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A LONG-TERM STUDY OF COMPETITION AND DIVERSITY OF CORALS

Joseph H. Connell,[1,4] Terence P. Hughes,[2] Carden C. Wallace,[3] Jason E. Tanner,[2] Kyle E. Harms,[1] and Alexander M. Kerr[1,2]

[1]*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2]*Department of Marine Biology, James Cook University, Townsville, Queensland 4810, Australia*
[3]*Museum of Tropical Queensland, Townsville, Queensland 4810, Australia*

Abstract. Variations in interspecific competition, abundance, and alpha and beta diversities of corals were studied from 1962 to 2000 at different localities on the reef at Heron Island, Great Barrier Reef, Australia. Reductions in abundance and diversity were caused by direct damage by storms and elimination in competition. Recovery after such reductions was influenced by differences in the size of the species pools of recruits, and in contrasting competitive processes in different environments. In some places, the species pool of coral larval recruits is very low, so species richness (S) and diversity (D) never rise very high. At other sites, this species pool of recruits is larger, and S and D soon rise to high levels. After five different hurricanes destroyed corals at some sites during the 38-year period, recovery times of S and D ranged from 3 to 25 years. One reason for the variety of recovery times is that the physical environment was sometimes so drastically changed during the hurricane that a long period was required to return it to a habitat suitable for corals. Once S and D have peaked during recolonization, they may either remain at a high level, or decline. In shallow water, with no deleterious changes in environmental conditions, S and D may not decline over time, because superior competitors cannot overtop inferior competitors without exposing themselves to deleterious aerial exposure at low tide. At other times and places, S and D did decline over time. One cause of this was a gradual deterioration of the physical environment, as corals grew upward into the intertidal region and died of exposure. S and D also fell because the wave action in hurricanes either killed colonies in whole or part, or changed the drainage patterns over the reef crest, leaving corals high and dry at low tide. At deeper sites, declines in S and D were sometimes caused by heavy wave action, or by interspecific competition, as some corals overgrew or overtopped their neighbors and eliminated them.

Key words: *algae; alpha and beta diversity; community dynamics; competition; corals; cyclones; disturbance; Great Barrier Reef, Australia; hurricanes; mortality; recruitment; species richness.*

INTRODUCTION

A fundamental question asked by ecologists and those interested in conservation is: ''What factors determine the level of diversity?'' Both natural processes and human activities that destroy habitats and organisms may reduce diversity. To evaluate the effects of human impacts, it is first necessary to understand the effects of natural processes. Natural disturbances such as violent storms, temperature extremes, and outbreaks of predators, pests, and diseases, as well as interspecific competition that could eliminate competitively inferior species, all tend to reduce local abundance and diversity, while recruitment and growth tend to increase it. Given that assemblages of corals often have high species diversity, the question of interest in the present study is: What factors determine it?

Our objectives were as follows. First, we will describe changes over 38 years in abundance, distribution, and recruitment of corals and macroalgae, under different environmental conditions. Second, we will describe interspecific competition, species composition, and diversity of corals. We measured species richness (S), the number of species per unit area, and diversity (D), an index based on the relative abundances of the different species. We calculated diversity at a single site (alpha diversity), and also the difference in species composition among two or more sites or times (beta diversity; Whittaker 1967). Third, we tested several hypotheses that could explain some of the mechanisms that produce these patterns in competition, alpha and beta diversity, and species composition.

Mechanisms affecting interspecific competition

Given that interspecific competition can eliminate colonies and so reduce abundance, S, and D, it is important to understand the conditions that determine its occurrence and strength. Interspecific competition for space in sessile marine invertebrates such as corals, barnacles, ascidians, etc., may take either of two forms. These are direct aggressive behavior, e.g., by overgrowth, shading by overtopping, digestion by mesenterial filaments, etc., or indirect defensive behavior, by

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[4] E-mail: connell@lifesci.ucsb.edu

preemption of space, i.e., defending it against encroachment by settling larvae or growth of neighbors (Connell 1961, 1973, 1976, 1983, 1990, Connell and Keough 1985, Lang and Chornesky 1990). Coral colonies may win over their neighbors because of inherent traits (e.g., age, size, ontogeny, growth rate, morphology, and aggressive ability), and/or because of the local environmental conditions, e.g., depth, time since last disturbance, recent weather, etc. (Connell 1973, 1976, Johnston et al. 1981, Bak et al. 1982, Connell and Keough 1985, Alino et al. 1992, Genin et al. 1994).

We tested the following hypotheses concerning interspecific competition in corals: (1) Regardless of their abundance, species may differ in their inherent ability to win in competition with neighbors. (2) Since competition for space takes place only between near neighbors, it would be expected to occur more often when coral cover was high. (3) Larger colonies might be expected to win over smaller ones more often than expected by chance. (4) Survival should be longest for those colonies that did not compete, less so for winners, and shortest for losers. (5) Commoner species would be expected to have more interactions with neighbors than would more rare ones. (6) Those species that engaged in more interactions should develop a greater degree of competitive ability, and so win a higher proportion of them. (7) If hypothesis 6 is true, then commoner species might be expected to win a greater proportion of their encounters than rare species would. (8) Because competition presumably requires the expenditure of energy, it will reduce the growth rate of colonies. (9) If competition is important in determining abundance, species superior in competitive ability should be commoner than those of inferior competitive ability.

