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Biology of Benthic Marine Organisms

Techniques and Methods as Applied to the Indian Ocean

Editors

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22. Field Studies of Life Cycles: Focusing on Individuals

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For an ecologist, the study of life cycles revolves around the problem of monitoring individuals in the field. This often time-consuming endeavor is justified when the species studied are of ecological or economic importance or is especially easy to follow, thereby providing a "model system" for testing hypotheses. Four important problems in the study of life cycles are reviewed: (1) how biological and physical factors influence postsettlement mortality of individuals under natural conditions; (2) the fate of larvae released into the plankton; (3) the extent of life-history variation among individuals; and (4) the meaning of the individual for species capable of clonal growth. I drew heavily on coral reef invertebrates for examples because of my familiarity with these organisms and because they are often particularly suitable for such studies.

INFLUENCE OF PHYSICAL AND BIOLOGICAL FACTORS AFTER SETTLEMENT

Approaches taken to this problem have been greatly influenced by scientific "fashion." An early focus on physical factors (particularly for intertidal organisms) was replaced by preoccupation with the effects of competition and predation on communities. With this shift came an experimental protocol involving monitoring changes in biomass or percent cover of structurally dominant species, following manipulations of predators or competitors (e.g., Dayton 1971). Although this approach revealed much about how species interact (Woodin, this volume), there are important limitations. First, the mechanisms responsible are often obscured because individuals are ignored. Second, it is difficult to assess experimentally the relative importance of various sources of mortality under natural conditions (including unusual but potentially critical events) because the number of experiments required to test all possible factors and their interactions would be enormous.

Thus, as Connell's studies of barnacles (1961a, b) have shown, a more effective approach may be to monitor individuals frequently enough to be

able to determine the agents of mortality, and over a period long enough to encompass most situations that an individual is likely to encounter. The appropriate time scales vary depending on the lifespans of the organisms chosen for study. Some species (e.g., epibenthic, sessile) are, of course, much easier to work with.

As an example of this approach for coral reefs, I will describe my ongoing research (with Judith Lang and Brian Keller) on the Caribbean branching coral *Acropora cervicornis* (Knowlton et al. 1981, Lang, unpublished). The basic technique is simply to draw individually identified colonies and measure the lengths of all their branches twice a year. This species offers the advantage of leaving behind a skeleton when it dies. It is often possible to assign causes of mortality with a fair degree of certainty when death has occurred within a few months of the observation. On the other hand, these corals can be quite long lived, making long-term observations essential. We were fortunate in being able to begin this study after a critical event of a type that most individual corals of this species probably experience but many investigators miss—the passage of a severe hurricane. We documented that much of the mortality associated with the storm was caused not by the immediate effects of breakage and abrasion but by the imbalance between corals and coral predators, which was produced by initial coral mortality stemming from the storm. Three years later, predation continued to exceed new coral growth in some areas, and these populations appeared to be heading towards local extinction. In other areas, in contrast, colonies were on the average doubling in size every year. The standard caging experiment (e.g., remove predators and monitor changes in the percent cover of coral) done under routine conditions could not have revealed this complexity of interaction between physical and biological sources of mortality. Further, the difficulties associated with cage construction and maintenance would have made multiple study sites logistically difficult or impossible. Yet, the kinds of subtleties revealed by this study must be understood if patterns of distribution and abundance are to be explained.

LARVAL ECOLOGY

Deficiencies in our understanding of mortality sources after settlement are, however, trivial when compared to our ignorance concerning what happens to planktonic larvae. Although we have learned a good deal about the fine tuning of settlement behavior (Scheltema 1974, Crisp 1976), we know much less about a rather basic problem—how far do planktonic larvae travel and what degrees of mortality do they suffer during their travels. We know from plankton tows that some larvae are capable of traveling great distances (Scheltema 1971), and several workers have docu-

mented maximum dispersal of introduced species by monitoring their spread (Mileikovsky 1971). But this does not tell us how far the surviving larvae, which settle, typically disperse.

Again, focusing on individuals helps to approach this problem. Gerrodette (1981) and Birkeland et al. (1982), for example, introduced adults of *Balanophyllia elegans* and *Pocillopora damicornis*, respectively, to areas previously lacking these species. They found enhanced recruitment in the immediate vicinity of introduced adults. There are two interpretations for such a result—either recruitment has a strongly localized component or widely dispersing larvae preferentially settle near conspecifics. To distinguish between these possibilities, adults, which are not releasing young, can also be introduced to an area to see if increased levels of recruitment persist in the immediate vicinity of adults, but in the absence of locally produced young. This technique was used to document localized recruitment in several species of symbiotic alpheid shrimp.

