from *C. stellatus* in the low shore to *C. montagui* in the high shore, while on sheltered shores the general paucity of *C. stellatus* meant *C. montagui* was the most abund-

ant chthamalid over all three shore levels, although its dominance increased with shore height.

LARVAL DISTRIBUTION

Stage II larvae were abundant in the water column throughout July to September with peak density in August, but were absent in samples taken in early October. Throughout the main settlement period densities were high, with an average of over 1000 and over 2500 m⁻³ of *C. montagui* and *C. stellatus*, respectively. *C. stellatus* stage II larvae were generally more abundant than *C. montagui* at both locations. However, the contribution of *C. stellatus* to the total chthamalid larval density differed between the exposed and sheltered sites (Fig. 4). The percentage abundance of *C. stellatus* averaged over the period of larval availability was 82% at the exposed

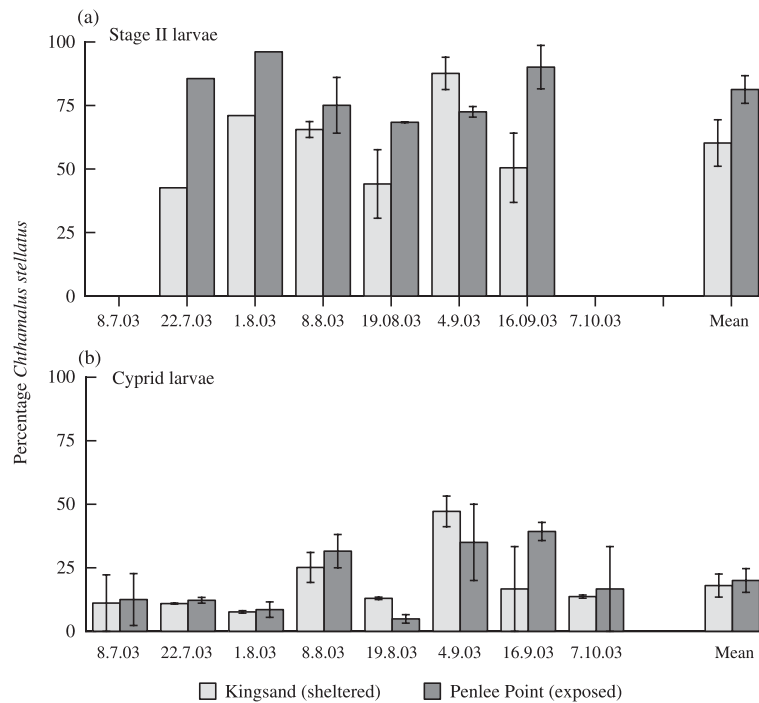


Fig. 4. Mean percentage abundance of *C. stellatus* larvae over the wave-exposure gradient at one sheltered (Kingsand) and one exposed (Penlee Point) shore at eight sampling dates during the summer of 2003. (a) Percentage abundance of stage II larvae. (b) Percentage abundance of cyprid larvae. Error bars ± 1 SE.

location compared to 60% in shelter. This pattern of greater proportional abundance of *C. stellatus* in exposure than shelter was consistent at five of the six sampling dates. One-way ANOVA using mean percentage abundance at each sampling date showed a significantly greater contribution by *C. stellatus* in exposure (d.f. 1,10; $F = 6.33$; $P < 0.05$).

The density of cyprid larvae was at least two orders of magnitude lower than stage II larvae and the rank abundance of the two species had changed, with greater mean abundance of *C. montagui* compared to *C. stellatus*. Throughout the main settlement period, the mean density of *C. montagui* over the wave-exposure gradient was 4 m^{-3} compared to a density of *C. stellatus* of less than 1 m^{-3} . In contrast to the pattern of stage II larval species distribution, cyprids showed no differentiation in the proportion of the two species over the wave-exposure gradient (Fig. 4). The mean proportion of *C. stellatus* was almost identical at Kingsand (18%) compared to Penlee point (20%) over the sampling period and no significant difference was found.

The transition from early larvae to the late-stage cyprid larvae in the near-shore waters sampled was accompanied by a large loss through mortality or dispersal. This loss was much greater in *C. stellatus*; on average, for every 4000 early *C. stellatus* larvae produced, only one cyprid survived. This compared with a ratio of 200 stage II larva to one cyprid in *C. montagui*. There was no consistent difference in the transition ratio for either species between exposed and sheltered sites.