Mechanisms affecting alpha and beta diversity

The intermediate disturbance model of diversity.—The intermediate disturbance model (Horn 1975, Connell 1978) predicts that diversity (*S* or *D*) will be lower in: (1) regimes of either high or low frequency of disturbance, or (2) very soon after, or very long after, a severe disturbance. In contrast, *S* or *D* will be higher in a disturbance regime of intermediate frequency, or at an intermediate time after a severe disturbance. The reasoning underlying this model is that abundance (both numbers of genets and cover), and therefore *S* and *D*, will be low in regimes of high disturbance frequency or very soon after a disturbance. With intermediate frequencies of disturbance or at an intermediate time after a disturbance, abundance, and therefore *S* and *D*, will have had time to increase. However, if a long time has passed after a disturbance, or in regimes of very low frequency of disturbances, we predicted that at the scale of our study, areas abundance will have increased until asymmetrical interspecific competition is strong enough to reduce and/or eliminate inferior competitors, causing *S* and *D* to fall. The model does not apply if interspecific competition is not strong, or is symmetrical (i.e., species are equivalent in competitive ability). In that case, *S* and *D* will not necessarily fall as abundance increases to high levels.

Compensation among species.—Compensation is defined here as any process that counteracts the effects of competitive superiority of some species over others (Connell 1978). For example, if inferior competitors are favored because predators preferentially attack the superior competitors, this would tend to keep the former from being reduced to low levels, even to local extinction, and so would tend to promote *S* and *D*. Any reduction in recruitment, growth, survival, or abundance of the superior species, relative to that of the inferior species, would be evidence of compensation.

Frequency dependence among species.—If the relative abundances of the more rare species increase while those of the commoner species decrease over an interval, *S* and *D* should be maintained. Such negative frequency dependence equalizes relative abundances, and thus reduces both the probability of local extinction of more rare species and the chance that commoner species will increasingly preempt space. The same applies if the recruitment rate of more rare species is greater than that of the commoner species.

Recruitment limitation.—The coral assemblage in some areas, particularly at the Inner Flat site, has many fewer species than at the other study sites. One possible explanation is that the recruitment rate of all species is much lower in some sites, thereby constraining their species pools. We also investigated the possibility that certain species might recruit less commonly at some sites than at others, again implying that limitation of recruitment could explain low *S* and *D* in the former sites.

Beta diversity.—To estimate variation in species composition over space and time, we calculated the degree of difference in species composition between study areas, which Whittaker (1967) called beta diversity. Two different locations could have the same alpha diversity, but if their species compositions were very different, the total diversity of both locations combined would be higher than if their species compositions were similar. We also extended the concept of beta diversity to time, comparing the species composition at different times at the same place.

METHODS

Study areas

Heron Island, Queensland, at 23°26′ S, 151°55′ E, is near the southern end of the Great Barrier Reef (Fig. 1), 65 km east of mainland Australia. It is a platform reef ~11 × 5 km in size, with outer slopes surrounding an almost flat upper surface, much of which is occupied by intertidal reef flats and a lagoon ranging from 1 to 8 m depth at low tide (Maxwell et al. 1964, Jell and Flood 1978). The outer edge of the platform is slightly

