

Adaptive Strategies of Coral-Reef Invertebrates

Coral-reef environments that are regularly disturbed by storms and by predation often favor the very organisms most susceptible to damage by these processes

The life history of any organism is described by the sequence of developmental stages from birth to death, and by the schedule of associated vital processes, including growth, reproduction, and mortality. Since the resources required for these processes are never in infinite supply, and since environments are always variable, an organism's life history is, to some extent, a compromise. For example, if an animal concentrates on increasing its ability to survive by investing most of the energy at its disposal in building a sturdy, well-defended skeleton, then it cannot also invest maximally in fecundity by producing vast numbers of eggs. Resources must be budgeted to potentially competing processes. Thus, an organism's schedule of life-history events can be thought of as the consequence of a pattern of investment—an investment "strategy"—that has been maintained over evolutionary time by natural selection.

One of the central problems of evolutionary ecology is to explain the adaptive basis and origin of various investment patterns and to demonstrate their association with particu-

lar environmental conditions. This paper will describe how the characteristic patterns of life histories among different morphologies of sessile (attached, immobile) coral-reef invertebrates are related to the distributions of these animals on tropical reefs.

Most ideas about the ecology and life history of sessile organisms on the sea floor are based on studies of animals, such as barnacles, mussels, and oysters, that dominate the intertidal zone, estuaries, or other marginal marine environments. These animals have simple life cycles, termed asexual; numbers of individuals in a population increase only through the sexual production of larvae, which typically are dispersed in the plankton before settlement (see Fig. 1). Individual animals are easily distinguished and counted, and there is ordinarily a genetically determined upper limit to body size, which may vary somewhat in different environments. In sufficiently favorable habitats, all surviving individuals grow to about this upper size limit, produce varying numbers of gametes or larvae, and eventually senesce and die. Such a life cycle is no different in its essential attributes from that of more familiar animals like humans or fruit flies.

Many marine environments, however, particularly coral reefs, are dominated by animals such as sponges, corals, and bryozoans whose life cycles are more complicated (Jackson 1977; Hughes 1984). These organisms are constructed of interconnected assemblages of genetically identical modules, such as coral polyps or bryozoan zooids, and are therefore termed clonal (Fig. 1). Single modules, like asexual individuals, can often survive on their own, as is al-

ways the case immediately after larval settlement and before modular budding begins. Although the size of each module may be limited as in asexual animals, the size of a collection of modules, such as a coral or bryozoan colony, is usually not intrinsically limited. The few exceptions are some mound-shaped and erect species that may suffer geometric constraints or accrue a burden of supportive tissues as they grow (e.g., Cheetham and Hayek 1983).

Sometimes, groups of modules from the same clone may become separated from one another by asexual division or through mortality of the modules between them (Hughes and Jackson 1980; Highsmith 1982). This tendency of clonal animals to live their lives in disconnected bits and pieces of their former selves greatly complicates the study of their demography. Unless clonal populations are observed repeatedly, it is frequently impossible to determine whether each physically separate colony is genetically distinct, or whether a single genotype is represented by more than just one colony.

We have studied the dynamics of populations of clonal corals, sponges, and bryozoans by revisiting the same colonies at regular intervals for almost 10 years. Our long-term measurements show that partial colony mortality and fission may increase numbers of colonies as much as or more than sexual reproduction does, and that clones can persist and increase in local abundance for long periods. In contrast to asexual organisms, the clonal animals we have studied also lack any signs of physiological deterioration caused by senescence, except for turnover of individual modular components.

Jeremy B. C. Jackson, staff biologist and Marine Coordinator at the Smithsonian Tropical Research Institute in Panama, received his education in biology and geology at George Washington University and at Yale University (Ph.D. 1971). Terence P. Hughes attended Trinity College, Dublin, and Johns Hopkins University (Ph.D. 1984) and is currently a postdoctoral fellow at the University of California, Santa Barbara. The authors wish to acknowledge the support of the NSF and of the Discovery Bay Marine Laboratory, which is operated by the University of the West Indies in Jamaica. Address for Dr. Jackson: Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republica de Panamá.

Ecology of clonal organisms

Besides the greater complexity of clonal life cycles, two basic ecological differences distinguish clonal from aclonal benthos (bottom-dwelling organisms). First, it appears from the differences in the rates of positive and negative growth between colonies of clonal coral-reef invertebrates that their schedule of life-history events is closely tied to their size as well as to their age. The ability to overgrow or resist overgrowth by neighbors, survive predation, regenerate in response to injury, or reproduce sexually, all increase with colony size. A large colony or clone that has decreased in size is more likely to die and less likely to reproduce than when it was larger; thus, it may demographically resemble other small colonies, whatever their age, more than its contemporaries that have remained large. In contrast, life-history parameters of aclonal animals vary with size to a much more limited extent, because of generally smaller limits in body size, lower tolerance of injury or fission, and shorter life span. Since most demographic theory has been based solely on age-dependent models, the extreme size dependence of the life histories of clonal animals is an important problem requiring new demographic techniques (Hughes 1984; Caswell, in press).

That life-history parameters depend on colony size is clearly

demonstrated by a population of the foliaceous (platelike) coral *Leptoseris cucullata* from our study site off Discovery Bay, Jamaica, at 35 m depth. Figure 2 shows the probabilities of transitions among 4 size classes by more than 100 colonies of this coral over 3 years. Consider first the fates of the corals in the smallest size class; 100% of these are accounted for by growth into the next two larger size classes (38%), by staying in the same size class (19%), and by death (43%). In contrast, the colonies in the largest size class increased to 317% of their original number, 67% of them remaining in the same size class while producing 250% of their original number in smaller colonies. Sex was not the primary means of producing new colonies in this population: over the 3 years of the study, 38 colonies formed by fission, compared to only 16 new colonies produced by the recruitment of larvae, which is the rare successful settlement of sexually produced larvae on the substratum. Similar relationships of size to survival and to fission have been shown for all corals, bryozoans, and other benthic clonal invertebrates for which adequate demographic data are available (e.g., Connell 1973; Bak et al. 1981; Sebens 1982; Winston and Jackson 1984).

The onset and continued capacity for sexual reproduction are also directly related to colony size in clonal animals. As an apparent response to initially high mortality, small colonies grow proportionately faster

than larger colonies and do not begin to reproduce sexually until they reach a certain minimum colony size, presumably because of a limitation of resources (Connell 1973; Hughes and Jackson, in press; Jackson and Wertheimer, in press). Thus, following a decrease in size caused by partial mortality, small portions of formerly larger colonies may lose their capacity to reproduce sexually until they grow back again to a larger size (Wahle 1983).

