# Case Study of Natural Population Collapse: Post-Hurricane Predation on Jamaican Staghorn Corals

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# ABSTRACT

Knowlton, Nancy, Judith C. Lang, and Brian D. Keller.    Case Study of Natural Population Collapse: Post-Hurricane Predation on Jamaican Staghorn Corals. *Smithsonian Contributions to the Marine Sciences,* number 31, 25 pages, 18 figures, 4 tables, 1990.—The staghorn coral *Acropora cervicornis,* formerly a dominant reef builder at intermediate depths along the Jamaican north coast, was devastated in 1980 by Hurricane Allen and its short-term aftereffects. Between 1982 and 1987, populations of *A. cervicornis* generally continued to decline at three monitored areas, approaching local extinction at one site. Feeding by the snail *Coralliophila* and the polychaete *Hermodice carunculata,* and "gardening" behavior of the damselfish *Stegastes planifrons* played important roles in the collapse of staghorn populations. All three consumers remained abundant seven years after the hurricane. Growth of algae following die-off of the urchin *Diadema antillarum* in 1983 and perhaps disease also contributed to the failure of *A. cervicornis* to recover. Although the timing and relative importance of these factors differed among sites, collapse of all three populations and substantial predator-associated mortality were the most striking features of these results. Threshold models of predation suggest that the hurricane increased the relative importance of predators, causing coral populations to continue to decline rather than return to their previous high densities. The generally patchy distribution of *A. cervicornis* in space and time throughout its range may reflect an ability to persist at either low or high densities with predators, interacting with fluctuations in density caused by extrinsic perturbations (e.g., storms, epidemic disease). Preliminary surveys provide evidence of events elsewhere in the Caribbean that are comparable to those documented for Jamaica. Sensitive coupling of unusually severe disturbance with routine biological processes may have long-term effects that limit our ability to explain local patterns of distribution, abundance and diversity in areas where this species has the potential to dominate.

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## Introduction

Although Caribbean coral reefs are cited as an example of a high diversity ecosystem (Porter, 1974), many of these reefs have large sections that are numerically dominated by a single species, e.g., *Montastrea annularis* (see Scatterday, 1977), *Madracis mirabilis* (see Bak, 1977; van Duyl, 1985), *Acropora palmata* (see Goreau, 1959; Scatterday, 1977; van Duyl, 1985; Liddell and Ohlhorst, 1987), *A. cervicornis* (see below). Many other species may be present, but they represent a much smaller proportion of the total live coral cover in these areas, so that the three dimensional structure of the reef is largely created by the dominant species.

Numerical dominance, as the converse of diversity, has indirectly received much attention, and patterns in diversity have typically been related to general characteristics of the physical and biotic environment, e.g., disturbance and light-determined growth potential (Huston, 1985b). Biological characteristics of the species themselves have largely been ignored in the search for general models. From this perspective, dominance by a single species is simply due to the lack of environmental factors promoting high diversity.

Dominance is more complex than the absence of high diversity, however, since the biological features of the dominant inevitably play a role in its local success. Moreover, since relatively few species achieve dominance, it is possible to explore the phenomenon of low diversity by examining the characteristics of the dominant species themselves, as well as the environments in which they succeed. Here we wish to focus attention on the attributes of a single Caribbean coral species, *Acropora cervicornis*, which, by virtue of its abundance or rarity, can have a major impact on the diversity of reefs, e.g., in Jamaica (Kinzie, 1973; Liddell et al., 1984). In doing so, we take advantage of a catastrophic event, Hurricane Allen, which fortuitously provided insight into the dynamics of dominance in this species.

The purpose of this paper is to document the volatile recent history of *A. cervicornis* reefs along the north coast of Jamaica, and in doing so to suggest a mechanism that contributes to the spatial and temporal patchiness of this sometimes dominant species. Our findings demonstrate the importance of Caribbean coral predators in dramatically slowing recovery from severe disturbance. The sensitivity of their impact to changes in coral abundance via threshold effects (May, 1977) may limit our ability to predict reef community composition based on prevailing physical conditions, even when some knowledge of the history of previous physical disturbances exists.

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## Natural History of *Acropora cervicornis*

### BASIC BIOLOGY

The staghorn coral *Acropora cervicornis* can dominate substantial areas of reef (Table 1*a;* Geister, 1977; Tunnicliffe, 1983). This potential for dominance is due to its high growth rate and its ability to disperse locally through fragmentation (Tunnicliffe, 1983). Each actively growing branch consists of an extending axial polyp from which radial polyps ramify (Wallace, 1978). Nutrients translocated from more basal sections support distal extension (Pearse and Muscatine, 1971; Gladfelter, 1983). Average linear growth rates of 10 cm per year from each branch are typical (Gladfelter, 1984), and individual branches may add more than 20 cm per year (Tunnicliffe, 1983). As a colony increases in size, shaded basal areas eventually die (Tunnicliffe, 1983). This dead area is subsequently fouled and invaded by boring organisms, and the weakened skeleton then fragments, particularly during periods of high wave energy (Tunnicliffe, 1979, 1982). Many fragments die (especially small ones), but often enough survive to result in the spread of the colony (Tunnicliffe, 1981). Larval recruits are relatively rare regardless of the abundance of adult conspecifics (Gilmore and Hall, 1976; Dustan, 1977; Bak and Engel, 1979; Tunnicliffe, 1979, 1981; Sammarco, 1982, 1985; Highsmith, 1982; Rylaarsdam, 1983). Direct competitive ability (sensu Connell, 1973) against other corals using the extracoelenteric digestive response is only intermediate (Lang, 1973). Nevertheless, high growth rates and fragmentation favor overtopping and abrasion (via loose pieces) of neighbors and rapid spread (Shinn, 1976; Tunnicliffe, 1979, 1981, 1983; Porter et al., 1981)._The speed with which this can occur has been documented by Davis (1982) for reefs in the Dry Tortugas. He found that a 220 hectare area, composed of sand and abundant gorgonians in 1881, was dominated by *A. cervicornis* in 1976. Farrell et al. (1983) also noted the existence of a conspicuous stand of staghorn coral that was not reported in a 1969 study.

Why then are all Caribbean reefs not dominated by *A. cervicornis*? Like any other species, this coral has physical limits beyond which mortality predictably exceeds growth.

Mortality is high in shallow, exposed areas where colonies are broken too frequently and extensively for fragments to survive and grow. In such habitats, one often finds the congener *A. palmata,* again in nearly monospecific stands (Geister, 1977; Tunnicliffe, 1983; van Duyl, 1985; Liddell and Ohlhorst, 1987). Growth rates eventually decline with depth, e.g., below −15 m in north Jamaica (Tunnicliffe, 1983). In regions subject to continual or seasonally extreme wave action, *A. cervicornis* is rare or absent at all depths (Adey, 1978). It is probably difficult for fragments of branching species like *A. cervicornis* to become established on steeply sloping surfaces (Highsmith, 1982; Tunnicliffe, 1983). In shallow lagoons it suffers if temperatures rise too high (Shinn, 1966) or if low tides expose the colonies (LeConte, 1875).

In addition to physical factors that regularly act to limit staghorn coral, the species occasionally suffers massive mortality due to unusual events in areas that are otherwise suitable for survival and growth. *Acropora cervicornis* is particularly sensitive to cold water (Mayer, 1914; Porter et al., 1982), and thus is periodically devastated at more northern latitudes, e.g., in 1977 at the Dry Tortugas reef discussed above (Davis, 1982; Porter et al., 1982). Major hurricanes are capable of severely damaging staghorn populations in their direct paths (Stoddart, 1963, 1969, 1974; Perkins and Enos, 1968; Bak and Luckhurst, 1980; Highsmith et al., 1980; Woodley et al., 1981; Kjerfve and Dinnel, 1983). Reconstruction of the probable impact of severe cold and storms from meteorological records is relatively easy. Disease apparently also causes severe mortality in some populations, e.g., in Curaçao and Bonaire (Bak and Criens, 1982; van Duyl, 1982, 1985), although it is poorly understood and its role is difficult to assess in retrospect. Extensive patches of *A. cervicornis* skeletons with little living coral attest to the recent demise of once healthy staghorn reefs in a variety of areas, e.g., in the San Blas, Panama (pers. obs.), the Bahamas (Pierce and Curran, in press), Colombia (Ramírez, 1986), the Florida Keys (P. Dustan, W.C. Jaap, E.C. Peters, and E.A. Shinn, unpublished data), and Los Roques, Venezuela (E. Weil, unpublished data). Whatever the cause, such observations reflect the potentially transient nature of dominance by this species.

These more sporadically acting factors help to explain some peculiar features of the distribution of staghorn coral. There are still, however, many puzzling areas where *Acropora cervicornis* has been rare for some time (Table 1*b*), or where it has failed to recover from disturbance at a rate predicted from its growth potential (Stoddart, 1969, 1974).

### HISTORY IN JAMAICA

Prior to 1980, the shallow coral reefs fringing the north coast of Jamaica were characterized by extensive accumulations ("haystacks") of the staghorn coral, *Acropora cervicornis* (see Goreau, 1959; Kinzie, 1973; Tunnicliffe, 1983; Liddell et al., 1984; Liddell and Ohlhorst, 1987). On 6 August 1980,

TABLE 1.—Examples of variability in abundance of staghorn coral: *a*, reefs dominated by *A. cervicornis; b*, reefs apparently physically suitable for staghorn growth, but where *A. cervicornis* is relatively uncommon. Data are drawn from papers where at least classes of numerical abundance were provided. Although a number of papers refer to nearly monospecific stands of staghorn (e.g., van Duyl, 1985; Farrell et al., 1983), they were not used unless percent cover values were given. Reefs in *b* were conservatively chosen; only intermediate depths were considered, and all reefs with steeply sloping surfaces, high exposure to wave action or heavy sedimentation were deliberately excluded, as were reefs where *A. cervicornis* was totally absent. Two of the reefs in *b* (Holandes, Lee Stocking Island) had large amounts of still standing, dead staghorn coral (at Lee Stocking Island, 25% of the absolute cover was dead *A. cervicornis*). Data varied in precision; where only abundance classes were provided, midpoints of each class were used for the calculations. Relative percent cover is the proportion of live coral made up by the species in question. Rank indicates the position of staghorn coral among all species recorded, where "1" is the most abundant. When staghorn was the most abundant, then the second most abundant species was listed (subdominant); otherwise, the dominant species was listed. References are (1) Liddell et al., 1984; (2) Huston, 1985a; (3) Liddell and Ohlhorst, 1987; (4) Davis, 1982; (5) Dustan, 1985; (6) Rogers et al., 1984; (7) van den Hoek et al., 1978; (8) E. Weil and J.B.C. Jackson, unpublished data; and (9) J.C. Lang, unpublished data. ND = no data available. *Millepora* species were excluded in calculations except for Davis (1982), where reef types were simply categorized as bank, coral head buttress, and staghorn.

| Site | Depth (m) | % live coral cover | A. cervicornis Relative % cover | A. cervicornis Rank | Dominant or subdominant Species | Dominant or subdominant Relative % cover | Reference |
|---|---|---|---|---|---|---|---|
| **a** | | | | | | | |
| Discovery Bay, Jamaica | | | | | | | |
| east forereef | 10 | 27% | 51% | 1/13 | *A. agaricites* | 14% | 1, 2 |
| west forereef | 10 | 42% | 33% | 1/11 | *A. agaricites* | 21% | 1, 2 |
| west forereef | 15 | 36% | 45% | 1/15 | *A. agaricites* | 20% | 3 |
| Dry Tortugas, FL | | | | | | | |
| general | 1–18 | 4% | 55% | 1/48 | *M. annularis* *S. siderea* | ND | 4 |
| Carysfort, Key Largo, FL | | | | | | | |
| forereef | 9–15 | 71% | 43% | 1/21 | *M. annularis* | 25% | 5 |
| **b** | | | | | | | |
| Salt River Canyon, St. Croix | | | | | | | |
| east wall | 9 | 12% | 5% | 6/11 | *M. cavernosa* | 51% | 6 |
| Piscadera Bay, Curaçao | | | | | | | |
| transect 1, community 5 | 6–13 | 46% | 1% | 16.5/18 | *M. mirabilis* | 24% | 7 |
| San Blas, Panama | | | | | | | |
| Aguadargana | 9–12 | 42% | 3% | 11/32 | *M. annularis* | 26% | 8 |
| Limones-1 | 9–12 | 43% | 3% | 6/18 | *M. annularis* | 60% | 8 |
| Holandes-1 | 9–12 | 12% | 1% | 13/21 | *A. agaricites* | 22% | 8 |
| Lee Stocking Is., Bahamas | | | | | | | |
| West Exuma Sound | 9–12 | 19% | <1% | 8.5/20 | *M. annularis* | 37% | 9 |

Hurricane Allen passed within 50 km of the Jamaican north coast (Woodley, 1980). Waves as high as 12 m were observed breaking in water 15 m deep over the reefs fringing Discovery Bay, where damage to shallow reef zones was extensive (Woodley et al., 1981).

The hurricane severely fragmented stands of *A. cervicornis* between depths of −6 to −20 m, and living cover of this species was reduced to approximately 40% of its previous level. Many

surviving fragments remained, however, of which over 250 in 6 m² were individually marked to follow their fates. More than 98% died within 5 months of the storm (Knowlton et al., 1981). Two 18 m² transects were established subsequently; together, they too showed a persistent decline in the number of living fragments and amount of live tissue for the period six to twelve months following the storm. Initially, an unidentified disease, first observed six weeks before the storm (pers. obs.),

probably played an important role in the mortality (see also Bak and Criens, 1982). Later, a significant source of mortality was predation by the gastropod *Coralliophila* (Knowlton et al., 1981). This post-hurricane decline was unexpected, since *A. cervicornis* often recovers rather quickly from even severe storm damage due to its rapid growth and normal success at propagation by fragmentation (Shinn, 1976, but see Stoddart, 1974, for an exception).

Subsequently, we extended our work to determine whether these trends would continue or be reversed, and to test the generality of the findings along the northern coast of Jamaica. To do this, we monitored for four years the fates of individually identified corals at three widely distant sites that had been subjected to different intensities of storm damage.