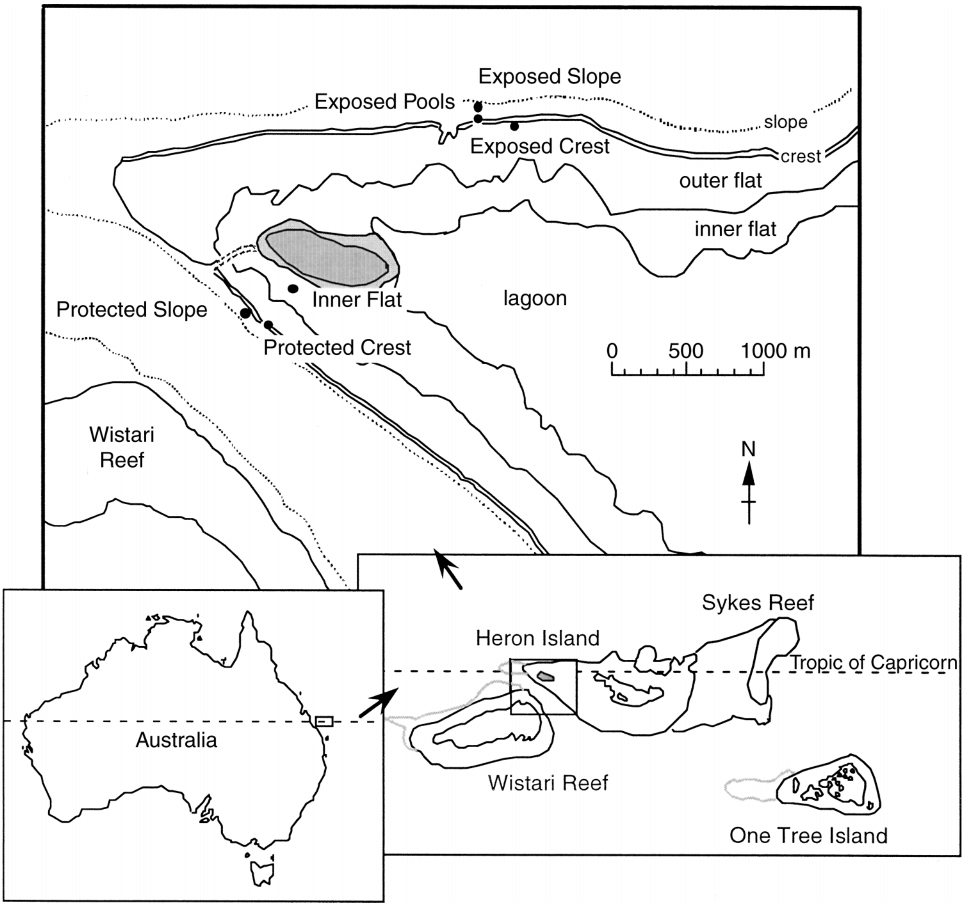

FIG. 1. Map of study areas on Heron Island reef, Great Barrier Reef, Australia. Dashed lines to the southwest of the island indicate a boat channel first dredged in 1966.

elevated to form an intertidal reef rim or crest, which retains a shallow pool of water over the outer and inner reef flat at low tide. There is a vegetated island or cay of ~19 ha near the west end of the reef. The climate, weather, occurrences of hurricanes, tidal amplitude, and currents are all described in detail in Connell et al. (1997).

We established permanent study areas in different habitats arrayed across the reef, from the inner reef flat close to the island, to the outer reef flat, reef crest, and beyond to shallow intertidal pools, and finally to the outer slopes (Fig. 1). There are several sites within each study area, each with samples in the form of permanently marked 1-m^2 quadrats, line-intercept transects, or belt transects. Three of the study areas were on the north (exposed) edge of Heron Island reef, where they were occasionally subjected to extreme wave forces during hurricanes (Fig. 1, Appendix A). These three study areas differed in depth: the Exposed Crest was uncovered at most low tides, the Exposed Pools, ~30 m seaward in a large intertidal pool, remain 0.5 m deep at the lowest tides, and the Exposed Slope site, ~20 m further offshore of the Exposed Pools, extended subtidally from 1 to 14 m depth. Two other study areas were on the opposite, southwestern, rim of the reef, which is sheltered by nearby Wistari reef from waves generated both by the SE trade winds, and by most of the extreme wave action of hurricanes. The Protected Crest was uncovered by most low tides, and, ~200 m west of it, the subtidal Protected Slope, on which sampling extended from 1 to 10 m depth. On this protected slope, tidal currents are swift, being channeled between Heron and Wistari reefs (Fig. 1). The protected Inner Reef Flat was ~350 m north towards the island from the Protected Crest site, and 70 m south of the shore of the cay (Fig. 1, Appendix A). This area is sandy and shallow, and it is likely to be a harsher physical environment for corals than the other five study habitats. Also, water temperatures fluctuate more and currents are slower, sedimentation rates are higher, and oxygen tension varies more widely, than on outer reef locations (Kinsey and Kinsey 1967, Potts and Swart 1984). In addition, nutrients from sea birds and humans are added to the Inner Reef Flat via seepage from the island, particularly close to the island (Staunton Smith and Johnson 1995). We also sampled the middle and outer portions of the south reef flat between the Inner Flat and the Protected Crest.

Estimates of abundance, spatial distribution, recruitment, and species composition of corals and macroalgae

Demography at the scale of individual corals.—To permanently locate coral assemblages for long-term study of individual colonies, we established replicate 1-m^2 quadrats using stakes (steel reinforcing bars, 9 mm diameter) driven in at the four corners. These quadrats were placed in one or more study sites within four of the study areas (Appendix A). At three of the study areas (Inner Flat, Protected Crest, and Exposed Crest) some of the permanent 1-m^2 quadrats were placed contiguously; this has the advantage of a smaller ratio of edge to area. At low tide, color slide photographs were taken of these 1-m^2 quadrats from vertically above, using a 35 mm SLR camera mounted on a tripod attached to a 1-m^2 frame that fitted over the steel stakes. Thus, photographs at different dates were comparable, being taken from the same position (see Connell, 1979, for a series of these photographs). Thirty-six visits to Heron Island were made in 26 of the 38 years between 1962 and 2000 (Appendix A). Photographs were taken in the months of July through February; most were taken in August through October. A complete set was available for all of the permanently marked quadrats for 23 of the 26 years in which censuses were made. In two yearly periods, September 1962–October 1963, and August 1971–September 1972, photographs were taken at intervals of 1 to 3 mo; all others were taken at intervals of 1 to 2 yr. All corals were either identified to species in the field, or a specimen was collected from a nearby colony of the same species outside the quadrat, for later identification in the laboratory.