CYPRID AND SPAT DISTRIBUTION

Analysis of samples collected in 2002 was restricted to metamorphs as cyprids were not collected in sufficient numbers. Owing to generally low recruitment levels, data from the weekly sampling was combined to provide an accurate estimate of the species ratio of early metamorphs during the middle of the main settlement period. The contribution of *C. stellatus* to overall abundance of chthamalid settlers showed a consistent pattern over the vertical shore gradient over all four shores, with a significant increase in proportion with declining height on the shore (Fig. 5, Table 2). It was absent from the high shore at three of the four locations, but made up between 20 and almost 70% at low tide levels. There was a significantly greater percentage contribution of *C. stellatus* on the two exposed compared to the two sheltered shores when averaged over shore heights. A similar pattern was found when metamorphs up to 1 month old were sampled although the results of the ANOVA were not as conclusive.

In 2003, sampling focused on four age classes, settled cyprids and metamorphs aged up to 1 day, up to 1 week and those which accumulated over the main settlement period from July through to the end of September.

Although cyprid data were collected from weekly sampling visits, there is a danger in these observations of incorporating individuals which have settled at some point during the 7-day period and failed to metamorphose, yet remained cemented to the substratum.

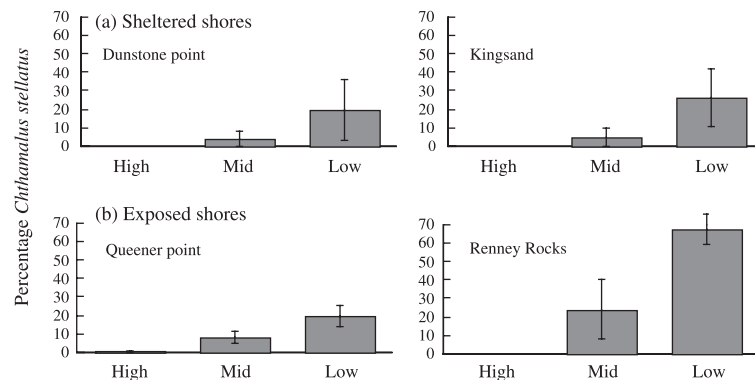


Fig. 5. Mean percentage abundance of 1-week-old *Chthamalus stellatus* recruits (percentage calculated as a total of all chthamalid recruits) over a 2-week period in August 2002 at three tidal heights within the barnacle zone at two sheltered and two exposed shores. Error bars ± 1 SE.

Table 2. ANOVA of abundance of *Chthamalus stellatus* metamorphs (as a percentage of both chthamalid species) up to 1 week old at three shore heights at exposed and sheltered shores in the environs of Plymouth Sound over a 2-week period in August 2002. Data are log-transformed. Cochran's $C = 0.25$; not significant. The factors exposure and height are fixed, shore is random

Source	d.f.	MS	F	P	F ratio vs.
Exposure	1	21.99	29.66	< 0.05	Sh(Ex)
Shore (exposure)	2	0.74	0.48	> 0.6	Residual
Height	2	37.60	29.67	< 0.01	He \times Sh(Ex)
Height \times exposure	2	5.19	4.09	> 0.1	He \times Sh(Ex)
Height \times shore (exposure)	4	1.27	0.83	> 0.5	Residual
Residual	60	1.54			