We chose this geographically broad, observational approach because we wanted to know what would actually happen to a set of communities showing variation in characteristics of obvious relevance to understanding the effects of major disturbances. We deliberately shunned the experimental approach traditionally favored by marine benthic ecologists for a number of reasons. First, the design of such experiments requires an intensive approach, both geographically and conceptually. It is no accident that the most successful experimental studies have involved relatively simple communities whose basic natural history was already well understood (see theoretical analysis of Bender et al., 1984). Thus we felt that we were likely to finish with a study on the wrong subject in the wrong place were we to commit ourselves to a single location and a limited number of manipulations at the outset. Second, no nearby reefs remained that could serve as undamaged, experimental controls. It would be both impractical and unethical to use an undamaged area to replicate (in replicate) the effects of a hurricane because of the amount of destruction that would be required. The results of small scale manipulations cannot necessarily be extrapolated to predict responses to regionally widespread, massive disturbances, because of the widely varying and unknown scales over which movement and larval recruitment of community members take place. Finally, as Yodzis (1988) has documented, the kinds of manipulations favored by marine benthic ecologists (e.g., in this case, the exclusion of predators) typically yield intuitively obvious results that also cannot necessarily be extrapolated to predict long-term effects.

## Methods

### STUDY SITES

Three primary sites along the northern coast of Jamaica were chosen. They were located near (1) the airport just east of Montego Bay, (2) the mouth of the Pear Tree River ("Pear Tree Bottom"), and (3) the coast between Priory and St. Ann's Bay. They will be referred to as our West, Central, and East Sites, respectively (Figure 1). We visited these sites nine times: in Aug 1982, Feb 1983, Jul–Aug 1983, Jan 1984, Jun 1984,
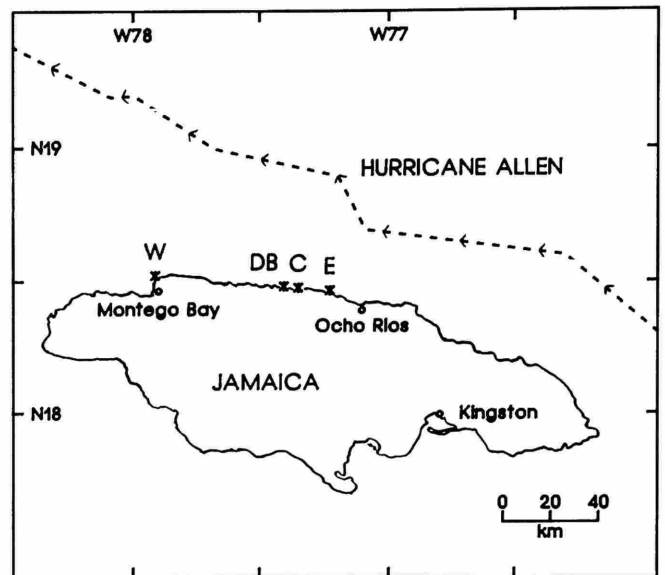


FIGURE 1.—Map of Jamaica, with track of Hurricane Allen (after Kjerfve et al., 1986) and locations of areas studied (W = West, C = Central, E = East, DB = Discovery Bay).

Feb 1985, Jul 1985, Jul 1986, and Jul–Aug 1987.

The three sites were generally comparable in structure and depth. All had buttress formations (Goreau, 1959) near shore (which Discovery Bay lacks), and large areas currently or formerly dominated by *Acropora cervicornis* in depths between −8 and −15 m (see below). Studied portions of the reefs were on the shallow end of the fore-reef terrace (sensu Liddell and Ohlhorst, 1981) seaward of the buttresses. Depths at the sites ranged from a minimum of −8 m at the Central Site to a maximum of −13 m at the East Site, with the bulk of the work at all sites between −9 and −12 m.

The East Site was most exposed, and the West Site least exposed to the force of prevailing seas (pers. obs.) and Hurricane Allen, both of which were northeasterly. The variation in exposure stems from differences in orientation of the reefs and in shelter provided by nearby headlands. We believe that these differences in exposure and the movement of the hurricane away from the coast as it travelled from east to west (Figure 1), are the primary reasons for the striking differences in live coral cover among the three sites observed at the onset of the study (see below).

These reefs were not, of course, identical in their other characteristics. The terrace was relatively wide at the West Site, narrow at the Central Site, and of intermediate width at the East Site; the heights of the reef lobes relative to adjacent sand channels were low, intermediate, and high respectively. The sites also differed in the relative importance of other species of corals (see below). Overall, however, they represented the best available compromise of widely varying degrees of damage to otherwise comparable staghorn reefs.

At each site, a particular reef (or reefs) bounded by sand

channels was selected haphazardly from an extensive system of similar reefs. To obtain percent cover estimates for these areas, we blindly dropped, while we swam, a weighted two meter line marked at 10 cm intervals onto the reefs a minimum of 10 times per site, and identified the benthic organisms lying below the marks. For more detailed information on *A. cervicornis,* we supplemented percent cover measures with data from m² quadrats haphazardly dropped in the same fashion in the same general areas. Numbers of quadrats per site and census ranged from 14 to 50, with most falling between 20 and 30. Data collected included: (1) counts of probable, recently settled recruits (circular to ellipsoid crusts of skeleton, occasionally with one or more small branches, that did not appear to have been derived from a broken branch), and (2) counts of all physiological isolates (defined by their continuous cover of living tissue) and measures of their maximum length, width, and height. At the West Site, it was not possible initially to collect all the above information from all quadrats due to the abundance of living staghorn (see below). The quadrats were also used to measure densities of some predators (see below). These procedures were done during the summers of 1982, 1984, 1985, 1986, and 1987. At the Central Site, data from two separate reef lobes are presented; elsewhere we took these measurements from a single reef.

In addition to our three primary sites, we continued to monitor previously established 18 m² transects at −9, −11, and −15 m at a fourth site on Dancing Lady Reef at Discovery Bay (Figure 1; see Knowlton et al., 1981), generally annually. We also surveyed a number of other locations between our West and Central Sites in 1982, using the methods described above. These data are presented when useful comparisons with our primary sites can be made.

### COLONIES OF *Acropora cervicornis*

At each site, individual colonies spanning the range of sizes available (see below) were chosen for study. All appeared healthy to the eye, although we could not rule out cryptic microbial infection (Peters et al., 1983; Peters, 1984). At the West Site (n = 80) and Central Site (n = 52), colonies were chosen haphazardly from among the many available; at the East Site (n = 28), all suitable colonies found were marked. Most marked colonies were separated by at least two meters from the nearest-neighboring, marked colony.

By colony, we mean a discrete expanse of skeleton that at the time of the initial census was connected by continuous living tissue. At subsequent censuses, such colonies might be entirely dead, or represented by one or more physiological isolates (Figure 2). Except for larval recruits (see below), the colonies consisted of one or more branches. They did not necessarily represent the entire extent of all living tissues descended from any single larva, because of prior clonal propagation through skeletal fragmentation or fission of tissue

(Hughes and Jackson, 1980, 1985; Neigel and Avise, 1983), a common event in this species (see above).

We limited our study to apparently healthy colonies to permit an assessment of maximum potential growth and survival at each site. By beginning with a standardized, healthy cohort, we were able to reduce unknown, detrimental effects of newly suffered mortality on future performance. Colonies were excluded if they showed evidence of recent mortality. Recent mortality is conspicuous because when the skeleton first loses its covering of live tissue, it appears as a bright, white area. After several days, the skeleton loses its whiteness as it becomes fouled by ephemeral algae (Shinn, 1976; Brawley and Adey, 1982). We also avoided colonies with the corallivorous snail *Coralliophila* or with the territorial damselfish *Stegastes planifrons* nearby (see below).

Plastic tags engraved with an identifying number were tied to the reef substratum near the colony. The colony itself was marked at the base, in a non-living portion, with a plastic cord or cable tie, and its location on the reef was mapped. During subsequent censuses, whenever the basally dead area became more extensive (often resulting in the production of physiological isolates), or when the skeleton itself fragmented, we added new cable ties to dead portions nearer the living tissue to increase the probability of relocation in the event of later fragmentation.

During censuses, we relocated as many tags and colonies as possible, and sketched all living colonies. We did not relocate the surviving colonies in 1987 because so few remained, and heavy algal growth (see below) made tags extremely difficult to find. The drawings were flattened representations of the three-dimensional structure (Figure 2), but because of the variable branching pattern, cable ties, and notations of orientation, we were nearly always able to identify corresponding branches at subsequent censuses with complete confidence. The drawings included (1) the positions of living (tissue covered) and dead portions of the colony and (2) the lengths of all living and recently dead (see above) portions. Colony size was calculated as the sum of the lengths of all live portions, and changes through time therefore reflect the combined effects of growth and mortality (i.e., net growth). Although costly in terms of underwater effort (over 1000 diver-hours associated with the project), these data could not have been accurately obtained from standard photographs because of the arborescent morphology of staghorn coral.

Although the net growth and survivorship of our marked colonies would presumably in the long run reflect patterns of population increase or decrease, a better immediate measure of the latter is the percent cover of staghorn coral through time. These measures (see above) were independent of the marked colonies; marked colonies represented such a small portion of the total area of the reefs sampled that they very rarely were recorded during percent-cover surveys.
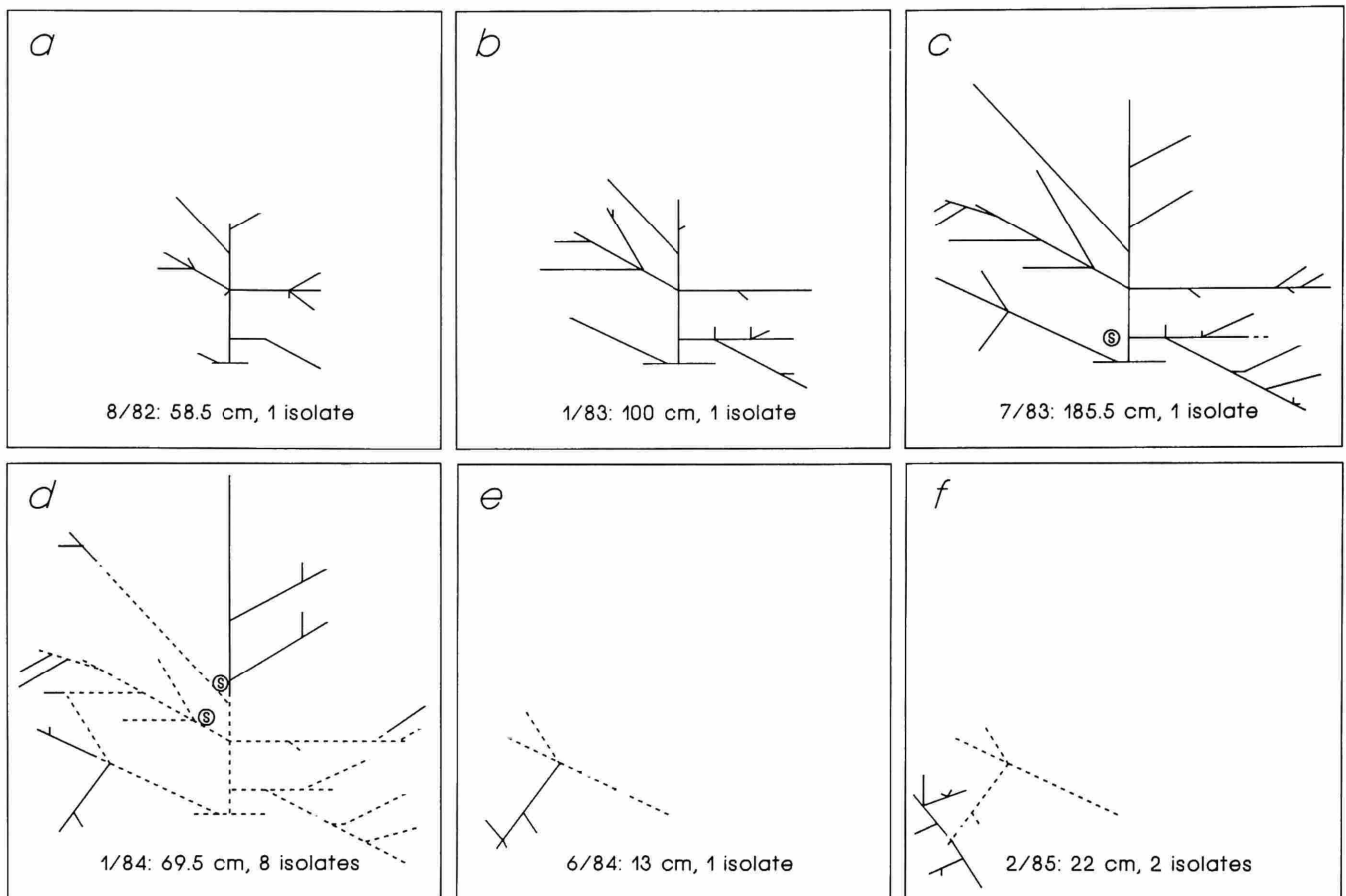
FIGURE 2.—Series of drawings of a marked coral at the East Site for all censuses when it was alive. Living branches, dead interconnecting skeleton (dashed lines), and positions of snails (S) are indicated. Branch lengths are drawn approximately to scale. Date, total length of living coral, and number of physiological isolates within the colony are indicated below each drawing.

### PREDATORS

Four animals known to be potentially important consumers of *A. cervicornis* in Jamaica are the snail *Coralliophila*, the polychaete *Hermodice carunculata*, the damselfish *Stegastes planifrons* (= *Eupomacentrus planifrons*), and the sea urchin *Diadema antillarum* (see Bak and van Eys, 1975; Shinn, 1976; Kaufman, 1977; Rylaarsdam, 1983; Tunnicliffe, 1983). They vary widely in their dependence on corals as a source of food (see below), but for simplicity all will be called predators since they all directly contribute to coral death by biting or sucking on coral tissue. For adults of these predators, *A. cervicornis* is a common and apparently preferred prey item, at least among scleractinian corals (Antonius, 1973; Bak and van Eys, 1975; Dustan, 1977; Itzkowitz, 1977; Kaufman, 1977; Williams, 1978; Waldner and Robertson, 1980; Rylaarsdam, 1983).

Predation pressure was assessed in different ways for each predator. Species of the snail *Coralliophila* cannot always be reliably distinguished without removal of the snail from the coral on which it is feeding. However, previous work and our general censuses suggest that most snails on *A. cervicornis*

have yellow opercula and are thus *C. abbreviata* (or perhaps occasionally *C. scalariformis*).