Since few clones appear to die of old age, and the chances of survival and of successful reproduction both increase with colony size, undisturbed populations may become dominated by relatively few, long-lived, highly fecund individuals (Jackson, in press). Indeed, many reefs today are dominated by corals up to thousands of years old; and corals probably lived many times longer when sea levels were more stable (Potts 1984). There are numerous exceptions, but aclonal organisms on coral reefs are generally rather ephemeral compared to clonal species.

The second basic ecological difference between clonal and aclonal benthic animals is in their patterns of distribution. Just as one might expect, given their chances of long-term survival, clonal species are generally more abundant and diverse in more stable and predictable environments than are aclonal species (Jackson, in press). For example, the surfaces of sediments, which are physically less

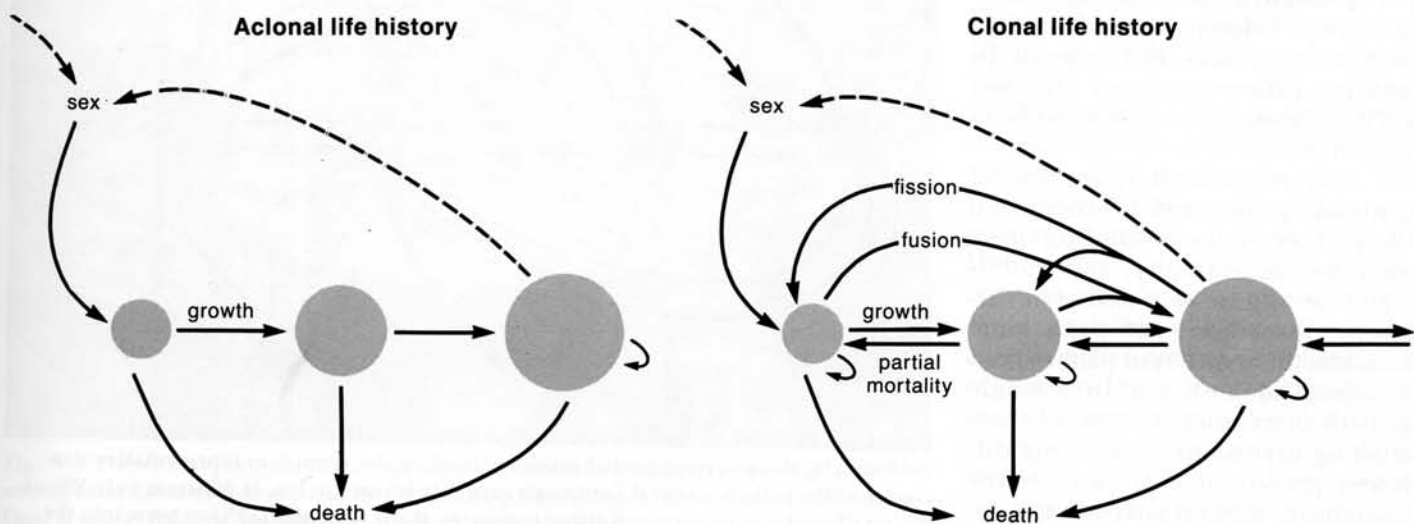


Figure 1. The two types of life histories of sessile organisms are represented schematically in terms of individual size, with the arrows indicating all possible transitions between size classes and mortality. Aclonal organisms, such as oysters or humans, have relatively simple life histories, increasing their numbers only by

sexual reproduction and their size only by growth, and having an upper size limit. In contrast, colonies of clonal organisms, such as corals and bryozoans, can increase their numbers by fission and their size by fusion, can decrease their size, either by fission or by partial mortality, and can grow indefinitely. (After Hughes 1984.)

stable than most rocky substrata, are dominated by clams, worms, and other aclonal animals. In contrast, hard substrata are typically dominated by clonal groups such as sponges, corals, and bryozoans, except in environments that are highly variable physically, such as the intertidal zone and estuaries. Physical conditions in tropical seas are generally much less variable than in the temperate zone, and diversity and abundance of clonal taxa increase relative to aclonal taxa toward the equator. For example, stony corals and ascidians are groups with both clonal and aclonal species; the ratio of clonal to aclonal species in these groups was found to be only 0.75 in waters off Great Britain, compared to 2.97 in the Caribbean (Coates and Jackson, in press).

Similarly, on a more local scale, as environmental conditions generally become more stable and predictable with increasing depth, the ratio of numbers of clonal to aclonal species increases accordingly. Estuaries are especially variable environments, and clonal to aclonal ratios also increase from estuarine into more stable marine environments (Jackson, in press).

Beyond the striking differences that distinguish the life histories and distributions of clonal from aclonal invertebrates, within each group there are also persistent and ephemeral taxa. Among clonal animals, the characterization of these differences is more complicated than among aclonal animals, because there are more parameters to account for, such as the tendency of clonal organisms to live in bits and pieces and to grow in widely different shapes (Jackson 1979; Hughes 1984; Coates and Jackson, in press).

Nevertheless, there are several contrasting patterns of correlated life-history traits—including morphology, demography, and mobility—that appear repeatedly in different clonal taxa. Although quite variable, these different patterns can be observed both within a single growth form, such as sheetlike encrusting bryozoans, and among different growth forms, such as the branching, mound-shaped, and foliaceous forms of corals.

This paper will focus on one distinguishing trait of particular importance among sessile clonal animals, the extent to which they

"move" about the substratum (Buss 1979; Jackson 1979). Although sessile organisms are incapable of active locomotion, sessile clones may still change position through growth and through passive dispersal of fragments, and different species vary enormously in the extent of this passive mobility. Rapidly growing clones are always on the move, exploring new areas of substratum, often far from where they settled as larvae. The youngest portions of these mobile clones tend to overwhelm most others they encounter, but they are rather weakly constructed and also tend to fall to pieces rapidly. In contrast, more stationary clones grow and take over space slowly, move about much less, and are built more sturdily. Despite these differences, however, individual clones of both mobile and stationary species may be extremely long lived and may cover quite large areas.

Mobile and stationary strategies occur commonly among all major taxa of clonal coral-reef invertebrates. We will first consider these strategies within single growth forms, using as examples foliaceous corals and encrusting bryozoans. Afterward, differences in life histories and mobility among different growth forms within the same taxa will be examined. Our examples are limited to Caribbean reefs, although we have

observed equivalent patterns on reefs elsewhere.

