INTERTIDAL ZONATION OF BARNACLES:
THE INFLUENCE OF PLANKTONIC ZONATION OF LARVAE
ON VERTICAL DISTRIBUTION OF ADULTS

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Abstract. The nonoverlapping vertical distributions of sessile species in the marine intertidal are usually considered to result from two interacting factors: (1) broadly restricted settlement of juveniles in the vertical horizon, and (2) postsettlement mortality which affects species differently. Investigated here is the role of larval behavior in molding the zonation of the acorn barnacles Balanus glandula and Balanus crenatus. I document the vertical distributions of: (a) adults, (b) newly settled spat, and (c) planktonic cyprid larvae. The data show that the vertical distribution of adults is a reflection of the vertical zonation of cyprids in the plankton and settlement patterns of spat. Although postsettlement mortality and substratum selection occur, pre settlement behavior can strongly influence vertical zonation of sessile organisms.

Key words: Balanus crenatus; Balanus glandula; habitat selection; intertidal zonation; settlement behavior.

INTRODUCTION

The vertical zonation of benthic organisms in the marine intertidal is a striking phenomenon long known to marine biologists (Audoin and Milne-Edwards 1832, Connell 1972, 1975, Stephenson and Stephenson 1972). Early explanations for intertidal zonation invoked the movement of the tides as the main determinant of vertical distributions (Colman 1933, Hewatt 1937, Doty 1946). It is now known that many interacting physical and biotic processes control vertical distribution and abundance of benthic organisms (Connell 1972, Menge and Sutherland 1976, Paine 1977).

There are four main ways vertical zonation of species can arise: (1) larvae may be nonselective and recruit over a broad vertical range, but those that do not chance upon suitable substrata die; (2) larvae may recognize attributes of substrata which vary according to intertidal height, and select those substrata; (3) mobile adults may migrate to particular zones; and (4) larvae may be stratified in the water column and consequently land at different heights. The first three processes have been most studied, whereas pre settlement processes are largely unexplored.

Prior to Matthews (1917) and Wilson (1932, 1948), it was assumed that planktonic larvae settled indiscriminately along the shore. Larval behavior was thought to be unimportant in determining vertical zonation. An increasing array of data indicates that larvae settle nonrandomly and can select habitats (Meadows and Campbell 1971, Scheltema 1974, Crisp 1976). Although habitat selection at settlement (i.e., substratum selection) could precisely cast distributions of adults, juveniles often recruit in a broader vertical range than that of surviving adults (Connell 1961a, b, Dayton 1971, Strathmann and Branscomb 1979). Because distributions are often dramatically altered between settlement and adulthood, much research has emphasized that distinct zones of adults result from species-specific susceptibilities to competition, predation, and physical factors (Dayton 1971, Connell 1972, Paine 1974, 1977, Lubchenco and Menge 1978, Underwood 1978, Grigg 1979).

The influence of postsettlement processes is undoubtedly important; however, pre set tlement processes (e.g., dispersion of propagules) can affect dispersion of sedentary adults independently of substratum selection and postsettlement events (Thorson 1950, Bousfield 1955, DeWolf 1973, J. D. Standing, personal communication, D. Wethey, personal communication). In this paper, I document the vertical distributions of adults, newly settled spat, and planktonic cyprid larvae of the acorn barnacles Balanus glandula Darwin and Balanus crenatus Brugiére, and show that the vertical distribution of cyprids in the plankton corresponds to the zonation of newly settled spat, and also to the subsequent zonation of adult conspecifics.

STUDY SITE

The data were collected in the Santa Cruz Small Craft Harbor at Santa Cruz, California, USA. This harbor is well protected above its seaward extreme. The study site, on pilings beneath a dock (0.8 km above the entrance to the harbor), was in shade, and therefore damp, for most of the day. Tidal data were reckoned from a calibrated tide staff at the dock (0 m indicates mean lower low water or MLLW).

METHODS

Adult distributions

Samples of adult barnacles were taken from two adjacent pilings at the study site. On each piling, two
10 × 10 cm quadrats were censused for barnacles at 0.3 m vertical intervals from −1.2 m up through +2.1 m. All barnacles of >5 mm basal diameter were counted and identified. The two quadrats at each level were treated as replicates in statistical analyses.

**Juvenile distributions**

Twelve 4-m poles were positioned vertically 25 cm apart and nailed to horizontal beams which connected the pilings. Each pole supported 12 asbestos-cement plates (each 10 × 10 × 0.3 cm). The plates were fixed to the poles by plastic roundhead machine screws run through holes in the centers of the plates. The center of the lowest plate rode at −1.2 m, and the remaining plates were set at ascending 0.3-m intervals up through +2.1 m. The study extended from 19 April 1975 through 31 May 1975. All plates from poles 1 and 2 were removed after 1 wk; those from poles 3 and 4 after 2 wk, and so on. Plates from poles 1 and 2 were considered replicates, as were those of poles 3 and 4, etc. After each set of plates was removed, a new set was positioned in its place to detect the continuing availability of cyprids. Cyprids of both *B. glandula* and *B. crenatus* were abundant throughout the study.