Each color slide was projected, and the boundaries of all coral colonies and clumps of macroalgae were traced to make a map at a scale of 30–50% of the original size. The corals were mainly scleractinians, but also included a few stony hydrozoans and soft corals (zoanthids, alcyonarians; see the species list in Appendix B). Coral colonies or algal clumps greater than ~0.5 cm^2 in area were discernible in the photographs; each was given a permanent number on the map when it first appeared, and was used on the maps of each successive census until it died. Thus, dates of first appearance (recruitment) and of death were recorded for each individual colony. To measure growth and percent cover, the projected horizontal area of each individual was measured with a digitizer program (tpsDig, version 1.31, F. J. Rohlf) at each census. A total of 8031 coral colonies were mapped and measured in successive censuses from 1 to 23 times each during the study period, with a total of 16 200 measurements. Areas of algal clumps, sand, rubble, and ‘‘free space,’’ i.e., solid substrate unoccupied by corals or algae, were also measured. Encrusting coralline algae were treated as free space, since corals and other invertebrates readily settle on them (Morse et al. 1988). Truly bare hard substrate probably occurs only briefly after storms or grazing, and is quickly reoccupied by sessile microorganisms.

Coral genets (individuals presumably derived from a single larva and genetically distinct) can undergo fission or fragmentation into separate daughter colonies called ramets. Each new coral colony that appeared on the permanent quadrats after the first census was presumed to be a distinct genet, unless it had clearly fissioned or broken off from an existing one. However, some colonies present at the first census of each permanent quadrat may have undergone fission previously. To identify which colonies in the original census of each quadrat were genets, we evaluated each instance in which there were two or more nearby coral colonies of the same species, and decided, from their color, shape, relative positions, and remains of skeletal connections, whether they were likely to be daughter colonies of the same genet. We judge that, of the 8031 individual colonies recorded between 1962 and 2000 on the permanent quadrats, over 95% were correctly identified as individual genets.

Abundance at larger scales.—To estimate abundance within particular habitats at spatial scales larger than individual m^2 quadrats, and to detect spatial autocorrelation, we used additional m^2 quadrats and belt and line transects, spaced up to 800 m apart within each study area. We also sampled the subtidal Exposed and Protected Slope study areas, by laying out down the slope, at 10-m intervals measured along the slope, a series of 20-m line transects parallel to the reef crest (Appendix A). These transects were relocated within 1–2 m of their previous location, using depth and natural features of the substrate, and sampled 10 times between 1972 and 2000. Since the tape was stretched taut over the corals, the length of tape intercepted by living organisms, unoccupied hard substrate, and sand/rubble, yielded estimates of horizontally projected percent cover, the same measure as in the photographs. We also used data collected by P. M. J. Woodhead, using three belt transects at depths of 3 to 5 m on the Exposed Slope in 1970 and 1971 (see Pearson 1981: Table 1).

In 1976, we established a permanent belt transect, 1.5 × 23 m, at the Exposed Crest study area to obtain adequate sample sizes after a hurricane in 1972 killed almost all corals over a large area of this crest. A second belt transect, 1 × 17 m, was established in 1978, 300 m east of the first on the same crest (Appendix A). At each census we sketched the position, and measured the maximum length × width, of all coral colonies larger than 1 cm in diameter; the area of each colony was calculated, assuming it had an ellipsoid shape. In these crest transects, plus those on the subtidal slopes, we made 8030 measurements of 3,250 colonies. We also analyzed a belt transect that had been sampled in the same way in 1969 by J. F. Grassle (*unpublished* *data*), near the permanent quadrats on the Inner Flat. In 1983, we sampled sites on the inner, middle, and outer south reef flat with large-scale photographs, each covering 3 × 5 m. A series of these overlapping photographs was made that covered a total area of 16 × 40 m at each site. Since these sites were sampled in the same way, and extend over much larger areas than the other sites, they are most comparable to each other. The number and dimensions of all transects and photographs, with the dates of sampling them, are shown in Appendix A.

Calculations of abundance, and rates of recruitment, growth, and mortality.—The abundance of corals at each census was calculated in several ways. Population density was expressed as the numbers of genets or colonies per unit area for quadrats or belt transects, or per unit length on the line transects. However, population density does not usually yield an accurate estimate of the degree to which corals occupy space, since colony size varies greatly, from <1 cm^2 to $>50\,000$ m^2, although $>90\%$ of the colonies were <200 cm^2. Therefore, we also calculated the percent cover of living corals and algae, as the percentage of either the area of a quadrat or belt transect, or the length along a line transect.