Investment strategies of corals

One of the commonest patterns of growth among stony corals is in the form of foliaceous colonies, such as those shown in Figure 3, which extend out horizontally over the substratum from a restricted area of attachment at the base to form single or multiple flattened discs or lobes. On Caribbean reefs at least 10 species characteristically show this form. *Montastrea annularis* is one of the most abundant foliaceous corals, particularly in depths greater than about 20 m; in shallower water, it also grows abundantly as massive and encrusting colonies (Goreau 1959; Dustan 1975). *Leptoseris cucullata* is another foliaceous coral common on Caribbean reefs, where it always grows as thin plates.

These two species represent opposite extremes in growth rates among foliaceous corals. Foliaceous *Montastrea* colonies, although they are often very large, up to several meters across, grow very slowly, usually only 0.5 to 1.0 cm laterally per year. In deep water, they are highly persistent locally and long lived. In contrast, *Leptoseris* colonies may reach 1 m or more in diameter,

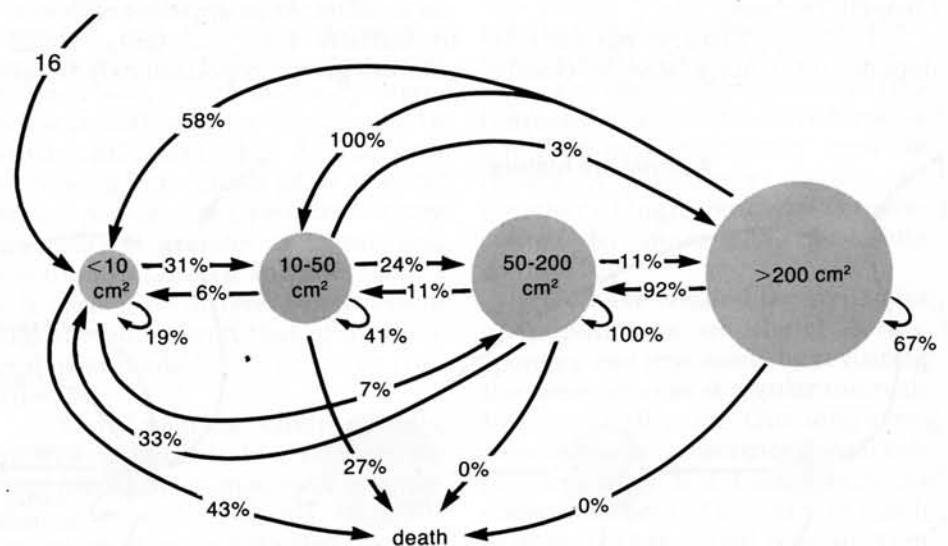


Figure 2. The correlation of the size of coral colonies with their ability to survive is indicated by these average probabilities of transition between four representative size classes of the foliaceous coral *Leptoseris cucullata* (shown in Fig. 3). Whereas only 57% of the smallest size class managed either to survive at the same size (19%) or grow into the next two larger size classes (31% and 7%), the transitions from the colonies in the largest size class amounted to 317% of their original number, with none of them dying. Over 100 colonies at 35 m depth off Discovery Bay, Jamaica, were observed over 3 years, during which time 16 new colonies were formed by sexual reproduction and 38 by fission. (After Hughes and Jackson, in press.)

but are usually much smaller; however, they grow laterally 5 to 10 times faster than *Montastrea*, at rates up to 5 cm per year.

Corals compete for space by direct and indirect means. Direct interactions are commonly aggressive: a dominant colony extends filaments armed with stinging cells onto the tissues of its less aggressive neighbors, which are subsequently di-

gested away (Lang 1973). Indirect interactions involve growth of one colony above another, thereby inhibiting the loser's access to light or food (Connell 1973). *Montastrea* is the most aggressive Caribbean foliaceous coral, capable of digesting the tissues of any other foliaceous coral with which it comes into direct contact. In contrast, *Leptoseris* is among the least aggressive corals and loses most of

its direct encounters with other clonal species. Instead, *Leptoseris* competes by rapidly growing up over its neighbors, as illustrated in Figure 4.

The two species of corals also have distinctive morphologies. Their skeletons, though similar in density, differ markedly in thickness; for average-size colonies at 30 m depth, foliaceous *Montastrea* skeletons have a mean thickness of 11 mm, versus 3 mm for *Leptoseris*. Consequently, *Leptoseris* colonies suffer far more in storms. For example, between 1977 and 1980 the mean percentage of tissue lost per year was about 5 times greater for monitored *Leptoseris* populations (112 colonies) than for *Montastrea* (75 colonies), with a rate of tissue turnover of 19% per year for the former compared to only 4% for the latter (Hughes and Jackson, in press). This suggests complete turnover of colony tissues after an average of every 5 years for *Leptoseris* versus every 25 years for *Montastrea*. Moreover, no *Montastrea* colony died completely in a single year, whereas whole *Leptoseris* colonies died every year. Another striking difference is in the larval recruitment of colonies, which was much higher for *Leptoseris* than for *Montastrea* (Rylaarsdam 1983); indeed, we have not detected a single larval recruit of *Montastrea* since 1977.

All these differences in life history are reflected in the contrasting distributions of foliaceous colonies of these species over the reef. Despite its more fragile construction, *Leptoseris* is relatively more abundant than foliaceous *Montastrea* at depths of 10 to 20 m; in these shallower waters, damage by storms and grazing predators, such as the sea urchin *Diadema antillarum* and damselfish, is greatest, and sponges, which are fierce competitors with corals, are relatively uncommon (Woodley et al. 1981; Jackson and Buss 1975). For foliaceous corals in shallow water, rapid growth is apparently more adaptive than strong skeletons and aggression. In contrast, at 35 m depth the foliaceous morphology of *Montastrea* is relatively more abundant than *Leptoseris*; in this deeper, less disturbed environment, the chance of persistence is increased by the reduced effects of storms and predators. Thus, just as they favor clonal over asexual species, stabler environments seem to favor the more