Plates were preserved in buffered 10% seawater formalin. On plates with 100 or fewer barnacles, all were counted and identified. On plates with >100 barnacles, all were counted but a limited census was made for identification in the following way: a transparent coordinate matrix was set over each plate and a random number table was used to locate 100 barnacles which were then identified. An estimate of the entire population was then made by extrapolation from the sample to the total number of barnacles on the plate. Barnacles were counted as dead if their shells were broken or gaping.

**Larval distributions**

Plankton samples were taken from a floating dock at hourly intervals for 24 h beginning at 1200 on 10 May, 17 May, and 24 May 1975. Three replicate samples of 20 L each were taken at four depths: (1) the surface, (2) 0.5 m below the surface, (3) 1.5 m below the surface, and (4) 3.0 m below the surface. As the tide oscillated, the sampling depths moved toward and away from the bottom. At lowest waters, the samples at −3.0 m were nearly at the bottom, whereas at highest waters, the −3.0 m samples were taken some 1.5 m above the bottom.

An air lift was used to gather samples. The air lift was made from a 5-m length of 1.9-cm (7/8-inch) Tygon tubing paralleled by 6 m of 0.5-cm (1/16-inch) Tygon tubing. An airstone, connected to the 0.5-cm tubing, was placed into a 15-cm (6-inch) funnel. The funnel was inserted into the bottom of the 1.9-cm tubing. The funnel mouth was anchored at each sampling depth with a 1.8-kg lead weight. The air lift was powered by a SCUBA tank fitted with a K-valve and an A-1 ac-

**Results**

**Adult distributions**

The vertical distributions of adult *Balanus glandula* and *B. crenatus* are presented in Fig. 1. *Balanus crenatus* was abundant at −1.2 m and −0.9 m, and was rare above these levels. In contrast, *B. glandula* rarely appeared below −0.3 m, but was abundant from that level up to +1.5 m. The maximum densities of adults of both species were ≈100 barnacles/100 cm². A partially nested two-way ANOVA (with pilings treated as blocks) shows highly significant differences (P < .001) between the numbers of each species according to tidal height. This confirms that adults of the two species are distributed differently; *B. crenatus* is abundant subtidally, whereas *B. glandula* is abundant intertidally with little vertical overlap between the species.

**Juvenile distributions**

The recruitment data for *B. glandula* are presented in Fig. 2a. Few spat ever settled below −0.6 m or
above +1.5 m. Settlement of this species was greatest from MLLW upwards through +1.2 m. Maximum densities reached 800 spat/100-cm² plate. Density increased through the 5th wk, then stabilized.

Fig. 2b illustrates the settlement data for *B. crenatus*. Spat were most abundant on the −1.2 and −0.9 m plates. Few spat ever settled above −0.3 m. As with *B. glandula*, total settlement increased throughout the study, but after the 5th wk of submergence, rates of recruitment rapidly declined. For both species, dead barnacles accounted for <5% of the population of any plate.

The results of a partially nested three-way ANOVA show a highly significant (*P* < .001) tidal height × species interaction. This supports what the figures document: there is little overlap at settlement between juveniles of *B. crenatus* and *B. glandula*. For both species, the vertical range of settlement of juveniles corresponds nearly exactly to adult zonation.

<table>
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<th>Source of variation</th>
<th>df</th>
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<tr>
<td>Residual</td>
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* Degrees of freedom for *F* test same as df column, with 192 df replicates.

Larval distributions

The data for the three samplings are presented in Figs. 3a, b, and c. On all three dates, at all hours, 94% of *B. glandula* cyprids were taken at the surface. In comparison, the cyprids of *B. crenatus* were never taken at the surface. In fact, 98% were collected at depths corresponding to an actual depth below MLLW.

Because the sampling depths moved vertically with the tide, the appearance of *B. crenatus* cyprids in 0.5-m and −1.5-m samples at low tides, and their absence from these depths at high tides, suggest that these cyprids remain at a fixed distance from the bottom. As the tide changes, different sampling depths intersect this cloud of cyprids.

Partially nested three-way ANOVA’s for each of the three dates show the same patterns of results. At each sampling, all of the depth × species interactions are highly significant (*P* < .001), confirming that the larvae of both species have very different vertical distributions. There were also significant (*P* < .005) interactions between total number of cyprids at each depth and time of day (depth × time) and between the total number of each species and time of day (species × time). As time of day is related to tidal cycle, it seems possible that the tide influences the relationships indicated by the ANOVA interaction terms. Such a possibility is also indicated by the second-order interaction terms (see Table 1).