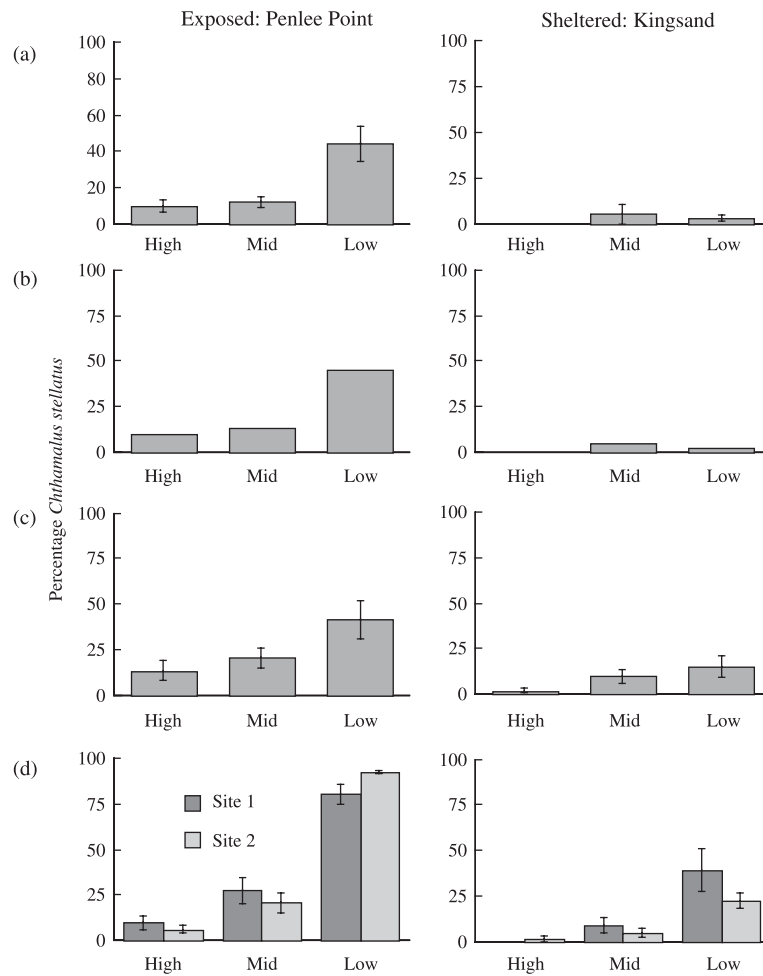


Fig. 6. Mean percentage abundance of *Chthamalus stellatus* settlers and recruits (percentage calculated as a total of all chthamalid recruits) during the summer of 2003 at three tidal heights within the barnacle zone at one sheltered and one exposed shore. (a) Mean abundance of cyprids collected daily over a 1-week period. (b) Mean abundance of metamorphs collected daily over a 1-week period. (c) Mean abundance of week-old metamorphs collected over a 4-week period. (d) Mean abundance of recruits in September at the end of the main settlement season. Error bars ± 1 SE.

For this reason only daily counts of cyprids made on rock cleared of all biota 24 h previously have been used in analyses.

Cyprids collected on 6 consecutive days from Penlee Point and Kingsand demonstrate a very clear difference in the settlement patterns of the two species over both vertical and horizontal gradients (Fig. 6a). There were very few *C. stellatus* cyprids settled at the sheltered Kingsand location, while at the exposed Penlee Point 23% of all chthamalid settlers were *C. stellatus*. These were found predominantly on the low shore. Two-way ANOVA using daily counts as individual replicates showed a significant interaction of exposure and shore height on the percentage abundance of *Chthamalus stellatus* cyprids. This was caused by differences between shore heights at the exposed location only and a difference between locations only on the low shore (Table 3). The proportion of *C. stellatus* metamorphs, identified in daily sampling, showed virtually the same pattern as the unmetamorphosed cyprids, indicating no selective mortality in the two species over the critical period of metamorphosis (Fig. 6b).

Table 3. ANOVA of abundance of *Chthamalus stellatus* cyprids (as a percentage of both chthamalid species) sampled daily at three shore heights at one exposed and one sheltered shore in the environs of Plymouth Sound over a 1-week period in August 2003. Data are untransformed. Cochran's C = 0.44; not significant. The factors location and height are fixed

Source	d.f.	MS	F	P
Location	1	1618.8	18.9	< 0.01
Height	2	886.9	10.3	< 0.01
Location \times height	2	756.8	8.8	< 0.01
Residual	12	85.7		

SNK of Location \times Height.

Penlee Point: Low > Mid = High.

Kingsand: Low = Mid = High.

Low: Penlee Point > Kingsand.

Mid: Penlee Point = Kingsand.

High: Penlee Point = Kingsand.

Older metamorphs (up to 1 week old) showed the same pattern as cyprids and 1-day-old metamorphs with a significantly greater proportion of *C. stellatus* settlers with decreasing shore height and increasing

Table 4. Abundance of different stages of *Chthamalus stellatus* settlers and recruits (as a percentage of both chthamalid species) at one exposed and one sheltered shore at three tidal levels

	Exposed shore: Penlee Point			Sheltered shore: Kingsand		
	Low	Mid	High	Low	Mid	High
Cyprids	45	14	11	7	13	0
1-day-old metamorphs	46	13	10	2	5	0
1-week-old metamorphs	36	17	12	14	9	2
Up to 3-month-old metamorphs	86	25	7	31	7	0.5

exposure (Fig. 6c, two-way ANOVA, exposure: $F_{1,18} = 10.7$, $P < 0.01$; height $F_{2,18} = 5.9$, $P < 0.05$). This pattern was maintained in metamorphs which had recruited over the whole settlement period up to the end of September and therefore included individuals from a few days up to approximately 12 weeks old (Fig. 6d). Sampling of these life stages was undertaken at two sites within each location and demonstrated the spatial consistency of the species ratio. Three-way ANOVA of these data showed no effect of the spatial scale site. There was a significant difference between the exposed and sheltered shores only at the lowest tidal level and differences between shore heights only on the exposed shore (SNK multiple comparison of the significant exposure–height interaction).