The recruitment, growth, and mortality rates of the corals were calculated from the sequential sets of photographs of the permanent quadrats, or from maps made at successive censuses of the permanently marked belt transects at the Exposed Crest. Recruits at each census were defined as new colonies that had arrived since the previous census and had survived until the present one. They arrived as propagules, mostly as larvae from the plankton, or as fragments carried from elsewhere. We did not include as recruits the daughter colonies produced by fission from existing colonies, since they remain adjacent and do not disperse, in contrast to the fragments. Recruits ranged in age from at least 6 mo after initial settlement (which corresponds to the approximate time required to grow to 0.5 cm diameter, the minimum size discernible in the photographs), up to 4 yr old, the longest interval between successive censuses. The mean interval was 1.45 ± 0.14 yr (±1 SE), median 1.08; all but one interval was <2.5 yr. The rate of recruitment was standardized as the number per square meter per year. The rate of growth (positive or negative) was measured as the change in area of each colony per unit of time, and of mortality, as the complete disappearance of colonies over time.

Competitive interactions between corals

Corals compete directly, for example, by overtopping, overgrowing, or digesting neighbors, or indirectly, such as by preempting space and so excluding larval settlers or encroachment by neighbors. We estimated the amount of the aforementioned direct competitive interactions between coral colonies by examining the maps for instances of junctures, in which either the border of a neighboring colony grew, or a new colony recruited, to within ~2 cm of another. We assumed that, within this distance, corals could interact, either with tentacles or mesenterial filaments. Some of these ''encounters'' were judged to be standoffs, if, over the succeeding interval of at least one year, the position of the borders of the colonies along this juncture either did not change position, or both borders retreated, or if each grew over the other at different places along the juncture. In that case, the neighbors were assumed to be equal in competitive ability (Connell 1976, Connell and Keough 1985). If, on the other hand, the edge of one colony advanced over some or all of the area formerly occupied by the second, this was scored as a win for the former, a loss for the latter. In some instances, the edge of one colony retreated but that of the other did not advance; this was not scored as an encounter. No pair of colonies was scored more than once, except when there was a standoff over one interval and a win or loss over the next interval (or vice versa).

For each species, we calculated the per capita rate of competition as the number of interactions recorded per 100 genets observed per square meter per census. Since encounters seldom occurred at the Inner Flat site, analyses of competition were made only at the other three sites with permanent quadrats. To judge whether interactions between particular pairs of species were asymmetrical (i.e., one species consistently won over the other), or not, and thus to investigate the degree to which competition was hierarchical and transitive, we tallied them as follows: When there was a clear winner, we assigned the winner a 1 and the loser a 0; a standoff was scored as a tie and assigned 0.5 win to each member of the pair (Connell and Keough 1985). We then applied the Binomial test to all pairs of species with at least six interactions, using a level of significance of $P < 0.05$. Since the direction of the outcome was not predicted, two-tailed probabilities were used.

To test the hypotheses about competition listed in the *Introduction*, we summarized the data for all the observed encounters between corals over all years in the study period as a matrix of the interactions among species at each site at each quadrat (Appendices C, D, and E). We also used the matrices to describe the competition in two other ways. First, to compare species, we tallied the outcome of interactions of each species with each of the other species, calculated the percentage of wins in the total of wins and losses (excluding standoffs), and used these percentages to rank species in competitive ability. We also used the percentage of wins to estimate how the competitive ability of species varied among different reef sites, as well as how colony size and species abundance affected its outcome. Second, we calculated the degree of complexity of the competitive interactions at each study site. In such a matrix of interactions, a greater proportion of symmetrical pairs, with many pairs equivalent in competitive ability, results in a more complex web with more links than if the species interacted in a strictly hierarchical manner. We calculated this proportion using only those competing species pairs with a reasonable sample size ($\geq$5 observed interactions). Last, we compared the abundances of superior competitor species and inferior competitor species at the start of the study.

We analyzed the effects of competition on coral growth rate by regressing, over all colonies at a site, percentage of change in area covered per year, against initial area of that colony. We did this for each of four groups of colonies: (1) those that were not observed to interact, (2) winners, those that won more often than they lost, (3) those that engaged only in standoffs, and (4) losers, those that lost more often than they won. If competition reduces growth, either because winners directly reduced the cover of losers, or because the competitive process used energy that would otherwise have contributed to growth, then growth would be expected to decline in the numerical order given.