Least squares regression analyses of: (1) total number of both species together (summed over all depths) vs. time, (2) total numbers of each species summed over all depths vs. time, and (3) total numbers of each species (and both species together) at each depth vs. time indicated no significant correlations in any of the comparisons (*P* > .5). Power spectrum analyses (Platt and Denman 1975) of all of the main effects revealed no periodicities that corresponded with tidal cycle. Because the samples were taken during a new moon.
half moon, and full moon, and the same patterns always emerged. Lunar effects seem unimportant.

**Discussion**

Connell (1961a, b, 1970) reported that the zonation of the barnacles *Chthamalus stellatus, Balanus balanoides, and B. glandula* was broadly determined by the settlement patterns of their respective cyprids. The most important factors which influenced adult distributions of these species intruded some time after settlement. Moyse and Knight-Jones (1967) obtained similar results for *Chthamalus stellatus*, but found that the settlement range of spat of *Elminius modestus* and *B. perforatus* corresponded with the vertical distribution of adults. Strathmann and Branscomb (1979) and Strathmann et al. (1981), trying to reconcile cases of precise and imprecise concordance of adult and juvenile zonation, examined differences in settlement behavior of *B. cariosus* and *B. glandula*. In 1979, they suggested that the relative precision of substratum selection depended upon the correlation of microfloral zonation with the suitability of their respective habitats. By 1981, it was clear that *B. glandula* could distinguish between transplanted substrata of high and low origins.

It remains unclear, however, how cyprids in particular, and more generally, how many other larvae distinguish between vertical heights (Meadows and Campbell 1971). Nevertheless, newly settled juveniles are often distributed nonrandomly. Which of many covarying factors lead to these distributions can be difficult to discern. The data presented here indicate that the vertical zonation of adult *B. glandula* and *B. crenatus* at Santa Cruz can be traced back through their life cycles to the vertical zonation of their late planktonic stages. This is shown by: (1) the nearly exact concordance between the vertical ranges of spat and of adults on pilings, and (2) the nonoverlapping vertical distributions of cyprids in the plankton. *B. glandula* cyprids, which nearly always settle intertidally, ensure this by riding the water’s surface as the tide oscillates. Thus, Connell’s (1970) speculation that *B. glandula* cyprids seek the water’s surface is confirmed. Remarkably, *B. crenatus* cyprids remain below a depth which corresponds to the upper bounds of the vertical range of adult survival.

The vertical zonation of adult *B. crenatus* and *B. glandula* reported here agrees well with the zonations reported by others, especially in locations where predation on barnacles is rare (MacDougall 1943, Pyefinch 1948, Stephenson and Stephenson 1972, Strathmann and Branscomb 1979). In places where the vertical ranges of adults are more restricted than those at Santa Cruz, such restriction seems to be a result of postsettlement processes, and not a consequence of different settlement patterns (e.g., Connell 1970).
The mechanisms which cyprids of *B. crenatus* and *B. glandula* use to locate themselves in the plankton are unclear. There are no apparent relationships between planktonic zonation and any diurnal events. Additionally, temperature profiles indicated that the water column was well mixed during this study. Possibly, cyprids of *B. glandula* seek pressure minima (Knight-Jones and Morgan 1966), respond to very low light levels (Crisp and Ritz 1973), or simply are buoyant (Bousfield 1955, DeWolf 1973). Any of these mechanisms could account for their presence at the surface. Planktonic zonation of *B. crenatus* cyprids is more difficult to explain, for their position remains constant in spite of tidal oscillations. Possibly, *B. crenatus* cyprids sink and are resuspended by the tidal flow.

The data demonstrate that the cyprids of *B. glandula* and *B. crenatus* are zoned even before settlement. Within their ranges of planktonic larvae, larvae may still select substrata (e.g., Knight-Jones 1953, Crisp and Barnes 1954). But it is not necessary to invoke substratum selection to explain these patterns of zonation. Similarly, although some young barnacles die after settlement, strong differential mortality does not always explain adult zonation patterns. Clearly, substratum selection and postsettlement mortality can influence patterns of zonation among some intertidal species. However, to these two kinds of processes ought to be added the planktonic zonation of larvae.

Acknowledgments

I thank B. Kennedy, A. T. Newberry, J. S. Pearse, M. W. Silver, and J. Standing for their advice and assistance. L. W. Buss, J. H. Connell, J. Germano, R. G. Harrison, S. Twombly, and an anonymous reviewer gave helpful criticisms of the manuscript. J. Arnold and J. A. Hartigan gave generously of their knowledge of statistics. This research was supported, in part, by National Science Foundation Dissertation Improvement Grant OCE8019304.

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