*Coralliophila abbreviata* is an obligatory cnidarivore that often feeds on scleractinian corals (Miller, 1981). It is relatively sedentary and typically rests at the margin between dead skeleton and live tissue (Ott and Lewis, 1972; Brawley and Adey, 1982); on *A. cervicornis* it characteristically feeds from the inner or basal portions of branches outward (Tunnicliffe, 1983; pers. obs.). The positions of snails on marked colonies (by design only present after the first census) were noted on the drawings, e.g., Figure 2c,d. During 1986 and 1987, overall snail densities were measured using the quadrats employed for estimates of damselfish and urchin densities (see below).

The polychaete *Hermodice carunculata* is an omnivore that often feeds on a variety of coelenterates (Ott and Lewis, 1972; Lizama and Blanquet, 1975; Sebens, 1982; Karlson, 1983; Witman, 1988). Individuals typically consume branching corals by "swallowing" branch tips temporarily and sucking off partially digested tissue (Glynn, 1962; Marsden, 1962; Ott and Lewis, 1972; Shinn, 1976). This leaves a highly

characteristic signature of intact skeleton at branch tips cleaned of soft tissues for up to 15 cm (Antonius, 1973; Shinn, 1976, figs. 9, 10), which is unique among the predators of *A. cervicornis*. For this reason, and because the worm is typically highly cryptic and therefore difficult to census during much of the day (Marsden, 1962; Lizama and Blanquet, 1975; Sebens, 1982; Witman, 1988), mortality due to *H. caruncula* was estimated indirectly in two ways. First, the numbers of dead tips were counted, excluding those that could not have been "swallowed" by the worm because they abutted directly onto other surfaces. Second, the amount of recent mortality of branch tips in the absence of *Coralliophila* was calculated. These methods probably underestimated predation by *Hermodice* because (1) the polychaete may have on occasion attacked corals with snails, and (2) some polychaetes may have attacked the colonies in less typical ways, e.g., a few very small *Hermodice* were observed crawling over recently killed basal sections of staghorn, and very large *Hermodice* can consume rings of tissue when attacking branches from the side (George Bruno, unpublished data).

The territorial damselfish *Stegastes planifrons* defends clumps of *A. cervicornis* (Itzkowitz, 1977, 1978; Williams, 1978) and kills the coral to provide space for its algal gardens (Kaufman, 1977; but see Sale, 1980; D. Ross Robertson, unpublished data). It has apparently done so at least since the Pleistocene (Kaufman, 1981). We noted whenever a marked colony was included in the territory of this species (unambiguously indicated by the presence of the fish and an algal lawn or "chimneys" on the coral (Kaufman, 1977, fig. 2; 1981, fig. 1; Liddell et al., 1984, fig. 14)). In addition, one-m² quadrats were used to measure the density of *S. planifrons* territories. For each quadrat we estimated the number of complete or partial territories present (e.g., two fish each with half a territory in the quadrat would yield a count of one territory for that quadrat). Territories were defined by algal gardens and activity patterns of the resident fish.

The sea urchin *Diadema antillarum*, although primarily a herbivore, does graze on living *A. cervicornis*, particularly basal or low lying areas (Bak and van Eys, 1975; Carpenter, 1981; Tunnicliffe, 1983); in doing so it removes both the living tissue and some of the underlying skeleton. The overall density of *D. antillarum* was measured by counting all individuals in the above-mentioned quadrats. Because the urchin shelters in crevices during the day and can move several meters in various directions while foraging nocturnally (Carpenter, 1984), we made no attempt to record associations between marked colonies and this urchin. *Diadema antillarum* suffered catastrophic mortality throughout the Caribbean during the course of our study (Lessios et al., 1984); the population crash occurred in Jamaica during our third census, in the summer of 1983 (Hughes et al., 1985).

## DATA ANALYSIS

All data were analyzed using the SPSS/PC software package.

The marked colonies at a site were not treated as a sample in the statistical sense, but rather as a cohort that was followed in its entirety. Descriptive statistics are thus the most appropriate means for describing the fates of the three cohorts. The reefs, however, were sampled in the statistical sense, and one can use inferential statistics to compare them. The comparisons strictly refer to the reef lobes themselves rather than the region in which they occur, since multiple lobes were not sampled (Hurlbert, 1984). It should be emphasized, however, that the similarities among the reefs we studied were far more striking than the differences, and that they can therefore be thought of as replicates describing the widespread collapse of staghorn populations along the north coast of Jamaica. Moreover, in pointing out differences among sites, we have limited ourselves to those patterns that were visually conspicuous and confirmed qualitatively throughout the area in which the sampled reef occurred. Our study sites were generally so similar to adjacent reefs that they were sometimes difficult to find.

We were able to assess the impact of snails and damselfish on particular colonies because these predators form persistent (Ott and Lewis, 1972; Thresher, 1976; Williams, 1978; Brawley and Adey, 1982) and unambiguous associations with particular colonies. Impact was measured in terms of net growth and changes in numbers of isolates. Because these predators could have exerted their influence both before and after a particular census t during which they were observed, we compared changes in colony size and number of isolates between consecutive censuses t−1 and t, and between censuses t and t+1.

Thus each colony at each census t had four measures of performance: (length at census t)−(length at census t−1), (number of isolates at census t)−(number of isolates at census t−1), (length at census t+1)−(length at census t), and (number of isolates at census t+1)−(number of isolates at census t). At each census, each colony was also assigned to one of four conditions: no predators, snails only, fish only, and simultaneous presence of snails and fish. This allowed us to compare performance measures among the four predator conditions. Not every colony experienced all four conditions during its history. Multiple observations for a single condition (e.g., four censuses without predators for a particular colony) were averaged so that each colony contributed only one value for each condition. These values are presented with descriptive statistics. To analyze inferentially the effect of snails, we used only those colonies that had never had associated damselfish, and for which we had recorded snails at some but not all censuses. We then used a Wilcoxon matched-pairs test (Siegel, 1956) to compare changes in size and numbers of isolates; that is, each colony provided a snail-present value and a snail-absent value that were matched for the analysis. Similarly for the damselfish, we used only colonies on which we had observed damselfish on some but not all censuses, but which had never had associated snails. Corals that had either no predators or both fish and snails at each census were not
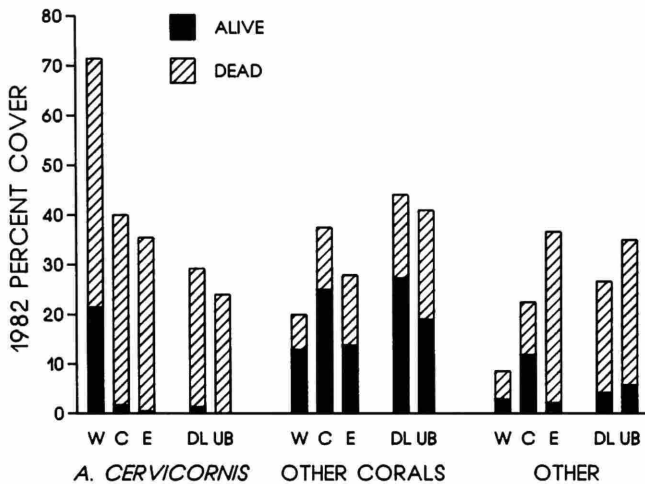
FIGURE 3.—Percent cover estimates in August, 1982, at our three study sites (W = West, C = Central, E = East) and at two reefs off Discovery Bay (DL = Dancing Lady, and UB = Upper Buoy). Depths at all sites were from 9–11 m. The dead portion of the category "other" was primarily pavement (consolidated dead-coral substratum) and includes pavement encrusted by coralline algae or foraminiferans. The two Discovery Bay sites were known to be dominated by *A. cervicornis* prior to the hurricane (see text), and were intermediate in exposure relative to our Central and East Sites (Upper Buoy is more exposed than Dancing Lady). Sample sizes (number of points) for the five areas were: W, 210; C, 240; E, 240; DL, 315; and UB, 300.

common enough to permit a comparable statistical analysis of the joint effects of damselfish and snails. Only the first seven censuses, which were separated by approximately equal time intervals, were used in this analysis (i.e., t = censuses 1 through 6 for t vs. t+1 comparisons, t = censuses 2 through 7 for t vs. t−1 comparisons).

## Results

### INITIAL COMPOSITION OF REEFS

In 1982, percent cover data (Figure 3) indicated that our three primary sites were or had been dominated by *Acropora cervicornis*. The sum of live coral plus dead rubble was higher for staghorn (35%–71% cover) than for all other species of corals combined, although only at the West Site did substantial amounts of living staghorn exist. The amount of live plus dead staghorn coral was higher at our three sites than at two Discovery Bay sites, also shown in Figure 3, which were known to be dominated by living staghorn coral prior to the passage of the hurricane (for Dancing Lady see Land, 1979, Knowlton et al., 1981; for Upper Buoy see Rylaarsdam, 1983). Indeed, the West Site had a higher percent cover of living *A. cervicornis* in 1982 (21%) than did one of these Discovery Bay reefs (Upper Buoy) before storm damage occurred (16% (Rylaarsdam, 1983)). There are no quantitative, pre-storm data for our primary sites (although Liddell et al., 1984, surveyed a reef at Pear Tree Bottom near our Central Site lobes, their

transects at −6 and −15 m largely missed the *A. cervicornis* zone). Divers visiting the Central and West Sites before 1980 have confirmed, however, the earlier dominance by staghorn coral at these sites (J.B.C. Jackson (pers. comm.) for the Central Site, P. O'Callaghan (pers. comm.) for the West Site).

Although our three primary sites were generally similar in having abundant living or dead staghorn, clear differences existed among them (categories: live staghorn, dead staghorn, live corals of other species, dead corals of other species, sediment or pavement (including surfaces with encrusting, coralline algae or foraminiferans), and other living animals or non-encrusting algae; $\chi^2 = 157$, 10 d.f., p<.0001; p<.0001 for all pairwise comparisons). The biggest contributors to the overall difference among the three sites, based on standardized, normally distributed $\chi^2$ residuals (in parentheses), were as follows: The West Site had excesses of both live and dead staghorn (7.6, 2.1) and a scarcity of pavement (−4.1). At the East Site, there was a scarcity of live staghorn (−3.9), an excess of pavement (6.4), and a scarcity of other animals and plants (−2.4). The Central Site was intermediate in scarcity of live staghorn (−3.2) and pavement (−2.6), but it had the highest excesses of living, non-staghorn corals (2.8) and of other living animals and plants (4.0). These patterns are generally consistent with expectations based on differences in exposure to Hurricane Allen, discussed above. The scarcity of live staghorn and the excess of pavement at the East Site presumably reflects the scouring effect of hurricane waves at this very exposed site, while the large amount of living staghorn at the West Site can be attributed to the much more limited effects of the hurricane there. The patterns also undoubtedly reflect differences in the relative abundance of the different species of coral before the hurricane (e.g., the apparent
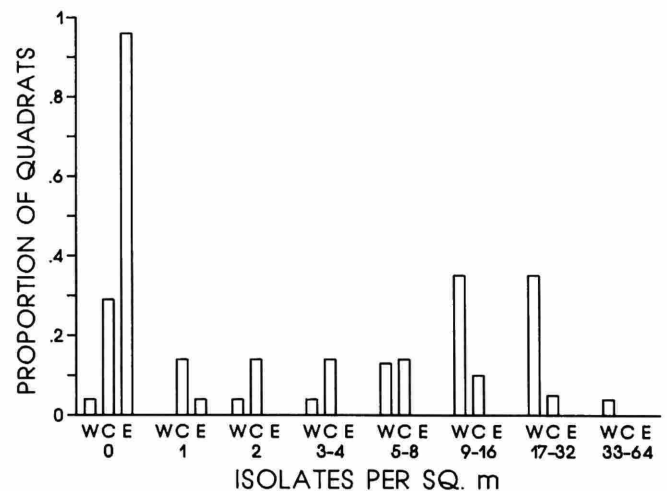


FIGURE 4.—Frequency distribution for density of staghorn isolates (numbers of isolates per m²) in 1982 at our three primary sites. Proportions sum to 1.0 for each site. Numbers of m² quadrats surveyed were 23, 21, and 26 at the West, Central, and East Sites, respectively.

greater dominance by staghorn at the West Site).

Measurements of percent cover are relatively inaccurate for rare species (e.g., living staghorn at the Central and East Sites), and in any case cannot distinguish between the effects of the size of colonies or fragments and their density. Density of *A. cervicornis* was highly significantly different among the three sites. Median numbers of isolates (see above) per m² (Figure 4) were 16, 2, and 0 at the West, Central, and East Sites respectively (p<.0001 for overall comparison and all pairwise comparisons, Kruskal-Wallis and Mann-Whitney U tests). Isolate size (Figure 5), on the other hand, was not significantly different between the West and Central Sites (median volumes (see "Methods") of 270 and 182 cm³ respectively; p>0.5, Mann-Whitney U test). At the East Site, our quadrats contained only one colony, making statistical tests impossible; it was, however, in the smallest size category, and the size distributions of marked colonies (see below) confirm that they were substantially smaller at the East Site.

Recently settled larval recruits (see "Methods") were relatively rare (Table 2, column 4). Densities at the Central and
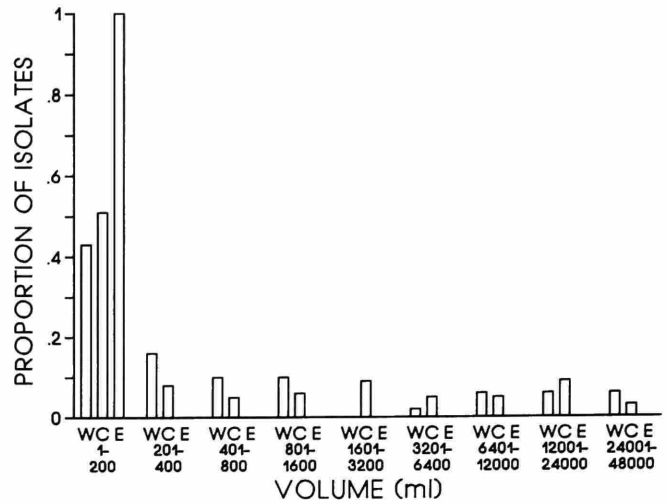


FIGURE 5.—Frequency distribution for isolate volumes (see "Methods") from m² quadrats in 1982 at our three primary sites. Proportions sum to 1.0 for each site. Numbers of isolates were 49, 79, and 1 at the West, Central, and East Sites respectively, and they were found in 2.5, 21, and 26 quadrats.