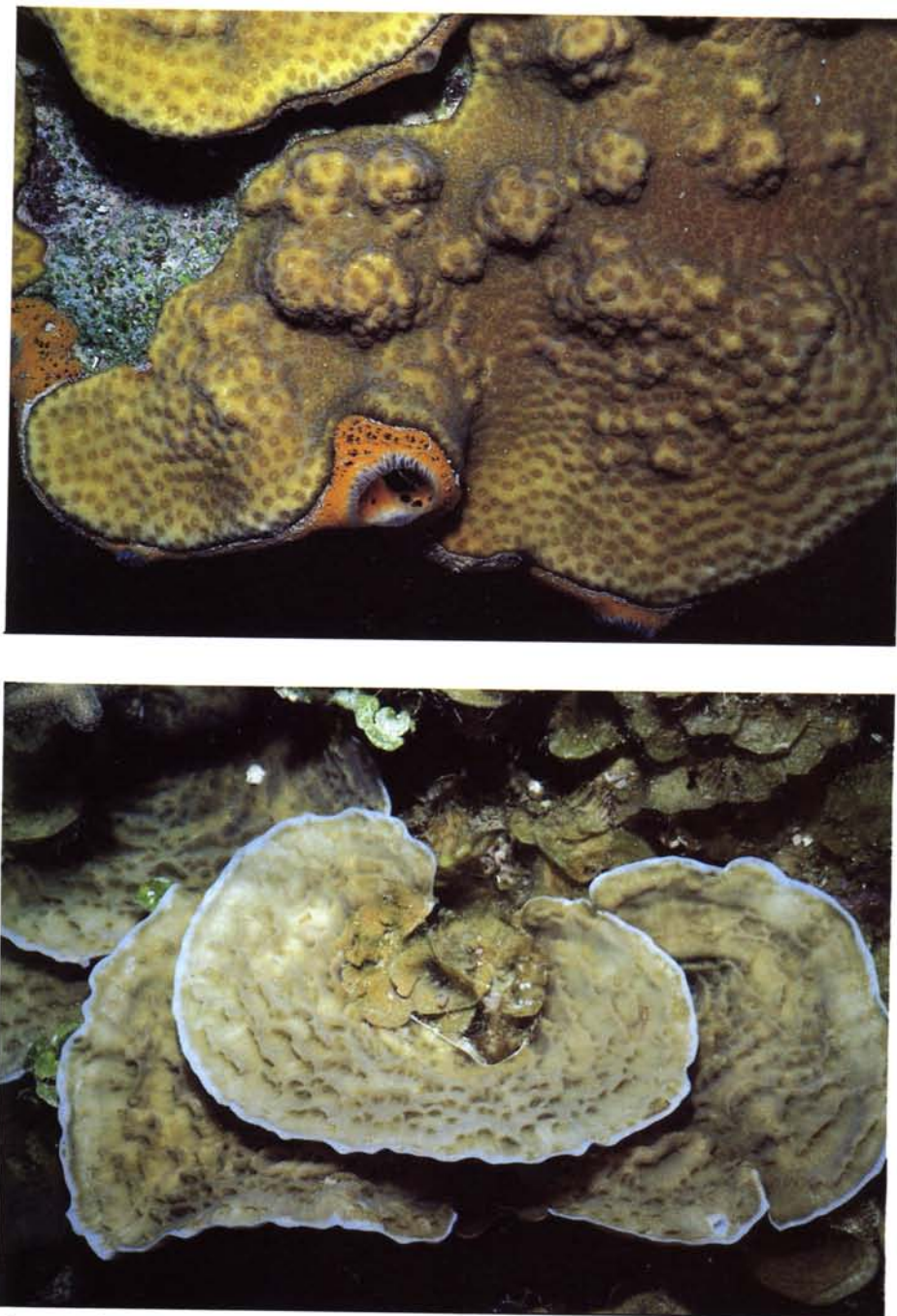


Figure 3. These two species of foliaceous corals represent opposite adaptive strategies among coral colonies that grow in this flattened, platelike form. *Montastrea annularis* (top) is relatively slow growing, but it is persistent in stable environments and successfully aggressive in direct encounters with other foliaceous colonies. (The orange creature near the bottom of the photograph is a sponge, *Mycale laevis*.) *Leptoseris cucullata* (bottom) is not aggressive and is much more ephemeral, but it nevertheless is more abundant than foliaceous *M. annularis* in highly disturbed environments, because of its greater mobility. (Photographs by G. Bruno.)

Investment strategies of bryozoans

A diverse community of sheetlike encrusting algae, bryozoans, sponges, corals, tunicates, and other sessile organisms lives on the undersurfaces of foliaceous corals such as *Montastrea* and *Leptoseris*, habitats where competition for space is so intense that the growth of any creature usually involves partial or complete death of another (Jackson and Buss 1975; Jackson and Winston 1982). Like their coral hosts, the encrusting organisms exhibit a wide variety of life histories that can be related to their patterns of distribution.

The two most abundant bryozoan species encrusting coral undersurfaces at our study sites in Jamaica are *Reptadeonella costulata* (Fig. 5) and a newly discovered species of *Steginoporella* (Fig. 6), both of which may occasionally grow to cover their entire substratum. *Reptadeonella*, a relatively stationary species, grows only 3 to 4 cm per year, forming fairly symmetrical colonies that are highly persistent. *Steginoporella*, in contrast, is extremely mobile, growing laterally at rates up to 11 cm per year, faster than any other encrusting bryozoan or foliaceous coral in Jamaica; the rapidly growing colonies form asymmetrical lobes or fans that sweep across the coral undersurface, rarely remaining in any one place for long, as can be seen in the 10-month sequence in Figure 6. In the same



Figure 4. The coral *Leptoseris cucullata* is able to compete successfully by virtue of its rapid growth, a capacity that permits it to grow over and around competitors for space, such as this *Agelas* sponge. Note that the coral is not in contact with the sponge, which may be toxic to the coral. (Photograph by C. Arenson.)

10-month period, a large *Reptadeonella* colony moved hardly at all, as shown in Figure 5.

Just as in the corals, these patterns of mobility are correlated with other demographic differences (Winston and Jackson 1984). Newly recruited *Steginoporella* colonies survive an average of only about 120 days, compared to an average of about 500 days for *Reptadeonella*. However, in addition to being more

mobile, *Steginoporella* also recruits more than 1.5 times faster than *Reptadeonella*, and large colonies of both species survive for many years.

