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INTERTIDAL ZONATION OF BARNACLES: THE INFLUENCE OF PLANKTONIC ZONATION OF LARVAE ON VERTICAL DISTRIBUTION OF ADULTS¹

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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, presettlement 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 (Audouin 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 presettlement 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, presettlement 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* Brugière, 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 tidestaff 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

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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 (3/4-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-

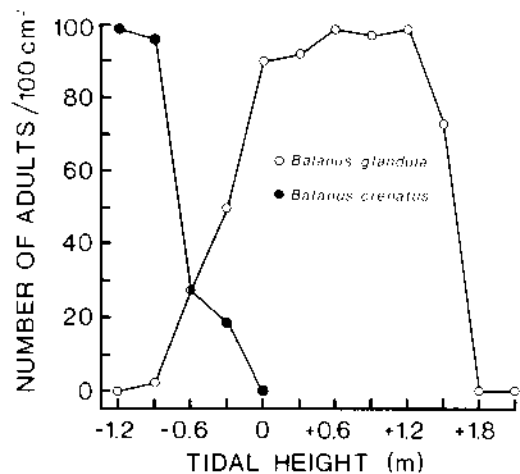


FIG. 1. The mean number of adult *Balanus glandula* and *Balanus crenatus* per 100-cm² quadrat according to tidal height (with 0 = mean lower low water). The range of samples at each height was within 7% of the mean for that height.

cessory inflator (Dacor Corporation, Northfield, Illinois) connected to the 0.5-cm tubing. Air pressure was regulated so that the flow out of the top of the air lift was 10 L/min. Samples were filtered directly onto a 10-cm disc of 160 μ m Nitex netting. The contents of the discs were carefully washed into 100 mL jars, and preserved in buffered 10% seawater formalin.

Cyprids were later sorted from the samples and identified. I used characters like those that Strathmann and Branscomb (1979) used to identify *Balanus glandula* cyprids. Pyefinch (1948) and Herz (1933) were used to identify *B. crenatus* cyprids. To confirm these identifications, I reared cyprids through metamorphosis until they were recognizable by their adult characters. Even before rearing, the cyprids proved easy to distinguish.

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 \approx 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

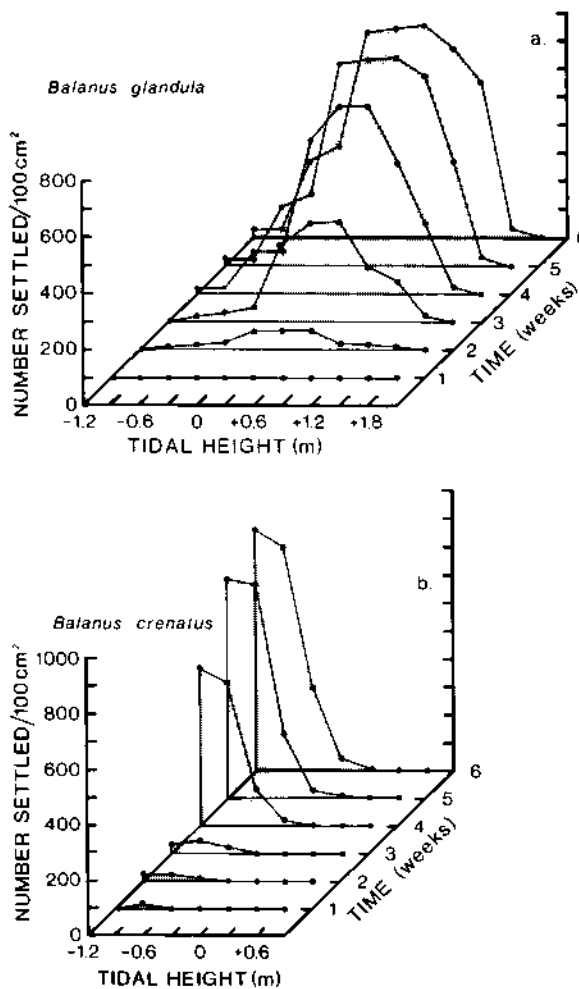


FIG. 2. The mean settlement of juvenile barnacles per 100 cm² plate according to tidal height, through time: cumulative settlement of (a) *Balanus glandula* and (b) *Balanus crenatus*.

above +1.5 m. Settlement of this species was greatest from M.L.L.W. 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 \times 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 1. Analysis of variance of the number of barnacle cyprids collected on 10–11 May 1975. The pattern of significant results was the same for the other two sampling dates.