As Crisp (1978) has emphasized, direct tests of assumptions about larval dispersal are hindered by our inability to mark individually and follow the larvae of most species. An exception to this is the recent work of R.R. Olson, still unpublished, who individually followed the large (2.5 mm) larvae of the colonial ascidian *Didemnum molle*, which are released at midday. He found that recruitment was localized because larvae traveled at the speed of the current (1-2 m/min in the Lizard Island Lagoon) and generally settled within 10 to 15 minutes.

There is clearly room for methodological improvement in the study of marine larvae. Perhaps techniques used to monitor pollen flow [neutron activation or the use of rare genotypes (Handel 1983)] could be applied. There is no question, however, of the importance of knowing where recruits typically come from, e.g., for interpreting geographic variation and formulating resource management policies.

INDIVIDUAL VARIABILITY

Most scientists are more interested in means than variances, but variation within a species is apparently quite common. In corals, for example, Stephenson (1931) and Harrigan (1972) reported variation in larval characteristics (e.g., larval behavior or egg size) that could lead to differences in dispersal capabilities.

A study of the selective significance of life history variation among marine invertebrate adults was recently completed by Grosberg (1982). He found that a population of the ascidian *Botryllus schlosseri* consisted of two types of colonies—one that produced a single, large clutch of young early in the season and then died, and another that produced several smaller clutches of young later in the season. The latter type is favored

wherever an introduced competitor occurs because it is better at resisting overgrowth by this competitor. This result would have been obscured had the analysis of clutch size been confined to mean population values.

As Grosberg emphasizes, understanding variations in life history characteristics is essential because they constitute the basic material on which natural selection acts. Moreover, theory predicts that evolutionary stable variation is often to be expected (e.g., Krebs and Davies 1981, ch. 8; Subramoniam, this volume).

CLONAL GROWTH AND INDIVIDUALITY

Many marine invertebrates, particularly on coral reefs, are capable of clonal growth, that is, an individual derived from a sexually produced larva can grow indeterminately. Often, through the process of fragmentation (for corals see Highsmith 1982), a single genetic individual or genet may consist of several or many separate "individuals" with no persisting physiological connection. One particularly important consequence of this is that there is no necessary connection between the size of an individual and its age. A small coral colony, for example, may be a new sexual recruit or a recently produced fragment of a much larger colony (Hughes and Jackson 1980). The same pattern holds for many species of sponges, bryozoans, hydrozoans, etc., implying that standard demographic analyses based on age are not appropriate for such species (Hughes and Jackson 1980).

There are two basic approaches for unravelling the complexity of individuality for species capable of clonal propagation. The first is to monitor individuals through time. Hughes and Jackson (1980), for example, photographically followed the growth, fissions, and fusions of several populations of platy corals to determine the fate of genets over a several-year period. From these data it was possible to determine the probabilities of transitions between different size classes under different ecological conditions (e.g., storm years versus nonstorm years). And, from these, predict expected size-distribution patterns for areas that, for example, differ in the frequency with which they are exposed to storms.

This method does not, however, indicate the genetic relationships among the colonies that formed the starting point of the observations. An increasingly popular method for assessing such relationships involves determining whether two physiologically separate colonies will fuse when placed together. It is a bioassay that takes advantage of the fact that fragments of colonies arising from the same original sexual recruit will always fuse. Failure to fuse is typically assumed to indicate genetic differences between two colonies, while fusion indicates that they may be genetically identical, although fusion does not imply genetic identity with

complete certainty (Curtis et al. 1982, Scofield et al. 1982, Ryland 1979).

A general pattern in such studies seems to be that fusion is more likely between colonies originally found close to one another (e.g., Neigel and Avise 1983a, 1983b, and references therein). Such a pattern is probably the result of asexual propagation through fragmentation. It could also reflect localized sexual reproduction if closely related individuals are capable of fusion, for example, some ascidians (Scofield et al. 1982). Nigel and Avise have used this technique, ecologically, to show that differences between areas in the clonal structure of a single species can be interpreted as the result of differences in recruitment success (1983a), and that differences between species in clonal structure are the result of species differences in habitat utilization (1983b).

A final complexity in the study of fusion concerns the behavior of recent recruits of clonal species. Fusions between recruits have been observed by several workers (Jackson unpublished). The low dispersal of larvae in many clonal species (Ryland 1981, Jackson unpublished) and the tendency of sibling larvae to settle gregariously (Keough unpublished) suggest that such fusions may often be between siblings. Whether many colonies in the field typically contain cells derived from more than one fertilized egg remains an intriguing open question (Buss 1982).

CONCLUSIONS

The study of the life cycles of individuals in the field reveals the mechanisms by which ecological patterns are produced. Without an understanding of mechanism, it is difficult to make predictions that go beyond the scope of particular studies. Evolutionary interpretations of species characteristics are impossible without information on the selective forces acting on individuals. In summary, although one may "fail to see the forest for the trees," one cannot really understand the forest unless some of the trees are looked at carefully.

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