As with the corals, there are also striking differences in the architecture and related biomechanical properties of the individual zooids of the two species (Best and Winston 1984). Each zooid consists of a feeding organ and other organ systems enclosed within a boxlike skeletal



June 1983

Figure 5. *Reptadeonella costulata*, one of the single-layered species of Bryozoa that encrust the undersurfaces of foliaceous corals, invests much of its resources in fortification and maintenance of its component zooids, but at the expense of rapid



May 1984

growth. Thus, this colony at 10 m depth near Rio Bueno, Jamaica, is relatively unchanged after 10 months, compared to the *Steginoporella* colony shown in Figure 6. The alligator clips are 5 cm long. (Photograph at left by J. Jackson; at right by G. Bruno.)



June 1983

Figure 6. *Steginoporella* is a highly mobile bryozoan, but at the expense of durability, as is indicated by these colonies – all probably members of the same clone – encrusting the undersurface of a foliaceous coral at 10 m depth near Rio Bueno, Jamacia. (First photograph by T. Hughes; other three by G. Bruno.)



September 1983

chamber. As Figure 7 shows, *Steginoporella* zooids are rather simple in form, with an enormous orifice through which the feeding organ protrudes, and they have thin roofs and walls, without much extra calcification for protection. In contrast, zooids of the more stationary *Reptadeonella* are more complex, having obvious surface fortifications, a relatively small orifice, and thick roofs and walls; consequently, *Reptadeonella* zooids are nearly 15 times harder to puncture, and their colony surfaces nearly twice as hard to crush, as *Steginoporella*'s (Best and Winston 1984).

All of these differences in life history are reflected in the distributions of the two species under corals (Jackson 1984). *Steginoporella* is relatively more abundant than *Reptadeonella* nearer the coral edges, where new space is more or less regularly created by lateral coral growth, and by the grazing of the sea urchin *Diadema antillarum* and of fishes. This is also where sponges, generally the best competitors under corals, are least abundant. *Reptadeonella* shows the opposite pattern, becoming far more abundant than *Steginoporella* away from the edges. Thus, just as for foliaceous corals, the mobile species *Steginoporella* predominates in less stable, more disturbed environments, and the persistent species *Reptadeonella* predominates in more stable ones.

We can gain insight into the underlying basis of clonal life histo-

ries by comparing the functional biology of mobile and stationary species. Among the bryozoans, *Steginoporella* colonies display marked gradients between younger and older regions, correlated with the apparent senescence of older zooids, whereas *Reptadeonella* does not show regional senescence or differentiation. Younger regions of *Steginoporella* colonies are brightly colored, unfouled by other organisms, and unbroken; older regions are dark, fouled, and broken, and individual zooids are filled with waste.

This deterioration appears to affect *Steginoporella*'s ability to function in at least three important ways. First, the ability of *Steginoporella* colonies to overgrow their neighbors is greatly diminished in older regions; for example, in encounters between the two species, young regions of *Steginoporella* usually overgrow *Reptadeonella*, winning 90% of the time, whereas old regions always lose. Second, younger *Steginoporella* zooids feed more frequently than older zooids in the same colony. Third, younger regions of *Steginoporella* colonies regenerate injuries an average of more than 4 times faster than older regions. No such variation is apparent in *Reptadeonella* colonies, which regenerate injuries at rates almost equal to young *Steginoporella* (Palumbi and Jackson 1982, 1983).

Steginoporella colonies survive through a balance of spatially partitioned growth and decay. The extremely rapid growth of younger regions results in exceptional competitive and regenerative ability, but at the apparent expense of localized senescence of zooids, which prevents the colonies from holding on to any particular patch of substratum for very long. Furthermore, *Steginoporella* colonies first become sexually re-

productive at 3 times the size necessary for *Reptadeonella* reproduction (a minimum of 8 versus 22 cm²) and have less fecund zooids (Winston and Jackson 1984; Jackson and Wertheimer, in press).

These patterns of life history and morphology can be interpreted in terms of the allocation of limited nutritional resources within colonies (Palumbi and Jackson 1983). *Steginoporella* apparently invests so much in growth that it has few resources left for reproduction until colonies become large, whereas *Reptadeonella* invests less in growth and more in fortification, maintenance of zooids, and sexual reproduction. The mechanistic basis of these differences probably lies in the extent and direction of translocation between zooids of stored nutrients needed for growth maintenance, and reproduction; this is suggested by circumstantial evidence, particularly by the marked polarity of regeneration in *Steginoporella* colonies, and by analogy with other clonal animals and plants (Tardent 1963; Taylor 1977; Pitelka and Ashmun, in press).

Mobility and growth forms

Differences in mobility between different morphologies of corals and of bryozoans greatly exceed those within any single growth form. Among corals, for example, mound-shaped colonies are generally far more stationary, and branching colonies far more mobile, than any foliaceous corals. *Montastrea annularis*, which is an abundant foliaceous coral in deeper water, is also the most abundant mound-shaped coral species in the Caribbean, occurring generally in depths about 10 to 15 m

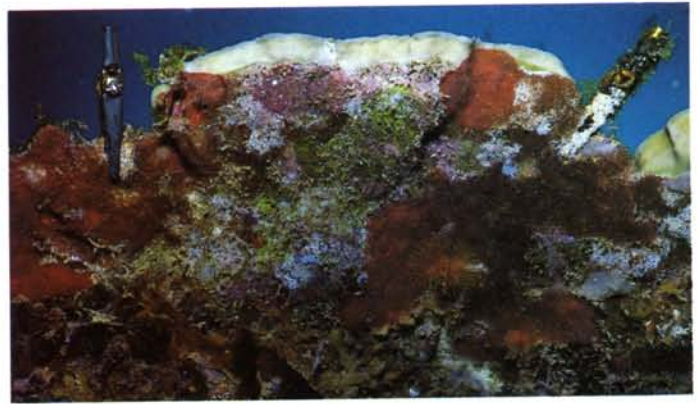


February 1984

shallower than where its foliaceous growth form predominates (Goreau 1959). Colonies are often several meters high and across, but they grow slowly, as in the species' foliaceous morphology, thickening usually at rates less than 0.5 cm per year (Dustan 1975). Both morphologies of *Montastrea* are highly persistent locally and long lived.

Staghorn coral, *Acropora cervicornis*, and elkhorn coral, *A. palmata*, are two of the most abundant Caribbean branching corals (Adey 1978). Colonies commonly reach 1 to 3 m in height, and a single clone may extend laterally for 10 m or more (Neigel and Avise 1983). In contrast to either morphology of *Montastrea* or to *Leptoseris*, they grow extremely rapidly; branches of *A. palmata* may lengthen at rates up to 11 cm per year, and *A. cervicornis* at rates up to 20 cm per year. Also in contrast to *Montastrea*, they are relatively poor aggressors in direct interactions with other coral species and compete most successfully by rapidly growing over their neighbors, which they may then harm indirectly by shading (Porter et al. 1981). Clones formed by these two species are extremely mobile, both through growth and through dispersal of fragments, and they may also be very long lived (Tunncliffe 1981).