Source of variation	df	MS	F*	Significance level (P)
Depth	3	25307.6	2569.0	<.001
Time	23	40.8	4.1	<.001
Species	1	5347.3	542.8	<.001
Depth \times time	69	97.2	9.9	<.001
Depth \times species	3	77400.0	7858.0	<.001
Species \times time	23	43.6	4.4	<.001
Depth \times species \times time	69	98.5	10.0	<.001
Replicates	192	9.2	0.9	>.5
Residual	192	9.8		

* 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 M.L.L.W.

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 \times 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 \times time) and between the total number of each species and time of day (species \times 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,

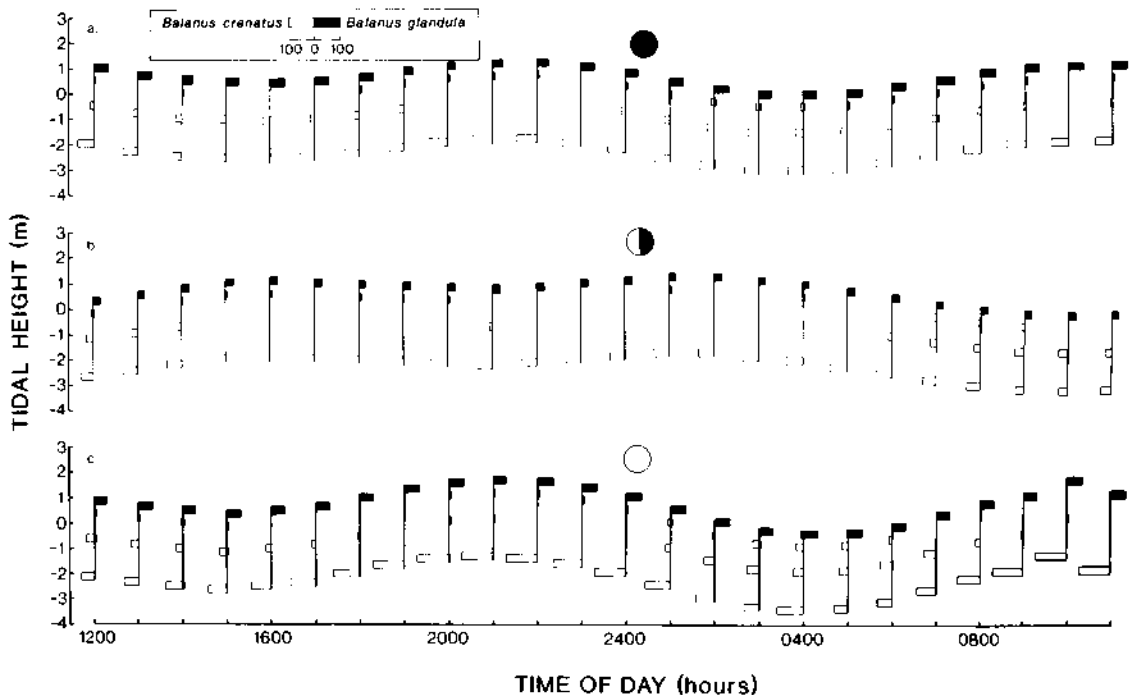


FIG. 3. The mean number of *Balanus glandula* and *Balanus crenatus* cyprids per 20-L sample at each sampling depth (at the surface and 0.5 m, 1.5 m, and 3.0 m below the surface). Samples were taken at hourly intervals for 24 h on three dates: (a) 10 May, (b) 17 May, and (c) 24 May 1975. All samples were taken at all scheduled times, though sometimes no cyprids were caught. The circular symbols depict lunar phase (solid = new moon; half open = half moon; open = full 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. Moyses 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. curiosus* 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 zonation, 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.