TABLE 2.—Density and relative importance of probable, recent recruits on reefs along the northern coast of Jamaica in July, 1982. Data for Falmouth (midway between Montego Bay and Discovery Bay, see Figure 1), Discovery Bay, and two of our primary sites are presented. Relative importance is measured in terms of (1) proportion of numbers of all isolates that were probable recent recruits, (2) proportion of summed volumes of all isolates from probable recent recruits, and (3) proportion of summed lengths of all isolates from probable recent recruits. For most sites, only one of the latter two measures is available; where both are available the differences reflect the non-linear relationship between length and volume measures. The number of recruits involved in these estimates can be calculated from the number of quadrats sampled (n) and the number of recruits per m² (note in particular only one isolate, a recruit, occurred in the 26 m² sampled at the East Site). For comparison, data from our marked colonies on the relative importance of recruits are also provided (for the East Site, the colony with *Coralliophila* was included). (ND = no data available.)

| Site | Depth (m) | n | Recruits per m² | Proportion of all isolates | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | | | Numbers | Volume | Length |
| Falmouth | | | | | | |
|   Half Moon Bay | 10 | 32 | 0.03 | 0.50 | 0.89 | ND |
|   Half Moon Bay | 13 | 26 | 0.23 | 0.20 | 0.01 | ND |
| Discovery Bay | | | | | | |
|   Gorgo City | 11 | 20 | 0.17 | 0.44 | 0.01 | ND |
|   Dancing Lady Reef | 9 | 18 | 0.19 | 0.18 | <0.01 | 0.03 |
|   Dancing Lady Reef | 11 | 18 | 0.38 | 0.13 | ND | 0.02 |
|   Dancing Lady Reef | 15 | 18 | 0.19 | 0.12 | <0.01 | 0.01 |
|   Upper Buoy Reef | 10 | 37 | 0.16 | 0.75 | 0.19 | ND |
|   Upper Buoy Reef | 13 | 78 | 0.14 | 0.79 | ND | 0.43 |
|   Upper Buoy Reef | 13 | 28 | 0.12 | 0.25 | 0.09 | ND |
|   East Forereef | 15 | 51 | 0.30 | 0.62 | 0.05 | ND |
| Central Site | | | | | | |
|   Reef survey | 10 | 21 | 0.14 | 0.04 | <0.01 | ND |
|   Marked Colonies | 11 | – | | 0.07 | ND | 0.01 |
| East Site | | | | | | |
|   Reef survey | 11 | 26 | 0.04 | 1.00 | 1.00 | 1.00 |
|   Marked Colonies | 11 | – | | 0.74 | ND | 0.19 |

East Sites were .14 and .04 per m² respectively; at the West Site, the number of quadrats censused was inadequate to provide a reliable estimate of recruit density. Surveys at other sites yielded densities of .03–.38 per m², values consistent with Rylaarsdam's (1983) pre-hurricane estimate of <.5 staghorn recruits per m².

The importance of these recruits relative to other physiological isolates of staghorn varied widely depending on the abundance of larger colonies (Table 2, columns 5–7, for estimates based on counts of individuals, volumetric measures, and measures of branch lengths, respectively). Recruits represented 4%–79% of the isolate counts, <1%–89% of all isolate volumes, and 1%–43% of the summed lengths (except at the East Site, where the only isolate encountered in the quadrats was a recruit). Recruits at the East Site (based on the marked colony data) were relatively more important than at most other sites sampled, while at the Central Site they were less important than at any other sampled site. At the West Site, recruits were undoubtedly of even less importance, due to the abundance of large colonies.

### INITIAL CHARACTERISTICS OF MARKED COLONIES

At the East Site, measurements of marked colonies provide a very accurate picture of the colonies on the reef, since all colonies initially found were measured (although the single colony with associated *Coralliophila* was excluded from most analyses; see "Methods"). The sampling scheme was haphazard at the other two sites. Nevertheless, the pattern of isolate volumes documented above is reflected in the size distribution of colonies chosen for individual monitoring (Figure 6). The sites differed overall in colony size (medians of 62, 42, and 3 cm total length at the West, Central, and East Sites respectively; p<.0001, Kruskal-Wallis one-way ANOVA), but this was due almost entirely to the small sizes of the colonies in the East (the difference between the West and Central Sites, although stronger, was again not significant, p>.09, Mann-Whitney U test).

Although both this paper and our previous study (Knowlton et al., 1981) document the decline of staghorn populations, there were important differences between the marked colonies in this study (generally upright and well established) and the fragments we monitored in Discovery Bay immediately following the hurricane. At the West and Central Sites, marked colonies were substantially larger than the previously studied fragments (median total length in the earlier study was only 17 cm). Moreover, all the fragments in the earlier study had just been detached by the hurricane's waves, whereas most of the colonies in the current study, begun two years after the hurricane, were firmly cemented or wedged in place (85%, 76%, and 93% of the marked colonies at the West, Central, and East Sites respectively). Finally, the previous study involved marking all living fragments in 6 m², many of which were deeply buried. In contrast, the colonies of the current
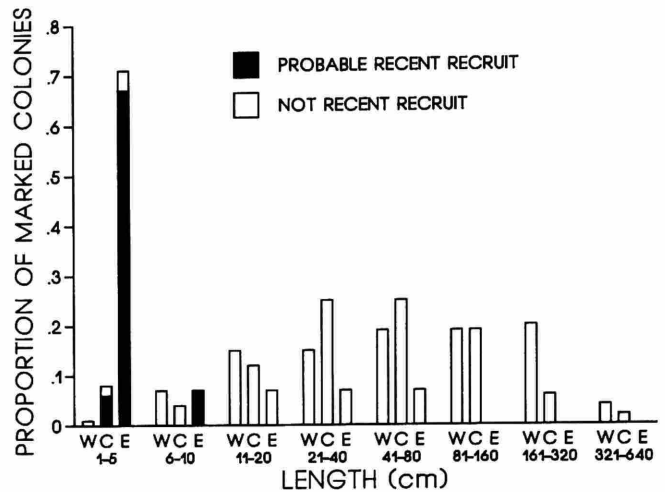


FIGURE 6.—Frequency distribution for marked colony sizes (sum of all living lengths—branches, or branches plus bases for recent recruits). Sample sizes are 80, 52, and 28 for the West, Central, and East Sites respectively. At the East Site, one colony was excluded from the analyses because of the presence of snails at the first census; its total length was 59 cm.

study often had some living branches that were well elevated. The median heights above the substratum of the highest, live branch of each marked colony were 43, 29, and 10 cm at the West, Central, and East Sites respectively, while the median heights above the substratum of the highest piece of staghorn (living or dead) in the quadrats at these sites were only 0, 9, and 17 cm above the maximum colony heights just listed.

No recently settled larval recruits were among the marked colonies at the West Site. At the Central Site, they made up 7% of the colonies and 1% of the combined total lengths. At the East Site, recently settled, larval recruits represented 77% of the original, marked colonies without predators, but even there they constituted less than 23% of the living tissue at the initial census.

### PATTERNS OF *Acropora cervicornis* MORTALITY

Overall, abundance of *A. cervicornis* decreased at all sites over the course of our study, with the steepness of the decline dependent on the 1982 abundance. In 1982, percent cover of live staghorn ranged from 21.4% at the West Site to 0.4% at the East Site (Figure 3), while in 1986 and 1987 abundance was so low that percent cover measurements yielded 0% at all sites. Observations on nearby reefs indicated that the decline was not limited to monitored lobes.

Survivorship of marked colonies was low in all three areas, ranging from complete elimination at the East Site, to reduction by 1986 to 2.5% and 7.7% of the original numbers at the West and Central Sites, respectively (Figure 7). Of the 154 colonies noted as dead over all censuses, the skeletons of all but 36 (23%) were relocated. For 17 of the latter, we found no living
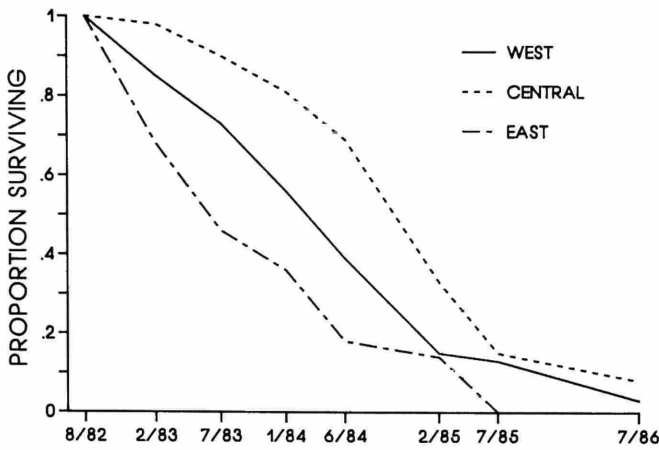
FIGURE 7.—Survivorship of the marked colonies through time (see previous legend for initial cohort sizes) at the primary sites.
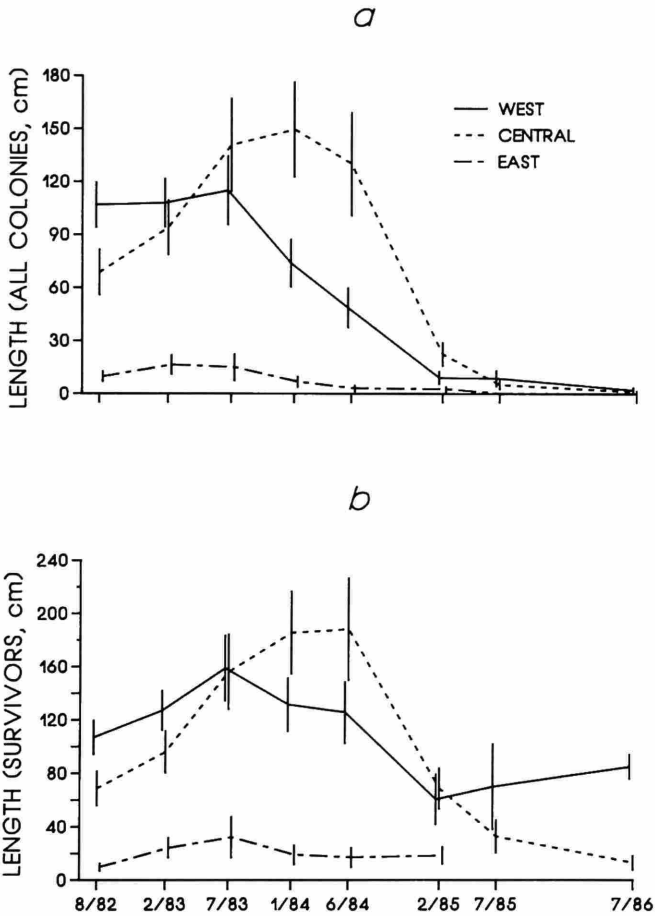


FIGURE 8.—Changes in sizes (means, standard errors) of marked colonies through time: *a,* all colonies included; *b,* only survivors at each census included. See Figure 7 to derive sample sizes for all figures concerning marked colonies.

coral within one meter of the tag marking the original location of the colony; in the remaining 19 cases, living corals in the vicinity did not correspond in shape to the drawings from the previous census. Even assuming the occasional survivorship of "missing" colonies, the gradual disappearance of the marked population was striking.

Colonies initially increased in mean total length of living tissue (Figure 8a); since we originally chose what appeared to be healthy colonies for our starting point, this growth is not surprising. With time, however, more colonies died or suffered levels of partial mortality that exceeded new growth, resulting in a net decline in total living length. This decrease began first at the East Site (census 3), then at the West Site (census 4), and last at the Central Site (census 5).

Looking at just the survivors (Figure 8b), mean colony length followed a roughly similar pattern, although the East (prior to total mortality) and West Sites showed a partial rebound in average living lengths for the few colonies surviving the initial declines. The similarity of pattern, whether or not entirely dead colonies are included in the calculation of average colony size, indicates that colony shrinkage and colony death were acting in a largely parallel fashion.

The changes in mean number of physiological isolates per living colony (Figure 9a) roughly resembled the pattern for mean colony size of survivors (Figure 8b). Isolate number increased proportionately more than colony size of the survivors at the West and Central Sites, however, resulting in a general decline in average isolate length at these sites (at the West Site, through February, 1985; at the Central Site, through July, 1986) (Figure 9b).

## PREDATORS

Although the cause of mortality could not always be assigned with complete confidence and undoubtedly included agents other than those investigated here, the overall importance of the predators we studied was clear. Of these, the two most conspicuous, due to their abundance throughout the course of the study and their sedentary and intimate association with staghorn, were the gastropod *Coralliophila* and the damselfish *Stegastes planifrons.* The effects of the polychaete *Hermodice carunculata* were also conspicuous at times, especially at the West Site. Below we present the details of these patterns (generally for censuses 2–7, since all colonies at census 1 were free of predators by design).