Alpha diversity

Descriptions of species richness and diversity.—Species diversity at one place in space and time, i.e., alpha diversity, was calculated in several ways. The simplest index of diversity is species richness, *S*, the number of species in a sample. We also calculated indices of diversity using the relative abundances of the different species. (Relative abundance is defined as the abundance of a particular taxon of corals divided by the total abundance of all corals.) We used the reciprocal of Simpson's index: $D = 1/\Sigma p_i^2$, in which relative abundance $p_i = n_i/\Sigma n_i$, and n_i refers to either the number of genets, or area covered, of species *i* in the sample. *D* represents the number of equally abundant species that would yield that diversity. In contrast to *S* or another commonly used index, $H = -\Sigma(p_i \log p_i)$, *D* is less sensitive to variation in the more rare species (Peet 1974, Magurran 1988). To compare the effects of sample size on *S* and *D* for corals in our present study, we regressed each of these indices against the number of genets, over all censuses at each site.

Because the area sampled varied among sites (Appendix A), to aid in comparing sites we calculated the percent cover, density, species richness, and diversity of corals for each m^2 quadrat on the permanently marked sites, then calculated the average and variance over all quadrats at that site. In addition, we calculated the overall species richness and diversity for each site from the combined data from all samples. We also used these various samples to discuss effects of variation in spatial scale (Connell et al. 1997), and to calculate beta diversity. To compare the species richness of the permanent quadrats with that on the belt or line transects, we tallied the number of species encountered on the transect for the same number of colonies found on the quadrat.

Hypotheses about mechanisms affecting alpha diversity

The intermediate disturbance model of diversity.—We tested two predictions of this model. First, at the scale of our study areas (several to few hundreds of square meters), *S* and *D* of corals will rise then fall with time after a severe disturbance. Second, *S* and *D* of corals will be lower at either low or high coral cover than at intermediate coral cover. The prediction that *S* and *D* will be smaller at low cover than at intermediate cover is not of great interest, since it can hardly be otherwise; after a drastic reduction in cover, *S* and *D* almost certainly will rise as recolonization increases coral abundance. However, the prediction that *S* and *D* will be less at high cover than at intermediate cover is more interesting, since it suggests possible mechanisms, such as strong and asymmetrical interspecific competition, species-specific preference among natural enemies, or random mortality among species and subsequent dominance by a few. Therefore, we tested only the latter prediction of the hypothesis, lower *S* and *D* at high cover than at intermediate cover. Since we were not testing the prediction that *S* and *D* increases from low to intermediate cover, we omitted all censuses with low ($<$20%) cover. The remaining censuses at each site were then divided into two sets, intermediate and high cover, each with equal numbers of censuses, and the means of *S* and *D* for the two sets were compared with a *t* test.

Compensation among species.—Evidence of compensation would be the abundance, or rates of recruitment, growth, or survival of the superior species during an interval, being equal to or less than those of the inferior species. If so, this would indicate that the inferior competitor either won over, or did not lose to, the superior competitor. We tested for the existence of compensation by first identifying the species of superior and inferior competitors by ranking the species in competitive ability, based on the numbers of wins, losses, and standoffs summarized in the matrices described in subsection *Competitive interactions between corals.* Superior competitors were defined as those that had won at least half their encounters with neighbors (excluding standoffs/ties); inferior competitors had won less than half. Competitive rankings are shown in Appendices C, D, and E.

We analyzed for the existence of compensation in two different processes: recruitment and changes in relative abundance. For recruitment, we compared the recruitment rates of the groups of superior and inferior competitors for each census interval. For each group, the relative recruitment rate (per unit area of adults) was calculated for each interval by dividing the absolute rate (number of new recruits in the given interval per square meter per year) by the abundance (cover) of adults of that group at the start of the interval. This is analogous to a per capita rate, but is superior for clonal organisms that reproduce as a function of number of modules, as in corals. If there were no compensation, the recruitment rate for each group should be unrelated to competitive ability. However, if compensation were occurring, the inferior group would have an equal or higher per capita recruitment rate than the superior group. (This procedure assumes that the two groups do not differ in their preference for recruiting near or far from their conspecific adults.) Abundance of adults was calculated in either of two ways: First, it was calculated as the percent cover at the focal site, which assumes that larvae do not disperse far from their parents. Second, it was calculated as the average of the cover at the three sites on the outer reef, which assumes that larvae could disperse considerable distances, so that they could have been produced anywhere on the western portion of Heron reef. In the field or in our photographs, recruits are visible at 0.5 cm^2, at about the age of 6 mo, and are identifiable to species at about the age of 1 yr. Therefore, we assumed that using the cover of resident corals at the start of the interval was the best index of abundance of those adults that produced the recruits. (Recruits not identifiable to species were not included in this analysis.)

A second analysis for compensation compared the changes in relative abundances of the superior and inferior competitor groups over each census interval. If this form of compensation were occurring, the abundance of the group of inferior competitors should stay constant or increase, relative to that of the superior competitors, during the interval. To estimate the frequency of occurrence of compensation, we calculated the percentage of change in abundance of the superior group minus that of the inferior group, for each census interval. If this difference was negative or $<10\%$ positive, inferior species were either increasing or remaining approximately constant, relative to the superior species, indicating that compensation was occurring.