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LITERATURE CITED

- Audoin, V., and H. Milne-Edwards. 1832. Recherches pour servir à l'histoire naturelle du littoral de la France. Volume 1. L. Martinet, Paris, France.
- Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bulletin of the National Museum of Canada (Biological Series 46) 137:1-68.
- Colman, J. 1933. The nature of the intertidal zonation of plants and animals. Journal of the Marine Biological Association of the United Kingdom 18:435-476.
- Connell, J. H. 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacles *Balanus balanoides*. Ecological Monographs 31:61-104.
- . 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710-723.
- . 1970. A predator-prey system in the intertidal region. 1. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49-78.
- . 1972. Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics 3:169-192.
- . 1975. Some mechanisms producing structure in natural communities: a model and some evidence from field experiments. Pages 460-490 in M. L. Cody and J. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.
- Crisp, D. J. 1976. Settlement responses in marine organisms. Pages 83-124 in R. C. Newell, editor. Adaptations to environment: essays on the physiology of marine organisms. Butterworths, London, England.
- Crisp, D. J., and H. Barnes. 1954. The orientation and distribution of barnacles at settlement with particular reference to surface contour. Journal of Animal Ecology 23:142-162.
- Crisp, D. J., and D. A. Ritz. 1973. Responses of cirripede larvae to light. I. Experiments with white light. Marine Biology 23:327-335.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-389.
- DeWolf, P. 1973. Distribution and dispersal of barnacle larvae. Netherlands Journal of Sea Research 6:1-112.
- Doty, M. S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. Ecology 27:315-328.
- Grigg, R. W. 1979. Reproductive ecology of two species of gorgonian corals: relations to vertical and geographical distribution. Pages 41-59 in S. E. Stancyk, editor. Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia, South Carolina, USA.
- Herz, L. F. 1933. The morphology of the later stages of *Balanus crenatus* Brugiere. Biological Bulletin 64:432-442.
- Hewatt, W. G. 1937. Ecological studies on selected marine invertebrate communities of Monterey Bay, California. American Midland Naturalist 105:1-12.
- Knight-Jones, E. W. 1953. Laboratory studies on gregariousness during settling in *Balanus balanoides* and other barnacles. Journal of Experimental Marine Biology and Ecology 30:584-598.
- Knight-Jones, E. W., and E. Morgan. 1966. Responses of marine animals to changes in hydrostatic pressure. Annual Review of Oceanography and Marine Biology 4:267-299.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 59:67-94.
- MacDougall, K. D. 1943. Sessile marine invertebrates at Beaufort, North Carolina. Ecological Monographs 13:321-374.
- Matthews, A. 1917. The development of *Acyonium digitatum* with some notes on early colony formation. Quarterly Journal of Microscopical Science 62:43-94.
- Meadows, P. S., and J. I. Campbell. 1971. Habitat selection by aquatic invertebrates. Advances in Marine Biology 10:271-382.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351-369.
- Moyses, J., and E. W. Knight-Jones. 1967. Biology of cirripede larvae. Pages 595-611 in Proceedings of the Crustacean Symposium at Ernakulam. Marine Biological Association of India, Bangalore Press, Bangalore, India.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.
- . 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Pages 245-270 in C. E. Goulden, editor. The changing scenes in natural sciences, 1776-1976. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.
- Platt, T., and K. L. Denman. 1975. Spectral analysis in ecology. Annual Review of Ecology and Systematics 6:189-210.

- Pyefinch, K. A. 1948. Methods of identification of the larvae of *Balanus balanoides* (L.), *B. crenatus* Brug., and *Veruca stroemia* O. F. Müller. *Journal of the Marine Biological Association of the United Kingdom* 28:353-369.
- Scheltema, R. S. 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica* 10:239-262.
- Stephenson, T. A., and A. Stephenson. 1972. Life between tidemarks on rocky shores. W. H. Freeman, San Francisco, California, USA.
- Strathmann, R. R., and E. S. Branscomb. 1979. Adequacy of cues to favorable sites used by settling larvae of two intertidal barnacles. Pages 77-89 in S. E. Stancyk, editor. Reproductive ecology of marine invertebrates. University of South Carolina Press, Columbia, South Carolina, USA.
- Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* 48:13-18.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society* 25:1-45.
- Underwood, A. J. 1978. A refutation of critical tide levels as determinants of the structure of intertidal communities on British shores. *Journal of Experimental Marine Biology and Ecology* 33:261-276.
- Wilson, D. P. 1932. On the mitraria larva of *Owenia fusiiformis* Delle Chiaje. *Philosophical Transactions of the Royal Society of London (Section B)* 221:231-334.
- . 1948. The relation of the substratum to the metamorphosis of *Ophelia* larvae. *Journal of the Marine Biological Association of the United Kingdom* 31:413-438.