The trend of increasing ratios of *C. stellatus* with decreasing shore height and increasing exposure showed consistency from the settling cyprid stage through to older (up to 3 months) juveniles. However, it is apparent that the ratio of *C. stellatus* to *C. montagui* increased substantially on the low shore at both Penlee Point and Kingsand when considering a mixture of early metamorphs and juveniles (up to 3 months old) compared to earlier stages (less than 1 week old (Fig. 6, Table 4). There was an increase in the proportion of *C. stellatus* from 36 to 45% up to 86% on the low shore at Penlee Point and from 2 to 14% up to 31% at Kingsand.

Discussion

A major thrust of recent marine ecological research has been to determine the importance of settlement variability in determining the size of subsequent adult populations (e.g. Connell 1985; Doherty & Fowler 1994; Menge 2000). In contrast, less effort has focused on understanding the relationship between larval supply/settlement and adult distribution. In the main, such work has focused on the distribution of adults over the vertical gradient of the shore (Strathmann, Branscomb & Vedder 1981; Grosberg 1982; Raimondi 1991) and less attention has been paid to horizontal distribution of benthic invertebrates (but see Raimondi 1991; Jenkins & Hawkins 2003).

The distributional pattern of *Chthamalus montagui* and *C. stellatus* across the wave-exposure gradient, and with tidal height described previously (Southward 1976;

Crisp *et al.* 1981; Burrows *et al.* 1992) was confirmed in photographic surveys of four shores in the Plymouth area. My results demonstrated clearly that the basic pattern of adult distribution of these two species is established at settlement, at the point planktonic cyprids irreversibly attach to the substratum. Schmitt & Holbrook (2002) recognize two broad categories of processes that create variation in settlement among different species, those that cause heterogeneity in larval concentrations and those that would produce variation even if larval pools were completely mixed. Strong differential patterns of settlement in the two barnacle species occurred in this case, despite a larval pool that was completely mixed; hence settlement patterns were dictated by larval choice rather than larval supply. Subsequent post-settlement mortality over a temporal scale of a few months appears to emphasize but not change this overall pattern.

The production of larvae across the wave-exposure gradient showed a pattern which reflected the distribution of adults. *Chthamalus stellatus* were proportionally more abundant in exposure compared to shelter (82% at Penlee point compared to 60% at Kingsand). Burrows *et al.* (1992) found that differences in the reproductive output (measured as egg production) of *C. montagui* and *C. stellatus* in the Plymouth area correlated with the distribution of *Chthamalus* species along the local environmental gradient of wave exposure. Calculations indicated that more *C. stellatus* larvae should be produced from wave-exposed sites and more *C. montagui* from sheltered sites. The patterns of early larval distribution observed in this study are in broad agreement with these calculations although *C. stellatus* larvae were numerically more abundant at both sites, even after correction for small biases in sampling against *C. montagui*.

Given the pattern of larval production across the wave-exposure gradient, and assuming limited dispersal from the site of production and no difference in relative levels of larval mortality between the two species in both environments, one can predict differential supply of cyprid larvae to exposed and sheltered sites. However, this was not the case; there was no difference in the proportion of cyprids of each species between the two environments. Differences in the species composition of larval production across the wave-exposure gradient

were eliminated during larval development. Additionally, the dominance of *C. stellatus* early-stage larvae (3 *C. stellatus*: one *C. montagui* averaged among sites) was replaced by dominance of *C. montagui* late-stage larvae (one *C. stellatus*: seven *C. montagui* averaged among sites), suggesting either enhanced levels of planktonic mortality or enhanced dispersive loss of *C. stellatus* from the near-shore environment. Both these explanations are consistent with a longer larval period in *C. stellatus*; cultured larvae of *C. montagui* reached nauplius stage VI in 11 days compared to 16 days in *C. stellatus* (Burrows *et al.* 1992).