We hypothesized that during periods when coral cover as a whole was high or increasing, colonies were likely to be in close proximity, so competition would ensue. As a result, superior competitors should win, and so should increase in relative abundance (the opposite of compensation). In contrast, when coral cover as a whole was either low or decreasing or remaining constant, competition is less likely. Therefore, the relative abundance of inferior competitors should either increase or stay constant (i.e., compensation should occur). We tested this hypothesis by tabulating the number of intervals when competition occurred or not, in relation to the change in total cover during the interval.

Frequency dependence among species.—If the relative abundances of the more rare species increase while those of the commoner species decrease over a time interval, thus tending to equalize relative abundances of species, S and D will be maintained or increased. Such negative frequency dependence reduces both the probability of local extinction of more rare species and the chance that commoner species will increasingly preempt space. The same applies if the recruitment rate of more rare species is greater than that of the commoner species.

We investigated the possibility of frequency dependence in two ways. First, we regressed the relative abundance of each species (in either numbers or area of colonies) at the end of a period (Y) against that at the start (X). If the slope of the regression was significantly <1.0, negative frequency dependence was occurring, i.e., the relative abundances of the more rare species had increased while those of the commoner species had decreased during the interval. If the slope was greater than or not significantly different from 1.0, negative frequency dependence was not occurring. We did such tests over the short time scale of the interval between successive censuses, and over the longer time scale of the entire study period. Second, for each census, we regressed the per capita number of recruits (recruits divided by the percent cover of conspecific adults in the previous census) against the percent cover of conspecific adults in the previous census. If the slope of this regression is significantly negative when adjusted for multiple comparisons, frequency dependence is occurring. We reasoned that, while it is extremely unlikely that these particular adults were the parents of those recruits, they represent our best estimate of the abundance of the true parents.

Recruitment limitation.—Perhaps individual species are specialized to recruit more successfully in certain habitats than in others. For example, the coral assemblage in some areas, particularly at the Inner Flat site, has many fewer species than at the other study sites. To test the hypothesis that this difference in species richness is due to recruitment limitation, we compared both the numbers, and the number of species, of recruits among all sites. We also investigated whether some species recruit more commonly at certain sites than at others, which could account for some of the variation in species composition among sites. The hypothesis predicts that sites with fewer numbers or species of recruits will have lower species richness of resident corals.

Limitation by mortality.—An alternative explanation for the low S at the Inner Flat is that it is due to poorer survival of corals there than at other sites. To test this hypothesis, we transplanted, from the Outer Flat to the Inner Flat, adult colonies of species either rare or common on the Inner Flat, and followed their survival; we transplanted several species of both of these types. As a control for handling during the transplanting process, as we carried the colonies into the inner flat, we paused at the halfway point and split each colony in half. Then we carried one half of each colony back to the outer flat and placed them in a control plot near where they were collected originally. These genetically identical controls, handled equally but not transplanted, were necessary to indicate whether the process of transplanting itself affected the two groups differently. The other experimental halves were carried on into the inner flat and placed in the experimental plot. Since there is little wave action on the reef flat, and many of the older corals there are not attached to the substrate, it was not necessary to attach the transplanted corals. This experiment was duplicated on both the north and south sides of Heron reef. The hypothesis predicts that species seldom found on the inner flat should survive more poorly there than those commonly found there naturally.

Spatial variation in species composition: beta diversity

Up to this point, we have calculated diversity for a single location or time. To estimate spatial variation in diversity and species composition, we averaged abundance data for each species of resident corals (number of genets or percent cover), over all quadrats at each study site, for each census on Heron Island reef. We then compared different sites, using the relative abundances of species from the combined data at each site, averaged over all censuses. We calculated the degree of difference in species composition between study areas, which Whittaker (1967) called beta diversity. Two different locations could have the same alpha diversity, but if their species compositions were very different, the total diversity of both locations combined would be higher than if their species compositions were similar. We used the average abundance of each species over all samples within each location and calculated beta diversity using the percentage similarity index (PS), which compares the relative abundance of each species in two samples. The equation for this index is $\mathrm{PS} = \Sigma\min(P_{1i}, P_{2i})$ with P_{1i} being the percentage of species i in sample 1 (Wolda 1981). Since sampling differed among sites, the most useful comparisons were between sites having similar sampling regimes, such as the four sites with permanently marked quadrats. Since diversity is greater when coral species at different sites are less similar, we calculated an index of beta diversity as (100 − mean percentage of similarity).