*Coralliophila* was regularly found on some of the marked colonies (Figure 10). The median census value for percent of colonies with associated snails ranged from 7.8% at the Central Site to 10.5% at the East Site. Snails were particularly abundant relative to the amount of staghorn coral at the East Site (Figure 11); the median census value for the mean numbers of snails per m of live tissue ranged from 0.1 at the West Site to 1.1 at the East Site. Only the last census had no marked colonies with snails, but by this census only six surviving corals
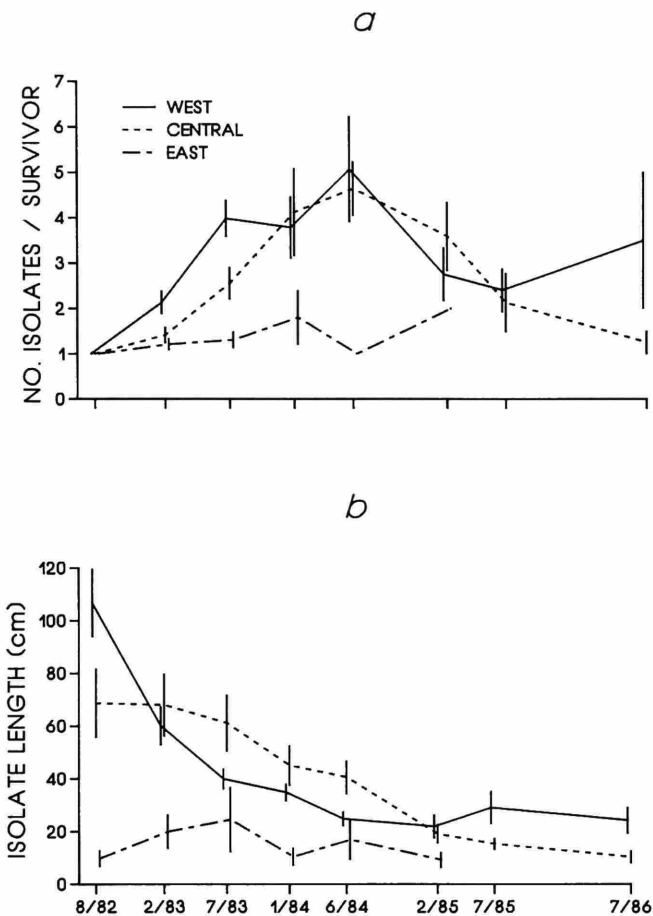
FIGURE 9.—Changes in isolates comprising marked colonies through time: *a*, mean number of isolates per colony; *b*, mean isolate lengths. At the first census, each colony consisted of one isolate, and hence isolate size equaled colony size. Bars indicate standard errors.



FIGURE 10.—Percentages of marked colonies with associated *S. planifrons* ("Fish") and/or *Coralliophila* ("Snails") at the primary sites through time. The first census is excluded since colonies were initially chosen to be predator-free. There are no data for the East Site after 2/85 because by then all marked colonies had died.

remained at all three sites combined.

Mortality in the presence of the snail (Figure 12, two left clusters) accounted for 43% of all recent mortality for all sites and censuses combined, and for 92% of all recent mortality at the East Site. Over 80% of recent mortality associated with snails was found away from branch tips, as would be expected from the known feeding preferences of the snail (Tunnicliffe, 1983).

Table 3 shows that the snails were associated with an increase in number of isolates from census t−1 to census t, with a decrease in number of isolates from census t to census t+1, and with a decrease in colony size (total living length) from census t to census t+1. That is, the effect was first the division of the colony into more numerous, smaller isolates and then the death of many of the newly generated isolates. Substantial tissue loss more often followed, than preceded, the observation of snails (e.g., see Figure 2*c,d*).

The damselfish was most commonly associated with marked colonies of *A. cervicornis* at the Central Site (Figure 10), where

the median census value for the proportion of all colonies in damselfish territories was 25%. The median census value was 9% at the West Site, while no marked colonies at the East Site were ever observed within a damselfish territory (perhaps due to the small size of colonies at this site; see Itzkowitz, 1978).

The quadrat data show a similar pattern (Figure 13*a*). The East Site always had the lowest mean density of territories of *S. planifrons*, while for all but one census, mean damselfish densities were higher at one or both lobes of the Central Site than at the West Site (overall differences in density among sites are significant at p<.0001, Kruskal-Wallis one-way ANOVA).
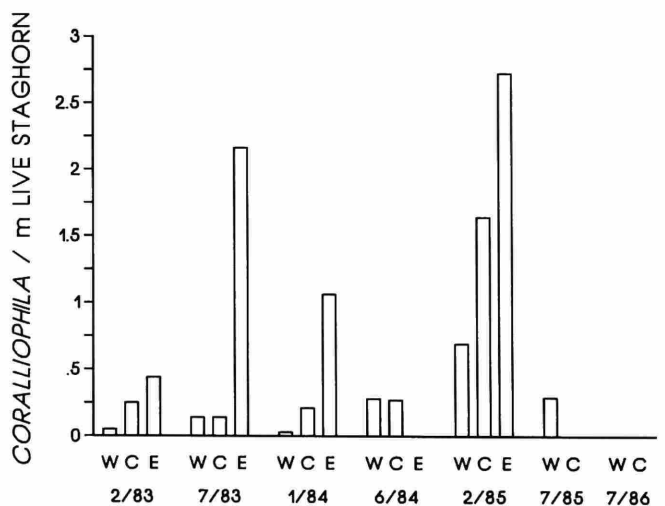


FIGURE 11.—Number of *Coralliophila* per m of live *A. cervicornis* on marked colonies at the primary sites through time (see legend to Figure 10).
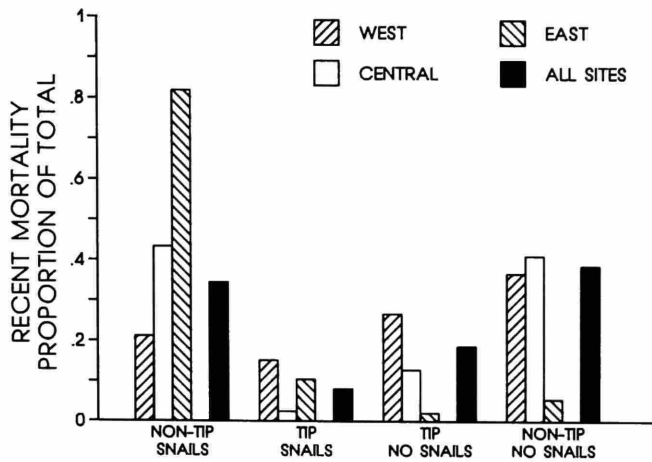
FIGURE 12.—Percentages of four types of recent death (white, unfouled skeleton without living coral tissue) found at each site (each site sums to 100) and overall. Tip death was the sum of the lengths of all recent mortality that included a branch tip, non-tip those lengths that did not include a branch tip. Either could occur on a colony that did or did not have an associated *Coralliophila*. Total recent death lengths were 593 cm at the West Site, 761 cm at the Central Site, and 24 cm at the East Site.

The impact of the damselfish on growth and colony fission was similar to that of the snail for changes following the observation of the predator; presence of a damselfish was associated with a significant decrease in the number of isolates and colony size over the interval following the observation relative to colonies without damselfish (Table 3). For the interval preceding the observation, damselfish had no significant effects on either number of isolates or colony size (Table 3).

The effect of the simultaneous presence of fish and snails is more difficult to assess, because most colonies that simultaneously had snails and fish also had one of these predators alone at other censuses. The means (Table 3, column 3), however, show a clear pattern of increased production of isolates prior to the observation of a joint occurrence of snail and damselfish, and a loss of tissue and isolates following the observation. It is not possible to state statistically whether the effect is greater than additive, although the data suggest that possibility (see also Knowlton et al., 1989). These two predators were not statistically associated in any census at any site.

Overall, the net growth of the corals at the three sites shows a striking, negative relationship with the frequency of these predators (Figure 14). Coral growth varied widely through time, and was negatively correlated with the percentage of corals that had associated damselfish or snails (Kendall rank correlation coefficient = −0.5, p < .005).

The polychaete *Hermodice carunculata* was probably also an important predator, but its impact is more difficult to compare with that of *S. planifrons* and *Coralliophila* because of the polychaete's diurnally cryptic habits (Marsden, 1962).
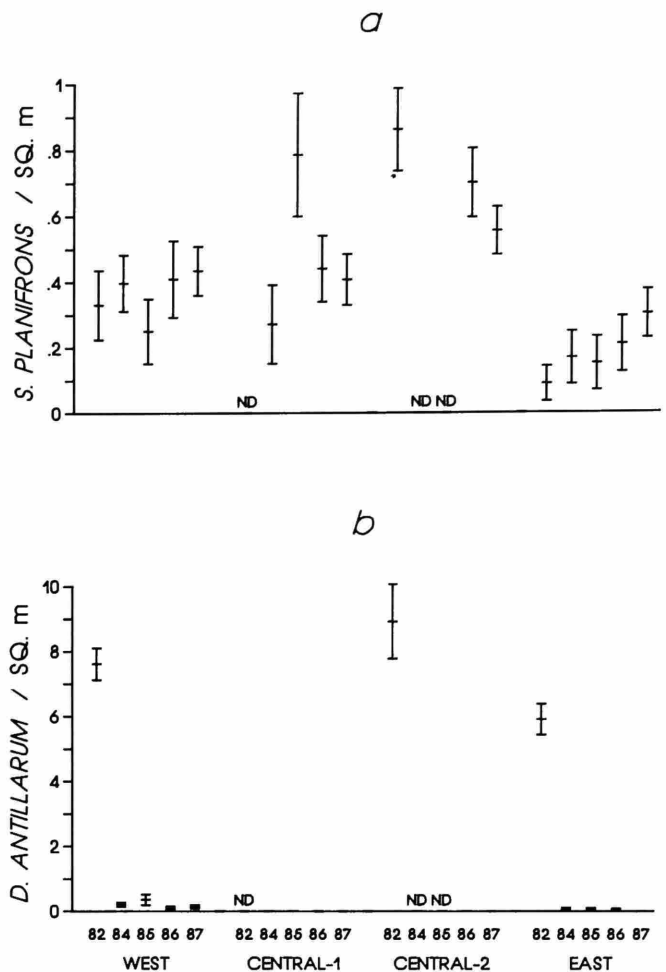


FIGURE 13.—Densities (mean, standard error): *a, S. planifrons,* and *b, D. antillarum,* at the primary sites through time. Data for the Central Site were collected from the area of our study reef (Central-1) and from an area approximately 200 m farther east (Central-2). ND = no data collected. Sample sizes (number of quadrats) were: West, 23, 35, 20, 22, 50; Central-1, ND, 14, 14, 25, 42; Central-2, 21, ND, ND, 26, 39; East, 26, 18, 20, 24, 35.

We never directly observed an attack on one of our marked colonies, although an adjacent colony was attacked during one of our censuses at the West Site, and we saw numerous instances of freshly killed branch tips at this location. The best measure of the relative importance of the polychaete is the amount of recent mortality of branch tips, particularly in the absence of *Coralliophila*. These data show that *Hermodice* was much more important at the West and Central Sites than at the East Site (tip death in the absence of *Coralliophila* represented 27% and 13% vs. 2% of all recent mortality respectively; Figure 12, third cluster). The same pattern is seen when the distribution of all dead tips is considered; the West Site generally had the highest percentage of colonies affected (6 of 7 censuses, Figure 15), and was the only site represented in the most severe damage category. Note that the pattern is

TABLE 3.—Analysis of the effects of *S. planifrons* and *Coralliophila* on changes in length of living tissue per colony and number of isolates per colony between consecutive censuses (measures of performance, see "Methods"). Descriptive statistics are based on all corals. Each coral contributed at most one value to each of the four conditions (no predators, fish only, snails only, both snails and fish; n1 = total number of corals contributing to descriptive statistics for each condition). Statistical tests for differences in performance as a function of the presence of predators (Wilcoxon matched-pairs) are comparisons based on a more limited set of corals (sample size n2) that had no predators and just one of the other three conditions. No coral was used more than once within each cluster of three statistical tests. (n.s.: p>.05, **: p<.01, ***: p<.001).

| Comparison | n1 | mean | std. dev. | Percentiles 25 | Percentiles 50 | Percentiles 75 | sig. | n2 |
|---|---|---|---|---|---|---|---|---|
| $census_t - census_{t-1}$ | | | | | | | | |
| length of tissue | | | | | | | | |
|  no predators | 160 | −24.9 | 60.2 | −27.1 | −8.9 | −2.4 | − | |
|  fish only | 27 | −18.9 | 125.5 | −60.3 | 1.7 | 35.0 | n.s. | 15 |
|  snails only | 34 | −14.9 | 93.2 | −50.9 | −14.7 | 15.9 | n.s. | 26 |
|  both | 9 | −24.7 | 148.6 | −161.1 | −5.0 | 63.2 | n.s. | 2 |
| no. of isolates | | | | | | | | |
|  no predators | 160 | −0.8 | 1.2 | −1.0 | −0.3 | −0.2 | − | − |
|  fish only | 27 | 0.5 | 4.5 | −1.0 | 0.5 | 3.0 | n.s. | 15 |
|  snails only | 34 | 1.9 | 3.5 | 0.0 | 1.7 | 4.2 | *** | 26 |
|  both | 9 | 6.3 | 4.2 | 4.0 | 5.0 | 8.5 | n.s. | 2 |
| $census_{t+1} - census_t$ | | | | | | | | |
| length of tissue | | | | | | | | |
|  no predators | 160 | −7.7 | 62.8 | −15.9 | −5.0 | −0.5 | − | − |
|  fish only | 26 | −110.4 | 238.0 | −157.5 | −87.1 | −25.9 | ** | 15 |
|  snails only | 34 | −72.9 | 104.0 | −99.9 | −43.4 | −13.5 | *** | 27 |
|  both | 9 | −361.0 | 367.6 | −536.0 | −234.5 | −83.0 | n.s. | 2 |
| no. of isolates | | | | | | | | |
|  no predators | 160 | 0.1 | 1.3 | −0.5 | −0.2 | 0.2 | − | |
|  fish only | 26 | −2.0 | 3.2 | −4.2 | −1.7 | 0.0 | ** | 15 |
|  snails only | 34 | −1.6 | 7.3 | −4.0 | −2.0 | 0.0 | *** | 27 |
|  both | 9 | −9.1 | 5.1 | −13.0 | −9.0 | −6.0 | n.s. | 2 |
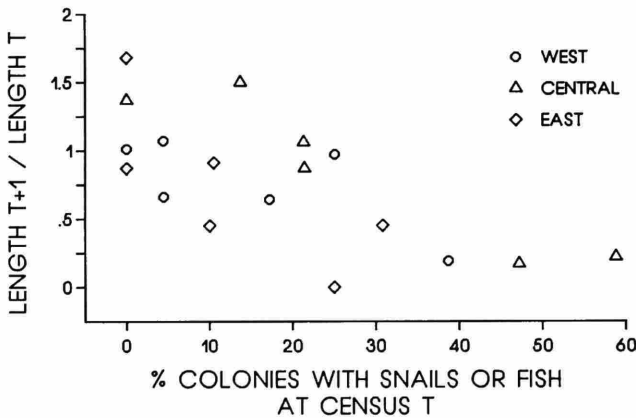


FIGURE 14.—Ratio of lengths at consecutive censuses (census t+1 / census t) as a function of percent of colonies with *Coralliophila* or *S. planifrons* at census t. Only the first seven censuses were used in order to maintain approximately equal census intervals.

not a simple reflection of colony size differences (e.g., in 1984 surviving colonies at the Central Site were on average larger than those elsewhere (Figure 8b) but did not have the highest proportion of damaged tips).