Mound-shaped skeletons are inherently much more resistant to toppling or breakage during storms than are branching corals (Highsmith 1982). For example, after the passage of Hurricane Allen in 1980, extensive populations of the two *Acropora* species, observed at 6 m depth near Discovery Bay, were reduced to less than 1% of their original cover, whereas 91% of the massive *Montastrea* mounds at this depth endured (Woodley et al. 1981).



May 1984

The functional biology of the different coral growth forms is intriguingly similar to what we have described for the two encrusting bryozoan species. Like *Steginoporella*, the branching *Acropora* species exhibit both very rapid growth at the edges of colonies—termed distal growth—and apparently higher rates of mortality (possibly due to local senescence) of older, basal regions (Tunncliffe 1981). This correlates well with the extremely high rates of distal translocation of nutrients and calcium observed in *A. cervicornis*; foliaceous *Montastrea* colonies also exhibit predominantly distal translocation, although not so unidirectionally as in *A. cervicornis* (Taylor 1977). Moreover, despite their slow growth rate, *Montastrea* colonies quickly regenerate damaged regions over most of the colony surface, whereas only the distal portions of the branches in *Acropora* regenerate rapidly, if at all (Bak et al. 1977; Tunncliffe 1981; Bak 1983).

Unlike corals, branching bryozoans are rare on coral reefs, and the most common forms other than sheetlike colonies are mound shaped. These grow by a series of processes, collectively termed frontal budding, that produce multiple layers of zooids, one on top of another, to form massive colonies superficially similar to those of mound-shaped corals (Cheetham and Cook 1983). Two abundant frontally budding bryozoans on Caribbean reefs are *Styloporoma spongites* and *Trematoecia aviculifera*. Both of these species grow more slowly and persist longer in any one place than do the single-layered colonies of *Steginoporella* or even of the more persistent *Reptadeonella*. Frontal budding is a strategy of persistence, providing greater resistance to both overgrowth and

disturbance compared with single-layered growth (Jackson and Biss 1975).

The surfaces of *Styloporoma* and *Trematoecia* colonies also lack any obvious signs of regional senescence. Moreover, *Trematoecia* zooids have very thick frontal walls, as can be seen in Figure 7, which are 1½ to 3 times harder to puncture than are those of *Reptadeonella* zooids, although colony surfaces are not harder to crush (Best and Winston 1984). Finally, *Styloporoma* and *Trematoecia* can regenerate injuries from live zooids below the surface layer, as well as laterally, which single-layered colonies cannot do (Lidgard, in press).

Investment strategies and distributions

The distributions of corals and bryozoans on reefs are strongly correlated with their life histories and growth forms, particularly as these relate to the animals' comparative mobilities over the substratum. In general, as we have seen, stationary growth forms are relatively more abundant in environments with low levels of disturbance, whereas mobile growth forms are relatively more abundant in environments with high levels of disturbance.

First consider two extremes in mobility, branching and mound-shaped corals. Branching *Acropora palmata* is by far the most abundant coral at and just below the reef crest, from 1 to 5 m depth, where the chances of damage caused by storms and by grazing predators is greatest (Adey 1978). Although mound-shaped corals are inherently much less susceptible to storm damage, they apparently cannot become established after hurricanes quickly