It is generally assumed that the presence of pelagic larvae in most benthic invertebrates ensures that most populations are 'open' and recruitment is independent of local production (see Caley *et al.* 1996 for review). However, recent work has suggested that local retention of larvae may be more common than is generally acknowledged (Jones *et al.* 1999; Swearer *et al.* 2002). Evidence comes from a variety of sources, including population genetics, the occurrence of endemic species, the persistence of introduced species and stock recruitment relationships. A relationship between adult stock and recruitment levels observed over small spatial scales may suggest retention of larvae near to adult production (see Swearer *et al.* 2002 for review). It is clear from the results of this study that a close relationship between adult stock abundance and recruitment either through space or time cannot be used as sole evidence for local larval retention. In this study such a relationship existed only because of larval behaviour at settlement. The lack of larval retention in the study area is consistent with the output of a 3-D hydrodynamic model of circulation patterns within Plymouth Sound. This shows that the sheltered area adjacent to Kingsand (Cawsand Bay), while showing some level of water mass retention, does exchange water with Plymouth Sound and the sea beyond (Siddorn, Allen & Uncles 2003).

Despite equivalent levels of supply of both species over the wave-exposure gradient, the overall level of settlement of the two species differed substantially between the exposed headland and sheltered bay. There was clearly a high degree of active substratum selection by cyprids of both species. Such selection operated not only over the horizontal gradient of wave exposure but also over the vertical gradient of the shore. Differential settlement between high and low shore levels can be caused by differences in vertical zonation of planktonic larvae. This has been demonstrated in acorn barnacles in sheltered areas on vertical substrata (e.g. Grosberg 1982). However, the extent to which fine-scale stratification of planktonic larvae in near-shore waters of open coastlines with shelving shores affects vertical patterns of settlement is unclear. Under these conditions it is likely that wave action on the shore line will typically breakdown any fine scale stratification in the surface layers (Denny 1988). Larval sampling in Plymouth Sound during 2004 showed no difference

in the vertical distribution of the two species (Jenkins unpublished data). Active substratum selection in barnacles can occur in response to a variety of different cues, including conspecific adults (Knight Jones 1953), predators of conspecific adults (Raimondi 1988), recently settled conspecifics (Wetthey 1984) and components of the epilithic microbial film coating the substratum surface (Strathmann *et al.* 1981). However, no study to my knowledge has demonstrated the degree to which such selection can change the relationship between supply of larvae and those actually choosing to settle. Raimondi (1991) used indirect evidence to suggest that settlement choice by larvae of *Chthamalus anisopoma* largely determines adult distribution, but direct measures of larval supply were not made. The cyprid stage in acorn barnacles is specialized to settle and as such is non-feeding. While settlement can be delayed until an appropriate benthic habitat is found, such delay cannot be indefinite. Rejection of habitat occupied by a congener demonstrates the strong selective forces operating to evolve settlement strategies to ensure settlement with a conspecific.

Post-settlement mortality in the early life of newly settled marine invertebrates can be extremely high and have a strong modifying effect on patterns of settlement (see Gosselin & Qian 1997 for review). For example, Strathmann *et al.* (1981) showed that high mortality following settlement of *Balanus glandula* to the low shore effectively limited the adult distribution to the high shore in part of its distributional range. In the present study the proportional abundance of the two chthamalid species were monitored at different ages following settlement, to determine the extent to which differential post-settlement mortality modified patterns set at settlement. In laboratory experiments Burrows (1988) showed that the mortality of *C. montagui* recruits increased with greater levels of immersion, in contrast to *C. stellatus* which showed the opposite response. In the present study the general pattern set at settlement was not changed, but was accentuated in 1-day-old, 1-week-old and 3-month-old juveniles. Thus, differential mortality of the two species does clearly have a role to play in setting adult distribution patterns. However, the results of this study contrast somewhat with the conclusions of Delany *et al.* (2003) who found that post-settlement mortality, not settlement patterns, dictated the vertical distribution of chthamalid barnacles in SW Ireland. The present study showed consistent differences in the pattern of settlement over the vertical gradient of the shore consistent with the pattern of adult distribution on both sheltered and exposed shores over two separate settlement seasons. The reasons for the differences in observations are unclear, but may be related to the confounding of differences between shores with differences between zones, as acknowledged by Delany *et al.* (2003).

In summary, this study demonstrates the powerful role of larval behaviour at settlement in nullifying the role of larval supply in setting adult distribution

patterns. Cyprid larvae of two invertebrate species were delivered in proportions which were equivalent over a local environmental gradient. However, larval choice ensured settlement differed substantially over this environmental gradient and ultimately dictated the pattern of early adult distribution. The results are of significance in considering the level of openness of benthic invertebrate populations. Clearly, at the spatial scale of the study, populations were open as differential patterns of larval production were not maintained. Future work should explore the generality of these observations at multiple spatial scales. This technique of monitoring the ontogenetic change in relative abundance of different species of planktonic larvae may prove useful in determining under what conditions local larval retention can occur.

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