The urchin was probably the least important of the four predators initially, because of its preference for algal turf (Carpenter, 1981) and its tendency to graze on basal areas (Tunnicliffe, 1983), which are not the zones of most active growth (Pearse and Muscatine, 1971; Gladfelter, 1983). Less than 1% of the recent mortality recorded prior to the die-off had the skeletal damage characteristic of grazing by *D. antillarum*. The urchin was obviously of negligible importance as a predator following the catastrophic drop in abundance during the summer of 1983 (Figure 13b), although the die-off had other, indirect effects (see below).

### CHANGES IN COMMUNITY COMPOSITION

At all sites, percent cover of five major groups (Figure 16a,b) changed significantly through time ($\chi^2$ analyses, p<.0001; counts for staghorn and other live coral combined for analyses of the Central and East Sites to meet requirements for numbers of cells with low expected values). The most striking aspect of the change was the increase in fleshy algae and the disappearance of bare or algal-encrusted substratum, which occurred after the virtual disappearance of *Diadema* at all sites in July 1983 (Figure 16a; see also Hughes et al., 1985; Liddell and Ohlhorst, 1986; Hughes et al., 1987; Morrison, 1988).

FIGURE 15.—Percent marked colonies with dead tips not in contact with other surfaces for the primary sites through time. Tips are defined as branch segments distal to the most distal branch nodes.
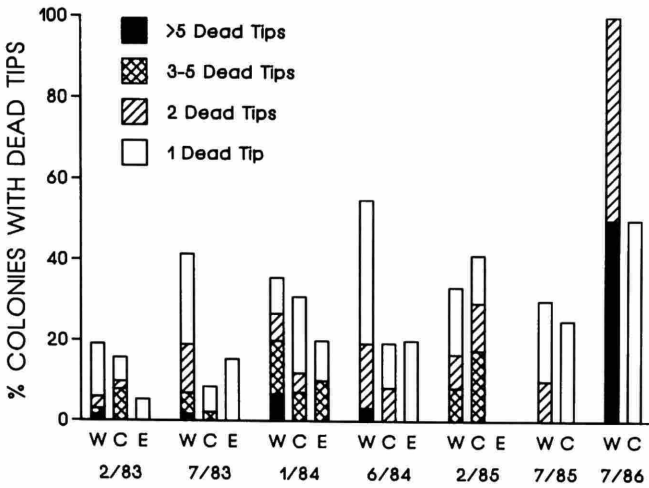
Standardized, $\chi^2$ residuals at the West, Central, and East Sites reflect these changes (the six most extreme values occurred in 1982 and indicated an excess of bare substratum (14.2, 14.9, 22.8) and a scarcity of fleshy algae (−11.7, −11.2, −12.1) relative to the censuses following the die-off).

Across sites, fleshy algae represented 82% to 88% cover in 1987 (Hughes et al. (1987) reported 94% coverage by fleshy algae at −10 m on the west forereef of Discovery Bay in 1986). The readily identifiable, dominant genera were *Lobophora*, *Dictyota*, and *Halimeda*; together they accounted for 30% to 96% of the percent cover of fleshy algae at the three sites in 1984–1987. These algae are avoided by herbivorous fishes but readily eaten by *Diadema* (Morrison, 1988). The West Site was dominated by *Lobophora* (median for 1984–1987 censuses of 63% of all fleshy algae), whereas the other sites had a more even pattern of algal species composition in which *Dictyota* was the most abundant (median of 21% of all fleshy algae).

At all three sites, changes in the percent cover of living coral (Figure 16b) also contributed to the significance of shifts in percent cover over time (following $\chi^2$ analyses based on categories as above, except all non-coral categories combined). Only the East Site showed a significant increase in the percent cover of living corals between 1982 and 1986 (p<.02), but even here no substantial increase in live coral cover occurred after the initial rise in 1984 (Figure 16b). At the West Site, live coral cover declined between 1982 and 1986 (p<.0001), due primarily to the decline in staghorn cover. At the Central Site lobe for which we have 1982 data, live coral cover also declined significantly (p<.0001) over this interval. Percent cover of living coral, including or excluding *A. cervicornis*, was lower in 1987 than in any other year (minimum, standardized, $\chi^2$ residuals occurred in 1987, and all were −2.7 or less). All sites showed declines in live coral cover between
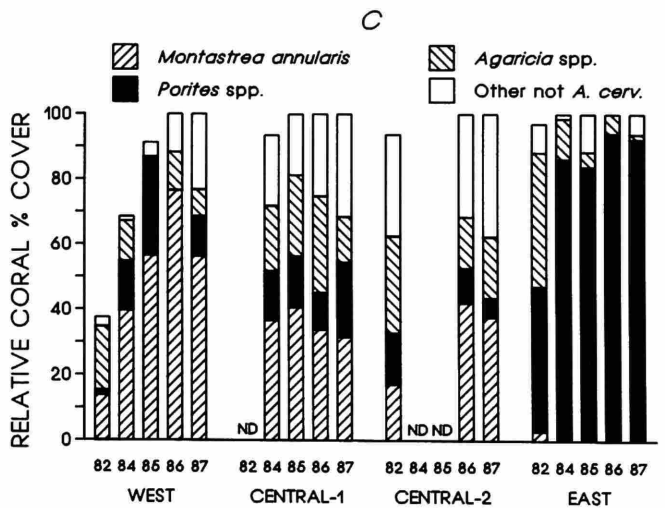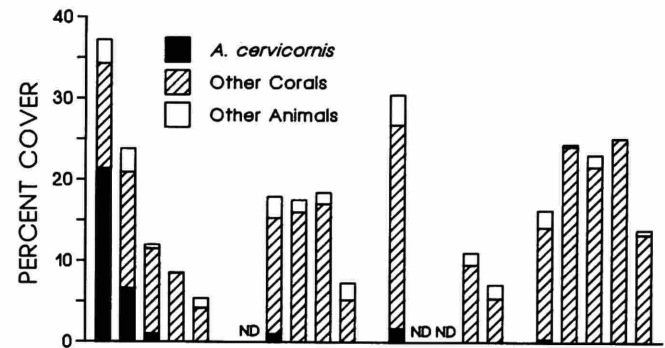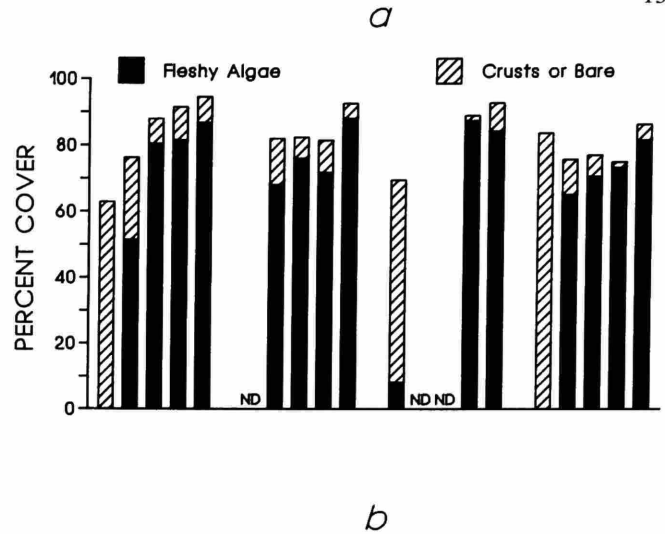


FIGURE 16.—Community composition for the three sites (see legend to Figure 13 for site information): *a*, absolute percent cover of algae (all but encrusting corallines are included in fleshy, and apparently living, encrusting corallines below dense beds of fleshy algae not included), encrusting foraminiferans and non-living substrata; *b*, absolute percent cover of animals; *c*, relative percent cover among corals and *Millepora* (*A. cervicornis* not plotted, with staghorn all bars would sum to 100%). Sample sizes (number of points) were: West, 210, 350, 200, 200, 581; Central-1, ND, 390, 200, 209, 546; Central-2, 240, ND, ND, 200, 634; East, 240, 300, 200, 200, 485.

1986 and 1987 (Figure 16*b*); these were significant at the West (p<.04) and East (p<.0004) Sites, and at one of two lobes at the Central Site (p<.0001).

Species composition of the coral community shifted significantly through time at some sites (Figure 16*c*, $\chi^2$ analyses with low abundance categories combined as required). At the West Site (p<.0001; categories: *A. cervicornis, M. annularis,* other corals) the relative importance of *Montastrea annularis* increased through 1986 (Figure 16*c*). This steady increase in relative importance was primarily due to the parallel decrease in staghorn coral over the same interval (Figure 16*c*). The absolute abundance of *M. annularis* fluctuated between 8% in 1984 and 2% in 1987 (standardized $\chi^2$ residuals of 2.6 and −2.9 for these years). At the East Site, *Porites* species increased and *Agaricia* species decreased markedly between 1982 and 1984 (p<.0001; categories: *Porites* spp. and other corals or *Agaricia* spp. and other corals). Branching and plating *Porites* have conspicuously dominated the coral community since then, with relative percent coverage of 84%–94% (Figure 16*c*). In absolute percent cover, *Porites* increased from 6% in 1982 to a peak of 23% in 1986, while *Agaricia* fell in absolute cover from 6% to less than 1% between 1982 and 1987. Both of these shifts in absolute abundance are also statistically significant (p<.0001; categories: *Porites* spp. and all other cover, or *Agaricia* spp. and all other cover). At the Central Site, neither lobe had significant shifts in coral composition through time (p>.15; categories: *M. annularis, Porites* spp., *Agaricia* spp., other corals).

## Discussion

### THE ROLE OF PREDATORS

The importance of predators on Indo-Pacific and eastern Pacific reefs has been recognized for some time (Chesher, 1969; Robertson, 1970; Glynn et al., 1972; Randall, 1974; Glynn et al., 1979; Neudecker, 1979; Wellington, 1982; Colgan, 1987) but in the Caribbean their role has received much less emphasis (Bakus, 1969; Porter, 1974). One reason for this neglect is the absence in the Caribbean of any predator comparable to the notorious *Acanthaster planci,* which is conspicuous due both to its highly variable densities and large adult size (Birkeland, 1982; Bradbury et al., 1985; Moran et al., 1985). Overall, the Caribbean supports a lower absolute diversity of fish and invertebrate predators on corals (Randall, 1974; Robertson, 1970). Although the diversity of coral predators relative to the diversity of corals may be comparable in the two regions, the lower absolute number of corallivorous species in the Caribbean may have contributed to their neglect by scientists. Finally, some of the best studied Caribbean reefs are heavily overfished, including those of the Jamaican north coast (Woodley, 1979; Munro, 1983), which has probably led to an underestimate of the potential importance of Caribbean fishes as coral predators. The lightly fished and well protected

reefs of Little Cayman, for example, have large numbers of adult corallivorous fishes, and corals there have numerous and obvious recent surface scars and skeletal breaks (pers. obs.; see also Glynn's (1973) description of fish predation on Caribbean corals in Panama).

Even documented Caribbean corallivores not harvested by man (*Hermodice carunculata,* see Glynn, 1962; Marsden, 1962; and *Coralliophila,* see Robertson, 1970) have often been described as relatively insignificant sources of mortality, however. Ott and Lewis (1972), for example, stated that both *Coralliophila abbreviata* and *Hermodice carunculata* were unimportant consumers of corals on Barbados reefs. Tunnicliffe (1983) also found relatively low percentages of *A. cervicornis* that showed signs of recent attack by these two predators (2%–5% and 0–2% respectively). This assessment as a general assumption has only recently been questioned for *C. abbreviata* on *A. palmata* by Brawley and Adey (1982), who suggested that the snails might be directly inhibited from feeding when potential fish predators were abundant. They pointed out that such a response could explain the relatively low predation rates by snails on corals observed by Ott and Lewis (1972) in Barbados, where fishing pressure is lower than on the Haitian reefs studied by Brawley and Adey. Snails on *Montastrea annularis* (which was much more abundant than *A. cervicornis* at the sites studied by Ott and Lewis) are also smaller than those on acroporids (pers. obs.) and may be less voracious corallivores (Rylaarsdam, 1983). In general, there is little published research on the population biology and behavior of these corallivores; Huston's (1985b) review, for example, does not even mention them.

Moreover, appreciation of the potential importance of the largely herbivorous *Diadema antillarum* and *Stegastes planifrons* as consumers or killers of adult corals in the Caribbean is relatively new (Bak and van Eys, 1975; Kaufman, 1977, 1981; Carpenter, 1981; Sammarco, 1982). Yet in Tunnicliffe's (1983) study of *A. cervicornis,* they were more likely to inflict damage (6%–32% of colonies attacked by damselfish, 2%–8% by urchins) than were the specialist corallivores (see above). She did not compare the amount of damage caused by the different predators, however.

In summary, predators have received relatively little attention in the Caribbean, and where studied they have usually been described as unimportant. Thus our findings (see also Knowlton et al., 1989) stand in contrast to most previously published work on Caribbean corallivores. The following discussion attempts to integrate these widely differing results with theoretical predictions for predator-prey systems.