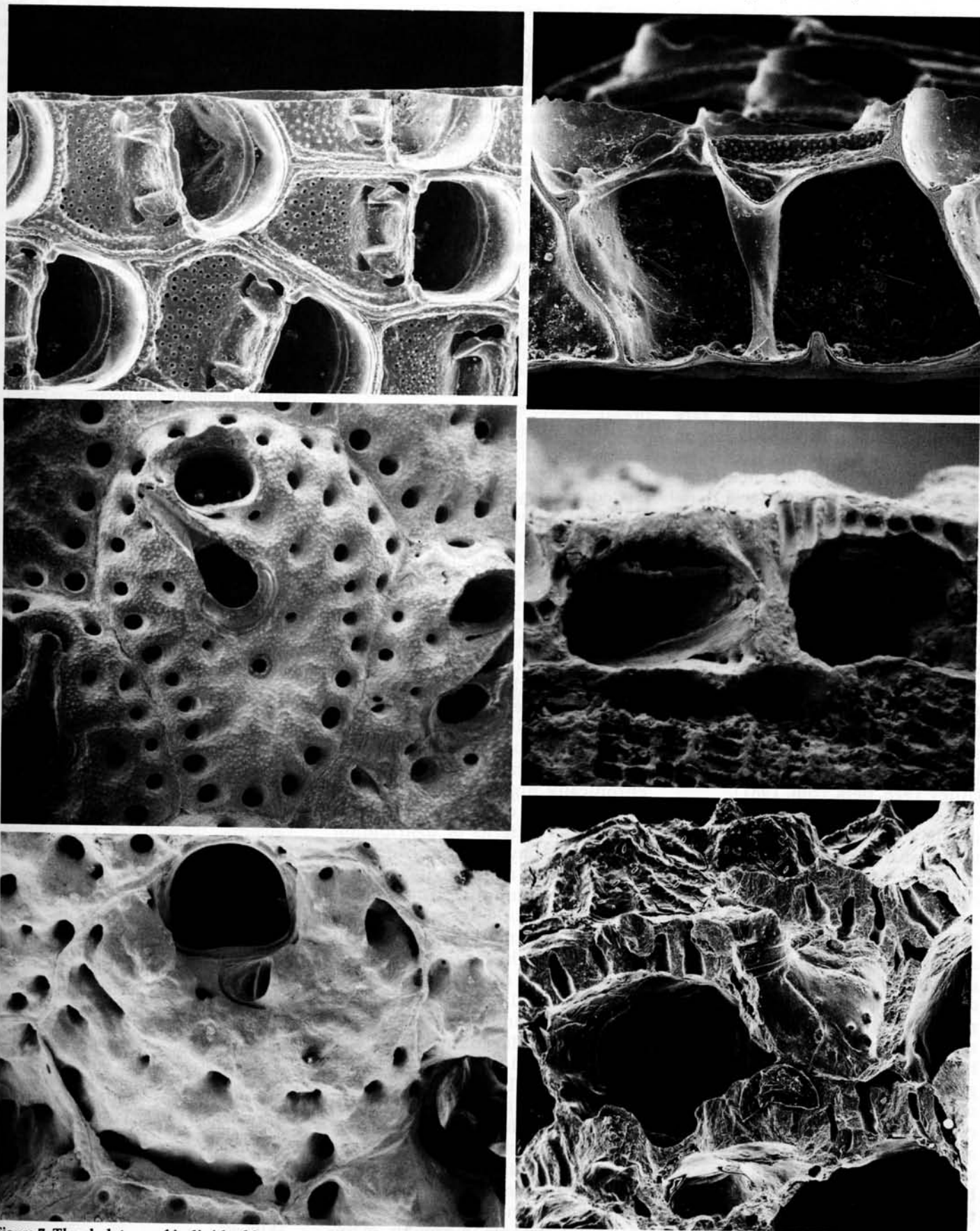


Figure 7. The skeletons of individual bryozoan zooids, shown in these scanning electron micrographs of their front surfaces (left) and transverse sections (right), clearly reflect the life histories of their respective species. The *Steginoporella* zooids shown in the top two photographs have a rather delicate skeletal structure, as would be expected in a highly mobile bryozoan that makes relatively little investment in the fortification and maintenance

of its zooids (each approximately 1.1 mm long). In contrast, the more stationary and highly persistent *Reptadeonella costulata* (middle) has substantially fortified zooids (~0.7 mm). *Trematoecia aviculifera* (bottom) is even more stationary and persistent than *R. costulata*, and its zooids (~0.8 mm) are accordingly more fortified and can grow in several layers one upon another. (Upper two photographs by S. Lidgard; lower four by J. Winston.)

enough to prevent repopulation by more rapidly growing *A. palmata*. Thus, mound-shaped corals occur in slightly deeper water, typically from 3 to 15 m. The delicate branching species *A. cervicornis* overlaps considerably in distribution with massive corals; however, in general, the rapid, mobile growth of the two *Acropora* species seems more successful in shallow environments than the more stationary and massive skeletons of mound-shaped corals. During storms, both branching species are broken up, and live fragments are locally dispersed (Tunncliffe 1981; Highsmith 1982). This appears to be their primary means of propagation, since larval recruitment by *A. palmata* and *A. cervicornis* is rare (Bak and Engel 1979; Rylaarsdam 1983).

However, although their strategy is highly successful, local *Acropora* populations can occasionally be so severely damaged by major hurricanes that recovery is extremely slow, or may not occur at all (Knowlton et al. 1981). Similarly, both *A. palmata* and *A. cervicornis* are rare in areas—such as most of the eastern Bahamas—that are swept each year by long-wave, open-ocean storms. Under these extreme conditions, all corals are excluded from shallow water, and massively crustose coralline algae predominate (Adey 1978, pers. com. 1981).

Foliaceous corals at shallow depths are typically less abundant than branching or massive corals and consist primarily of more mobile colonies, such as of *Leptoseris*, *Agaricia agaricites*, and *Porites astreoides*. Below about 20 m, the more stationary foliaceous colonies of *Montastrea*, *Agaricia lamarcki*, and *A. grahamae* become dominant, a pattern similar to the replacement of branching corals by more stationary massive species below about 5 m. However, at depths greater than about 50 m, where levels of light are very low, these foliaceous corals give way again to more fragile and more mobile foliaceous species such as *Agaricia undata* and *A. fragilis*, both of which grow 5 times faster than foliaceous *M. annularis*. Thus, on the deepest reefs, the generally positive correlation between levels of disturbance and mobility appears to break down, probably because of intrinsic physiological limitations on coral growth and morphology (e.g., Goreau 1963).

The distribution patterns of bryozoans on reefs change with depth in a manner very similar to those of corals. As we have seen, mobile *Steginoporella* is most common in the more disturbed habitats near coral edges, while the more stationary *Reptadeonella* is relatively more abundant farther back in the less disturbed sites. In deeper water, where predators are less prevalent and where foliaceous corals are also much longer lived, *Steginoporella* and *Reptadeonella* are replaced as the most abundant bryozoans under foliaceous corals by the potentially massive *Stylopoma*, which can form very large colonies 1 cm or more thick (Jackson and Wertheimer, in press).

If levels of predation are extremely high, however, single-layered encrusting species are excluded, and bryozoans are limited to a few massive, stationary species, such as *Trematoecia aviculifera*, which commonly forms colonies more than 10 cm thick. In contrast to other bryozoans in Jamaica, *Trematoecia* occurs most commonly on open reef surfaces, where most bryozoans are excluded by physical damage and by grazing sea urchins and fishes. Thus, *Trematoecia* seems similar to massive crustose coralline algae found on crests of exposed reefs, where branching corals are excluded by chronically high levels of physical and biological disturbance.

These patterns of distribution suggest that physical disturbance and predation, in addition to strongly affecting community structure and diversity of coral reefs, have profoundly influenced the evolution of different life-history strategies of bryozoans and corals (Connell 1979; Woodley et al. 1981). Patterns of growth form and life-history variation very similar to these have also been described for terrestrial plants (Lovett-Doust 1981; Cook 1983); this suggests that these kinds of investment trade-offs in space and time may be characteristic of all sessile clonal organisms. Although both clonal and aclonal animals and plants vary widely in their relative energetic investments in growth, maintenance, and sexual reproduction, the two additional components of life histories that are peculiar to clonal species are the spatial patterns of their growth and their local persistence or mobility over time.