### THRESHOLD EFFECTS

Stoddart (1974), noting that recovery was rapid following moderate hurricane damage but prolonged following severe damage, suggested that reefs might respond in a threshold manner to disturbance. Our study points to a biological
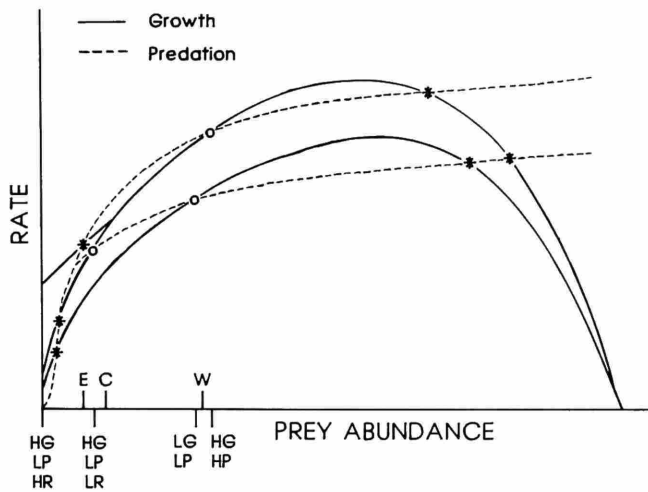
FIGURE 17.—Model for threshold response of coral prey to predation (after May, 1977). Solid lines show two rates of coral growth in absence of predation. The height of the Y-intercept indicates the extent to which new colonies arrive via larval recruitment. Two recruitment levels are shown for the upper growth curve; generally the lower of these would more accurately reflect the biology of *A. cervicornis*. Dotted lines show rate of loss due to predation for two predation intensities. Both rates are graphed as a function of prey abundance, which will increase whenever growth exceeds mortality, and decrease whenever mortality exceeds growth. Given the appropriate curves, this can lead to a variety of stable equilibria (asterisks) and breakpoints (open circles) separating domains of attraction. Hypothetical *A. cervicornis* abundances at the West (W), Central (C) and East (E) Sites at the outset of our study are shown by the ticks above the horizontal axis. Ticks below the horizontal axis identify the breakpoints (above, where curves cross) from which recovery to high abundance could occur for combinations of high (H) and low (L) growth (G), predation (P) and recruitment (R); there is no high equilibrium, and therefore no threshold for recovery, for the combination of low growth and high predation. Note that the response of staghorn at the West and Central Sites could have critically depended on the prevailing intensity of predation and rate of growth; the area with the highest initial post-hurricane abundance would not necessarily have had the highest probability of recovery. If the effect of the die-off of *D. antillarum* were to lower net growth rates in the absence of predation (e.g., from upper to lower solid line), then some populations previously above thresholds for recovery would subsequently decline.

mechanism consistent with his general perspective, and provides an additional reason for the conflicting assessments of the role of predators on Caribbean reefs: the relative importance of predators can change radically in a threshold fashion depending on the population size of the prey. In theory (Figure 17; May, 1977) such a system can have two stable population densities of prey: a high equilibrium, at which predators are relatively scarce, and a low equilibrium, at which predators are relatively common. These two equilibria are separated by a breakpoint; should the prey population fall below this point for whatever reason, it will continue to decline until it reaches the lower stable value of prey density.

The assumptions of this model are not particularly stringent. Most important are (1) growth rate of the prey must first increase and then decrease as a function of prey abundance,

(2) impact of the predators must increase at a decreasing rate as their prey become more abundant, i.e., their feeding must be limited by something other than food abundance when prey are at high density, and (3) predation intensity must in some cases be intermediate in strength relative to prey growth rate (otherwise only one equilibrium, high or low, will exist).

The biological characteristics of *A. cervicornis* and its predators are consistent with this model. For the coral, rates of mortality at the bases of the colonies must eventually approach growth rates at the tips (perhaps, in part, due to self-shading; Tunnicliffe, 1983), generating a growth curve resembling that illustrated. If this were not the case, the thickness of the living layer of staghorn would be far greater than any actually observed. The low level of larval recruitment apparently characteristic of *A. cervicornis* (see above; Table 2) makes the existence of a low stable point more likely as well (see Figure 17).

At least some of the predators also appear to be controlled by factors other than the amount of staghorn when this species is abundant, as required by May's (1977) model. Tunnicliffe's (1983) estimates of percentage of colonies with identifiable damage by snails (4%) and damselfish (6%) on a comparable reef dominated by staghorn before the hurricane are lower than most of our post-hurricane estimates (Figure 10), despite the fact that ours is a more conservative measure (damage in absence of predator is not included in Figure 10). Robertson et al. (1981) found that *S. planifrons* was not limited by the amount of staghorn in an area of dense staghorn growth in Panama. Snail densities along the Jamaican north coast six and seven years after the initial destruction (Table 4) are still comparable to those reported by Ott and Lewis (1972) for intact reefs in Barbados. Although the two sites in Discovery Bay where pre- and post-hurricane estimates of snail density are available (Table 4, rows 13–16) indicate declines to 50% and 60% of pre-hurricane values, the abundance of staghorn has generally declined to a much greater extent. For example, in Discovery Bay pre-hurricane estimates of 14%–16% absolute staghorn cover (Rylaarsdam, 1983; Table 1a this paper) exceed our estimates in 1987 of 0.2%–1.2% cover on Dancing Lady by approximately an order of magnitude, and even our maximum value (2.6% cover on Arena reef) is less than 20% of the lowest pre-hurricane estimate for these reefs. Similarly, the densities of *S. planifrons* at the West Site (Figure 13a) showed no signs of decline over the course of our censuses, while staghorn abundance dropped dramatically during the same period (Figure 16b). Taken together, these data suggest that abundance of staghorn relative to the abundance of these predators is routinely higher when staghorn is at high density, which would lead to the kinds of curves illustrated in Figure 17.

The initial impact of Hurricane Allen was much greater on *A. cervicornis* than on its predators (Knowlton et al., 1981; Williams, 1984), both because of immediate mortality and the delayed effects of fragmentation (including possibly the

TABLE 4.—Mean density, distribution, and species and size patterns for the snail *Coralliophila*. Sites (see "Methods," Figure 1) are our main sites (W = West; C = Central (C-1 is the reef with marked corals; C-2 is a reef approximately 200 m farther east); and E = East), and several locations off Discovery Bay (DB). The latter are represented by three permanent transects on Dancing Lady Reef (DL) and two additional sites for which pre-hurricane data are available (Dancing Lady and Long Term Sampling (LTS) reefs). Host corals listed are, in order, *Acropora cervicornis*, *Montastrea annularis*, *Agaricia agaricites*, *Porites* spp., *Madracis mirabilis*, and others. ND = no data available; n = number of square meters censused. Note that previously reported pre-hurricane densities (Knowlton et al., 1981) were for snails on *A. cervicornis* only. Percent yellow is the percent of snails with yellow opercula (i.e., probably *C. abbreviata*, see "Methods"). Size distributions (percent of snails greater than 9 mm in total length) are based on visual estimates of snail sizes.

| Site | Depth | Date | n | No. /m² | % Distribution by Host | | | | | | % Yel. | % > 9 mm |
|------|-------|------|---|---------|------|------|------|------|------|------|--------|----------|
|      |       |      |   |         | A.c. | M.a. | A.a. | Por. | M.m. | Oth. |        |          |
| W      | 10–12 | 1987 | 50 | 0.7 | 0  | 65 | 21 | 0  | 3  | 12 | 71  | 53  |
| C-1    | 9–12  | 1986 | 22 | 0.7 | 0  | 40 | 53 | 0  | 0  | 7  | ND  | ND  |
| C-1    | 9–12  | 1987 | 42 | 1.9 | 0  | 55 | 33 | 0  | 11 | 1  | 89  | 38  |
| C-2    | 9–11  | 1987 | 39 | 0.6 | 0  | 73 | 27 | 0  | 0  | 0  | 86  | 55  |
| E      | 10–12 | 1986 | 24 | 1.7 | 0  | 7  | 50 | 36 | 0  | 7  | 88  | 43  |
| E      | 9–12  | 1987 | 35 | 1.3 | 0  | 0  | 83 | 13 | 0  | 4  | 91  | 26  |
| DB-DL  | 9     | 1986 | 18 | 1.7 | 10 | 53 | 37 | 0  | 0  | 0  | ND  | 37  |
| DB-DL  | 9     | 1987 | 18 | 3.8 | 41 | 44 | 15 | 0  | 0  | 0  | ND  | 38  |
| DB-DL  | 11    | 1986 | 18 | 1.3 | 26 | 30 | 39 | 0  | 0  | 4  | ND  | 48  |
| DB-DL  | 11    | 1987 | 18 | 1.3 | 17 | 52 | 30 | 0  | 0  | 0  | ND  | 61  |
| DB-DL  | 15    | 1986 | 18 | 0.4 | 0  | 12 | 87 | 0  | 0  | 0  | ND  | 25  |
| DB-DL  | 15    | 1987 | 18 | 1.6 | 24 | 10 | 34 | 3  | 28 | 0  | ND  | 31  |
| DB-DL  | 13    | 1975 | 40 | 1.0 | ND | ND | ND | ND | ND | ND | 100 | ND  |
| DB-DL  | 13    | 1986 | 38 | 0.4 | 0  | 40 | 47 | 0  | 0  | 13 | ND  | ND  |
| DB-LTS | 9     | 1975 | 40 | 1.2 | ND | ND | ND | ND | ND | ND | 100 | ND  |
| DB-LTS | 9     | 1986 | 46 | 0.6 | 7  | 38 | 52 | 0  | 0  | 3  | ND  | 36  |

intensification of ongoing disease; see Bak and Criens, 1982). Thus the hurricane can be viewed as an event that lowered the density of *A. cervicornis,* at some sites below the breakpoint separating theoretical, high and low density equilibria, thereby resulting in further decline rather than recovery.

Near the East Site in June, 1984, we attempted to demonstrate a threshold effect by monitoring the survival of experimentally introduced colonies of *A. cervicornis* that were either solitary (low density, n = 12) or surrounded by other introduced, conspecific colonies (high density, n = 12). Three lobes with four measured colonies each were used for each treatment (randomly assigned), and negligible amounts of live staghorn occurred on the lobes prior to the introductions. After six months, both low and high density treatments had very high numbers of *Coralliophila.* Mean number of snails per m of live staghorn ranged from 4.4 on the high density experimental corals to 9.3 on the low density experimental corals, and the percentages of living colonies with snails were 44% and 75% respectively (although the trend was in the expected direction, no significant differences between treatments were found). All of these figures greatly exceed maximum values observed during the censuses (1.1/m and 31% respectively), and confirm the importance of *Coralliophila* documented for other lobes in the region. By twelve months total mortality was 50% for the high density corals and 67% for the low density corals; overall total length of living tissue

on monitored corals was less than one third its initial value, and only two of the surviving colonies showed net growth exceeding 10%. In 1987 total densities were still substantially below initial levels, with many of the "high density" areas totally lacking live staghorn coral. In sum, the attempt to produce experimentally a threshold effect failed because we were unable to increase local density of staghorn sufficiently to swamp the predatory activities of the snail, even though the high density treatments involved collecting all sizable, living *A. cervicornis* colonies from surrounding reefs (without their predators) to place around the monitored colonies.

This rapid response by the snails suggests a low probability of recovery for *A. cervicornis* at the East Site unless snail densities decline substantially or massive recruitment of staghorn occurs. Densities of snails six and seven years after the hurricane were still relatively high (Table 4, rows 5, 6). Although the sampled snails at the East Site were found exclusively on other corals due to the extreme rarity of staghorn, they remained potentially available to attack new colonies of *A. cervicornis*; indeed the only staghorn colony seen at the East Site during the 1987 visit had four *Coralliophila.* Swamping such high densities of predators by sexual recruitment seems unlikely given the typical low density of *A. cervicornis* recruits (see above; Table 2), although the possibility of an unusually massive recruitment event cannot be completely ruled out (e.g., see Dayton and Oliver, 1980).

## DIE-OFF OF *Diadema antillarum*

Although *Diadema antillarum* can be a predator on corals (Bak and van Eys, 1975; Carpenter, 1981), the net effect of its grazing would appear to be to prevent the overgrowth of corals by algae, particularly on Jamaican forereefs where large herbivorous fish and other grazing echinoids are relatively uncommon (Sammarco, 1982; Hughes et al., 1987). For established colonies of *A. cervicornis*, the most important effect of the algae would be to inhibit propagation through fragmentation. Low-lying pieces (and the occasional recruit) can be easily overgrown (Rosesmyth, 1984; Liddell and Ohlhorst, 1986); rapidly growing branch tips on large, upright colonies are usually unaffected (pers. obs.). The question remains, however: if *D. antillarum* were still abundant, would predators have prevented the recovery of *A. cervicornis*?

At our East Site the answer appears to be yes, since the amount of living tissue on marked corals was declining for six months before the die-off occurred (Figure 8*a*, censuses 2/83–7/83). Moreover, the primary role of the snail *Coralliophila* is unambiguous at this site. The average decline of –2.2 cm per colony from 2/83–7/83 becomes an increase of 4.1 cm per colony when colonies with associated snails in February are excluded. Recent mortality in February and July, 1983, totaled 0.1% and 4.9% of all living branch lengths respectively, and 94% of this recent mortality occurred on colonies with snails.

At the West Site, although average colony size increased before the die-off, the initial net growth of coral did not show the exponential increase one would expect in a recovering population in the absence of substantial partial colony mortality (Figure 8*a*; total length of living branches increased by only 1% from 8/82–2/83 and 7% from 2/83–7/83). Here recent mortality in July, 1983, totalled 2.8% of the amount of living tissue, and 72% of this recent mortality could be attributed to *Hermodice* (branch tips) or was found on colonies associated with *S. planifrons* or *Coralliophila* (there was no recent mortality at the 2/83 census). Other factors may have been contributing to mortality at this site prior to the die-off (perhaps disease) and net decline in the size of marked corals had not occurred as of July, 1983. Yet here too, the importance of predators and the relatively poor growth of the population suggest that predator-mediated collapse might also have occurred even with normal densities of *D. antillarum*.

In the Central Site, however, growth was very high for the two intervals before the die-off occurred (Figure 8*a*; increases of 37% and 50% for the two census intervals prior to the die-off). Recent mortality was 0.3% and 2.5% of living tissue lengths in February and July, 1983, and only 27% and 30% of recent mortality at these two censuses was attributable to *Hermodice* or on colonies with *S. planifrons* or *Coralliophila*. Here the combined effects of predators and algal growth may have been required to prevent recovery.