References

- Adey, W. H. 1978. Coral reef morphogenesis: A multidimensional model. *Science* 202: 831-37.
- Bak, R. P. M. 1983. Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Mar. Biol.* 77:221-27.
- Bak, R. P. M., J. Brouns, and F. Heys. 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. In *Proceedings of the 3rd International Coral Reef Symposium* 1:143-48.
- Bak, R. P. M., and M. S. Engel. 1979. Distribution, abundance, and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* 54: 341-52.
- Bak, R. P. M., J. Sybesma, and F. C. van Duyl. 1981. The ecology of the tropical compound ascidian *Trididemnum solidum*. II. Abundance, growth and survival. *Mar. Ecol. Prog. Ser.* 6:43-52.
- Best, B. A., and J. E. Winston. 1984. Skeletal strength of encrusting cheilostomes. *Biol. Bull.* 167:390-409.
- Buss, L. W. 1979. Habitat selection, directional growth, and spatial refuges: Why colonial animals have more hiding places. In *Biology and Systematics of Colonial Organisms*, ed. G. Larwood and B. R. Rosen, pp. 459-97. London: Academic Press.
- Caswell, H. In press. The evolutionary demography of vegetative reproduction. In *Population Biology and Evolution of Clonal Organisms*, ed. J. B. C. Jackson, L. W. Buss, and R. E. Cook. Yale Univ. Press.
- Cheetham, A. H., and P. L. Cook. 1983. General features of the class Gymnolaemata. In *Treatise on Invertebrate Paleontology, Part G (Revised)*, ed. R. A. Robison, pp. 138-207. Univ. of Kansas Press.
- Cheetham, A. H., and L.-A. C. Hayek. 1983. Geometric consequences of branching growth in adeoniform Bryozoa. *Paleobiology* 9:240-60.
- Coates, A. G., and J. B. C. Jackson. In press. Morphological themes in the evolution of clonal and aclonal marine invertebrates. In *Population Biology and Evolution of Clonal Organisms*, ed. J. B. C. Jackson, L. W. Buss, and R. E. Cook. Yale Univ. Press.
- Connell, J. H. 1973. Population biology of reef-building corals. In *Biology and Geology of Coral Reefs*, ed. O. A. Jones and R. Endean, vol. 2, pp. 205-45. Academic Press.
- . 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. In *Population Dynamics*, ed. R. M. Anderson, B. D. Turner, and L. R. Taylor, pp. 141-63. Oxford: Blackwells.
- Cook, R. E. 1983. Clonal plant populations. *Am. Sci.* 71:244-53.
- Dustan, P. 1975. Growth and form in the reef building coral *Montastrea annularis*. *Mar. Biol.* 33:101-07.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40:67-90.
- . 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Annals N. Y. Acad. Sci.* 109:127-67.

- Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* 7: 207-26.
- Hughes, T. P. 1984. Population dynamics based on individual size rather than age. *Am. Nat.* 123:778-95.
- Hughes, T. P., and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713-15.
- . In press. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.*
- Jackson, J. B. C. 1977. Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am. Nat.* 111:743-67.
- . 1979. Morphological strategies of sessile animals. In *Biology and Systematics of Colonial Organisms*, ed. G. Larwood and B. R. Rosen, pp. 499-555. London: Academic Press.
- . 1984. Ecology of cryptic coral reef communities. III. Abundance and aggregation of encrusting organisms with particular reference to cheilostome Bryozoa. *J. Exp. Mar. Biol. Ecol.* 75:37-57.
- . In press. Distribution and ecology of clonal and aclonal benthic invertebrates. In *Population Biology and Evolution of Clonal Organisms*, ed. J. B. C. Jackson, L. W. Buss, and R. E. Cook. Yale Univ. Press.
- Jackson, J. B. C., and L. W. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. *PNAS* 72:5160-63.
- Jackson, J. B. C., and S. P. Wertheimer. In press. Patterns of reproduction in five common species of Jamaican reef-associated bryozoans. In *Bryozoan Biology and Paleontology*, ed. C. Nielsen and G. P. Larwood. Fredensborg, Denmark: Olsen and Olsen.
- Jackson, J. B. C., and J. E. Winston. 1981. Modular growth and longevity in bryozoans. In *Recent and Fossil Bryozoa*, ed. G. P. Larwood and C. Nielsen, pp. 121-26. Fredensborg, Denmark: Olsen and Olsen.
- . 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. *J. Exp. Mar. Biol. Ecol.* 57:135-47.
- Knowlton, N., J. C. Lang, M. C. Rooney, and P. Clifford. 1981. When hurricanes kill corals; evidence for delayed mortality in Jamaican staghorns. *Nature* 294:251-52.
- Lang, J. C. 1973. Interspecific aggression by scleractinian corals. II. Why the race is not always to the swift. *Bull. Mar. Sci.* 23:260-79.
- Lidgard, S. In press. Budding process and geometry in encrusting cheilostome bryozoans. In *Bryozoan Biology and Paleontology*, ed. C. Nielsen and G. P. Larwood. Fredensborg, Denmark: Olsen and Olsen.
- Lovett-Doust, L. 1981. Population dynamics and local specialization in a clonal perennial *Ranunculus repens* I. The dynamics of ramets in contrasting habitats. *J. Ecol.* 69:743-55.
- Neigel, J. E., and J. C. Avise. 1983. Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: Self-recognition analysis and demographic interpretation. *Evolution* 37:437-53.
- Palumbi, S. R., and J. B. C. Jackson. 1982. Ecology of cryptic coral reef communities. II. Recovery from small disturbance events by encrusting Bryozoa: The influence of "host" species and lesion size. *J. Exp. Mar. Biol. Ecol.* 64:103-15.
- . 1983. Aging in modular organisms: Ecology of zooid senescence in *Steginoporella* sp. (Bryozoa: Cheilostomata). *Biol. Bull.* 164:267-78.
- Pitelka, L. F., and J. W. Ashmun. In press. Physiology and integration of ramets in clonal plants. In *Population Biology and Evolution of Clonal Organisms*, ed. J. B. C. Jackson, L. W. Buss, and R. E. Cook. Yale Univ. Press.
- Porter, J. W., et al. 1981. Population trends among Jamaican reef corals. *Nature* 294: 249-50.
- Potts, D. C. 1984. Generation times and the Quaternary evolution of reef-building corals. *Paleobiology* 10:48-58.
- Rylaarsdam, K. W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar. Ecol. Prog. Ser.* 13: 249-60.
- Sebens, K. P. 1982. Competition for space: Growth rate, reproductive output, and escape in size. *Am. Nat.* 120:189-97.
- Tardent, P. 1963. Regeneration in the Hydrozoa. *Biol. Rev.* 38:293-333.
- Taylor, D. L. 1977. Intra-colonial transport of organic compounds and calcium in some Atlantic reef corals. In *Proceedings of the 3rd International Coral Reef Symposium* 1:431-36.
- Tunncliffe, V. J. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. *PNAS* 78:2427-31.
- Wahle, C. M. 1983. The roles of age, size and injury in sexual reproduction among Jamaican gorgonians. *Am. Zool.* 23:961.
- Winston, J. E., and J. B. C. Jackson. 1984. Ecology of cryptic coral reef communities. IV. Community development and life histories of encrusting cheilostome Bryozoa. *J. Exp. Mar. Biol. Ecol.* 76:1-21.
- Woodley, J. D., et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-55.