In sum, a potential range of responses among the sites, depending on the interaction of prevailing growth and predation rates, may have been reduced to a nearly uniform decline due to the negative effects of the increased algal cover associated with the *Diadema* die-off (see Figure 17). Ironically, by sharply reducing overall coral cover, the eventual effect of the urchin die-off may be to cause the decline of the predators to such a point that *A. cervicornis* can recover from a relatively few remaining large colonies (although there are many other potential effects as well).
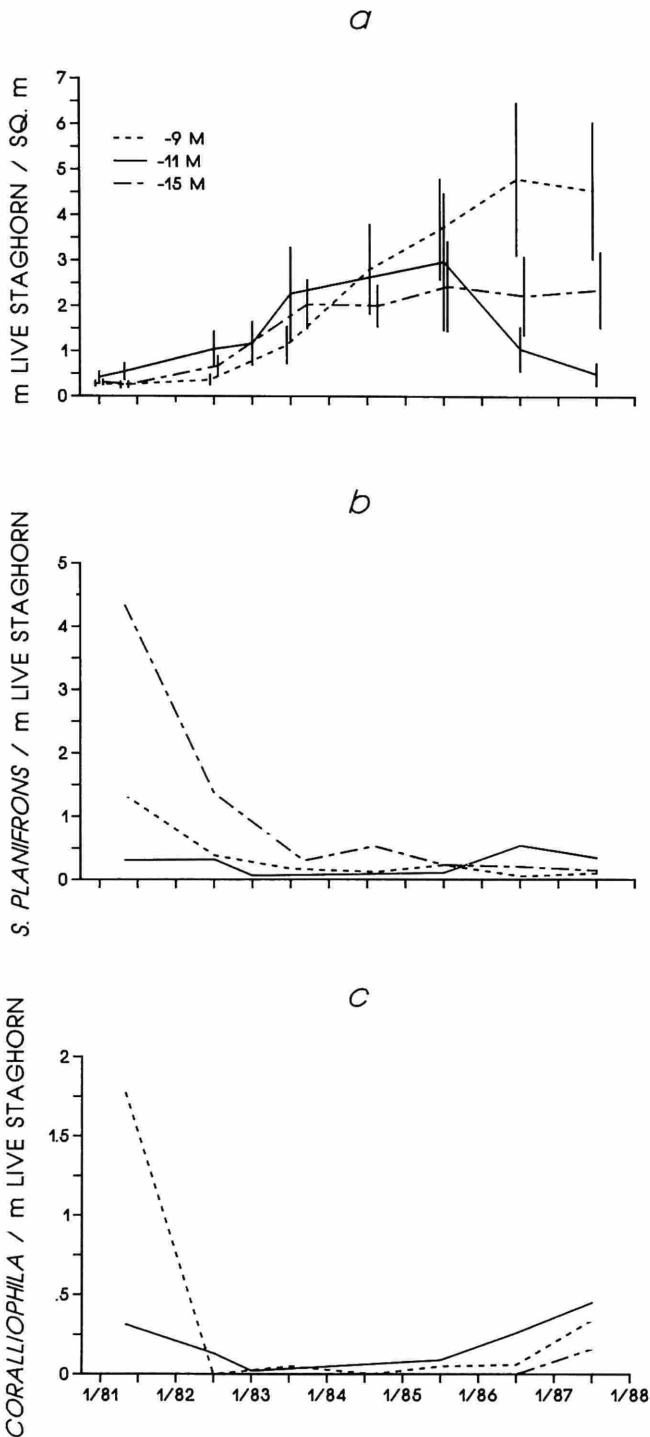
## PROSPECTS FOR FUTURE RECOVERY

The prognosis for eventual recovery of staghorn reefs along the north coast of Jamaica is uncertain. The essential question is whether the current low densities of staghorn will persist, that is, will these transformed reefs be an example of an alternate stable state (e.g., Sutherland, 1974; Connell and Sousa, 1983)?

The response of predators is critical and potentially complex. As May (1977) indicated, a particular threshold analysis (e.g., Figure 17) is not necessarily valid indefinitely. Except in the case of man-controlled harvesting, one cannot assume that predator populations will not collapse following long-term low densities of their prey. Predator collapse and recovery of the prey is not inevitable, however. Stable persistence at low densities of a prey is more likely if the prey is preferred but exploitation of isolated individuals is delayed, and if the predators can persist on other, less preferred prey. The known natural history of staghorn coral and its predators (see above) is apparently consistent with these requirements.

It is clearly too early, however, to predict with any confidence what the long-term behavior of these populations will be. This unpredictability is well illustrated by data collected at three depths on Dancing Lady Reef at Discovery Bay over the same period (Figure 18). Here predators were initially very abundant relative to their staghorn prey in comparison to pre-hurricane estimates (see legend), but subsequently declined substantially, at least until 1986. Notably, the –11 m transect showed the poorest growth of *A. cervicornis* from 1984 to 1987, and during the same interval suffered a heavy attack by *H. carunculata* and had generally higher densities of snails and more recently damselfish (Figure 18). Indeed, even using conservative estimates of pre-hurricane abundances of staghorn (Figure 18 legend), in 1987 the densities of damselfish and snails relative to the abundance of staghorn were 4.2 and 5.6 times pre-hurricane estimates at this depth. Graus et al. (1984) predicted recovery of Discovery Bay reefs within eight to ten years, but they ignored the now clearly important role of biological interactions.

Overall, Discovery Bay performed in a distinctly different manner from our main sites. Percent cover of live staghorn there rose from 1% in 1982 to 3% in 1986, in contrast with the fall to 0% cover at the West, Central, and East Sites over the same period. We cannot assume that our transects are on the

*a*

*b*

*c*

FIGURE 18 (left).—Changes in coral and relative predator abundances at Dancing Lady Reef, Discovery Bay, Jamaica, for three 18 m² transects located at −9, −11, and −15 m; shallow and deep transects are those described in Knowlton et al. (1981): *a*, Mean cm living *A. cervicornis* per m². Much of the drop between 1985 and 1986 at −11 m was apparently due to predation by *H. carunculata* (50% of colonies affected). Pre-hurricane staghorn abundance was at least 8 m per m². Tunnicliffe (1980) reported a mean of 7.2 m of live staghorn per m² for the entire undisturbed *cervicornis* zone of a nearby reef, suggesting over 60% recovery for the −9 m transect. This seems unrealistic, however, because percent cover of staghorn never exceeded 4% during our surveys at this depth, while pre-hurricane estimates for nearby reefs range from 14%–16% absolute cover (Rylaarsdam, 1983; Table 1*a* this paper). Additionally, one third of this transect in 1987 was devoid of living staghorn, while 4 of 18 m² exceeded Tunnicliffe's maximum densities by 21%–85%; maximum densities on a local scale were known to have reached 21–25 m/m² (Land, unpublished data from 1975). *b*, Number of *S. planifrons* territories per m of staghorn coral. Pre-hurricane densities were maximally 0.08, 0.08, and 0.23 damselfish per m of coral at −9, −11, and −15m (based on Kaufman's (1979, 1981) counts of damselfish at these depths and a conservative estimate of 8 m of staghorn per m²). *c*, Number of *Coralliophila* on staghorn per m of staghorn coral. Pre-hurricane density was maximally 0.08 per m coral (based on Knowlton et al. (1981) counts of snails per m² on staghorn and a conservative estimate of 8 m staghorn per m²).

## OTHER EXAMPLES

Explicit tests for the generality of our findings are required. Of particular importance are similar occurrences in areas not heavily influenced by man. In the absence of such examples, one might argue that our observations were due to the scarcity of predators on corallivores (Brawley and Adey, 1982) caused by overfishing along the northern coast of Jamaica (Woodley, 1979; Munro, 1983).

Stoddart's (1963, 1969, 1974) qualitative surveys of lightly fished (Hay, 1984) reefs off Belize following the passage of Hurricane Hattie are consistent with our observations in Jamaica. Rendezvous Reef was in the direct path of the storm and severely damaged; eleven years later, little regrowth by *A. cervicornis* had occurred (although "fast-growing" *A. palmata* was noted as recovering). Moderately damaged Carrie Bow Cay, on the other hand, was described as completely recovered after the same interval. Although Stoddart (1974) attributed the difference to problems associated with recruitment in the more devastated area, predators were not monitored.

Much stronger support for the generality of our findings comes from more recent studies in the Chichime Cays, San Blas, Panama, where fishing pressure is also relatively light (pers. obs.). On the leeward sides of some islands, extensive beds of still standing but dead *A. cervicornis* were found in 1987. The cause of the extensive mortality is unknown. Hurricanes do not normally occur in this part of the Caribbean, and the mild warming event of 1983 had relatively little effect on staghorn (Lasker et al., 1984). The epidemic causing extensive mortality in Curaçao and Bonaire (Bak and Criens, 1982; van Duyl, 1982, 1985) may have occurred unrecorded in the San Blas.

A 180 m² stretch of one of these reefs at a depth of −6 to −7

brink of collapse (as perhaps suggested by the 1987 data), or alternatively, that the 1983–1986 increase in staghorn abundance will resume. Whether or not the Discovery Bay reefs diverge or converge with our main sites over the coming years, their divergence to date makes clear the importance of monitoring a diversity of sites.

m was surveyed in 1987. One of us (NK) recorded 29 *C. abbreviata* on 39 isolates of staghorn that were grouped in 10 clusters. Each of the clusters had at least one snail, and there were on average 2.3 snails per meter of live staghorn and 1.5 snails per m² of reef. Fifty percent of the isolates were also within the territories of *S. planifrons*. Six months later, we found only 18 isolates in 6 clusters, and total living length of coral had dropped to 44% of the previous amount. Although none of the colonies were still in damselfish territories, snail densities remained high (1.6 snails per m of live staghorn).

The densities of snails recorded at this site in the San Blas are comparable to those recorded at the East Site in Jamaica, where the role of *Coralliophila* was so conspicuous. One of us (JCL) has also observed that the few fragments of *A. cervicornis* that survived the Fall, 1987 bleaching event between −9 and −12 m at Lee Stocking Island, Bahamas, were the apparent focus of attack by *Coralliophila* in January, 1988.

Thus events such as those documented in detail for Jamaica are likely to be a regular feature of the biology of *A. cervicornis*, due to its susceptibility to occasional catastrophic mortality. Sources of mortality include not only acute wave damage as documented for Jamaica (Woodley et al., 1981), but other agents such as temperature extremes, foul water, and certain epidemic diseases, to which *A. cervicornis* is particularly sensitive (Mayer, 1903, 1914; Stoddart, 1963; Porter et al., 1982; Bak and Criens, 1982; van Duyl, 1982, 1985; Peters, 1984). Reefs might also respond dramatically to slight decreases in staghorn growth rates (e.g., through reductions in light levels, to which the species is notably sensitive; Rogers, 1979) or minor increases in predator abundances or human disturbance (the latter suggested by van Duyl, 1985, Chavez et al., 1985, and Ramírez, 1986, as the reason for the declines of staghorn reefs in Curaçao and Bonaire, the Yucatán Peninsula and Colombia respectively). These shifts could result in a transition from a double to single, low equilibrium condition if predation levels were already relatively high (Figure 17, e.g., high predation with high growth vs. high predation with low growth).

Similar patterns may be characteristic of the congener *A. palmata*. Like staghorn, it grows rapidly (Bak, 1976; Gladfelter et al., 1978) and is susceptible to occasional severe mortality from storms (Stoddart, 1963; Roberts, 1974; Woodley et al., 1981; Rogers et al., 1982) and disease (Gladfelter, 1982; Peters et al., 1983; Peters, 1984; Dustan, 1987). It also suffers from predation by the predators on staghorn (Glynn, 1962; Bak and van Eys, 1975; Waldner and Robertson, 1980; Brawley and Adey, 1982). Historical and paleontological records indicate that *A. palmata* can decline markedly in areas where it was formerly abundant. In the Dry Tortugas, coverage fell from 44 hectares to less than 600 m² between 1881 and 1976 (Davis, 1982); in Barbados the species has been uncommon for at least forty years, but was abundant in 1918 and forms a major part of the reef framework dating back to 2,300 years B.P. (Lewis, 1984). *Acropora palmata* differs from staghorn, however, in an apparently greater ability to recover via sexual recruitment

(Stoddart, 1969, 1974; Rosesmyth, 1984; pers. obs.; and by cautious extrapolation from patterns discussed in Wallace, 1985), and may thus rebound more reliably from low abundances (e.g., in Figure 17 for the combination of high growth, high recruitment, and low predation).

Currently, the kinds of interactions we suggest for *A. cervicornis* may also be occurring with other coral species along the Jamaican north coast, now that coral percent cover is generally so low. At the East Site in 1986 and 1987, for example, 66% of the *Coralliophila* were found on *Agaricia agaricites* (Table 4, column 8, rows 5–6), which represented less than 4% of the coral cover (Figure 16c); this species of coral has declined significantly since 1982 (see above). These data caution against assuming that the increase in algal biomass is necessarily alone responsible for the species-specific patterns of mortality observed since the die-off of *D. antillarum* (e.g., de Ruyter van Steveninck and Bak, 1986; Hughes, 1989).

Glynn's (1985a,b) study of the increased importance of predation on eastern Pacific reefs following massive coral mortality from an unusually severe El Niño is strikingly parallel in its pattern and implications to our own. Suggestively, the dominant coral on these reefs, *Pocillopora damicornis*, also has relatively rapid growth, little larval recruitment, and is a preferred prey of some of the important predators (Glynn et al., 1972; Richmond, 1985).

Other candidates may include some of the extensively fragmenting, Indo-Pacific acroporids. For example, *A. longicyathus* and *A. horrida* recruit rarely, may be very abundant or absent in preferred habitats, and have high adult mortality rates from predation (Wallace, 1985), although the species were not studied from the perspective presented here. Colin (1987) discusses and illustrates gardening by *Stegastes nigricans* on large, monospecific beds of an unidentified, staghorn *Acropora* in Enewetak. The patterns are strikingly similar to those produced by *S. planifrons* in areas dominated by *A. cervicornis* (e.g., compare Colin's fig. 24 with Kaufman's (1977) fig. 11). One of us (NK) also observed elevated densities of the predator *Drupella* on staghorn survivors of an *Acanthaster* outbreak, compared with staghorn from areas not recently affected by the starfish (1988, central Great Barrier Reef).

In general, *A. cervicornis* and species like it pose problems for ecologists trying to interpret patterns of abundance and diversity. Post-hoc studies demonstrating marked changes in abundance in such species (including those based on paleontological data) cannot alone be used to infer large, permanent changes in environmental conditions; transitory or minor environmental events, difficult to reconstruct after the fact, can potentially trigger long term and substantial changes in abundance. Similarly, studies that ignore the biology of these potential dominants are unlikely to explain observed patterns of diversity correctly.

*Note added to proof:* See Lang et al. (in press) for a brief review of catastrophic effects of Hurricane Gilbert (12 Sep 1988) on staghorn coral populations in Discovery Bay.

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