We also assessed the similarity of recruits to resident coral assemblages in three tests. First, we calculated for each site the mean percent similarity across years of the number of recruit genets to the percent cover of residents of the same species from the previous year. (In clonal, colonial organisms such as corals, the number of recruit genets (larvae) produced by a species is proportional to the coverage (number of polyps) of conspecific colonies, and hence these are the appropriate units of comparison here.) These mean similarities within each site were compared via a two-tailed Student's *t* test (adjusted for multiple comparisons), to the similarities between recruits at the focal site and residents from distant sites. This comparison tests whether recruit composition at a site is more (or less) similar than expected to the local assemblage, than to assemblages at other sites. However, when the relative abundances of species in the two sites are compared, some of the difference may simply be due to the fact that some species are not shared between the two sites. In such a case, a lower between-site similarity could occur even though the species that are shared at the two sites all have identical relative abundances, as when recruits are drawn from a common larval pool. To distinguish between these possibilities, this first analysis was repeated using only species held in common at the two sites being compared. Significant results from the test using all species, and that using only those species held in common at the two sites, would indicate that higher within-site than between-site similarity of recruits to adults is independent of the difference in some species presence at only some sites. This might suggest that the latter may be experiencing very different recruitment dynamics from others in the community.

Significant results in these two tests may obtain under several relationships between recruits at a site and their local assemblage. For example, recruits may be more similar to their local assemblage than to more distant ones, but still quite dissimilar on average to the local assemblage, as when recruitment is local, but temporally variable between species. Hence, to see how closely the species composition of recruits at each site resembled that of their local residents, a third test was performed. For each site, the mean within-site percent similarity between recruits and residents of the previous year was calculated. The significance of this value was assessed via a two-tailed randomization test, that is, by noting the proportion of times the observed mean equaled and exceeded (or was less than) those garnered by randomly reassigning the number of recruit genets within years and across recruit species 10^4 times. This tests the hypothesis that within a site the recruit and resident assemblages are no more similar than expected by chance. If all tests find that recruits are significantly more similar to adults within than among sites, one must infer either that (1) most recruits were the offspring of site residents and dispersal distances are quite short, or that (2) recruits are drawn from a pool of larvae at a larger spatial scale, but recruit composition is determined by settlement preferences, or by post-settlement survival favoring larvae of the same species as local resident corals.

Temporal variation in species composition

We extended the concept of beta diversity to time, comparing the species composition over time at the same place, using the percentage similarity index. To estimate temporal variation in species composition, we first investigated how the relative abundances of corals differed after a complete change in genets, comparing the relative abundance of each species between the start and end of the 37-year study period. (We first excluded

TABLE 1. Per capita rates of interaction, the equivalence of competitive ability (standoff encounters), and the sizes of genets at three study areas at Heron Island, Great Barrier Reef, 1962–1990.

Sites	No. observations					Standoff encounters (%)	Genet size		
	Interactions	No. genets	No. square meters	Censuses	Overall mean observations†		Area (m^2)‡	1 SE	*N*
Exposed Pools	348	489	2	13.5	2.64	25*	36	3.85	489
Exposed Crest	382	537	3	12.66	1.87	30*	43	4.4	908
Protected Crest	276	952	2	17	0.85	51	17.5	1.64	1476

† Overall mean observations are the mean numbers of interactions per 100 genets per square meter per census.

‡ Tests for mean genet size: Exposed Crest vs. Protected Crest ($t = 6.31$, $P < 0.001$), Exposed Pools vs. Protected Crest ($t = 5.13$, $P < 0.002$), and Exposed Crest vs. Exposed Pools ($t = 1.05$, $P > 0.1$).

* Percentage significantly different from 50% by a binomial test ($P < 0.05$).

the single colony that had survived the whole period, so the comparison represents a complete change in the colonies of all species.) Second, to look for trends over the period, we compared, for each site, the abundances at the initial census to that at each subsequent census.

Third, we examined how often the identity of the dominant (most common) species changed from one census to the next. We tallied the numbers of such shifts, excluding any census that contained only one species, or in which there was no clear dominant, i.e., when the two common species were nearly equal, differing by <2%. Fourth, we used presence–absence data to measure the changes in all species at each site and at all sites combined. We tallied the proportion of species that (1) persisted throughout the study period, (2) went extinct, being present at the start but disappearing during the study period, (3) were transient, appearing and then disappearing during the study period, and (4) invaded, appearing after the start and persisting to the end. Such estimates are, in part, a function of the length of the study period; invaders in a short study could become transients in a longer study.

RESULTS

As outlined in the *Introduction*, we will first describe the variations that we observed among corals in interspecific competition, abundance, species composition, alpha diversity, and beta diversity, and use these results to test several hypotheses that could account for such variations over time and space.

Interspecific competition for space

We will first discuss the factors determining the overall rates of competition among corals, and then those determining its outcome. The absolute per capita intensity of competition varied among the study sites, being highest at the Exposed Pools, intermediate at the Exposed Crest, and least at the Protected Crest (Table 1). The lower per capita intensity at the Protected Crest may be due in part to the fact that genets are much smaller there, so that at the same density, they are less likely to encounter each other than where their size is larger (Table 1). Since competitive encounters occur only when the edges of colonies come into close proximity, the per capita rate of encounter between colonies would be expected to be a function of coral cover. For two of the three sites there was a strong positive correlation between coral cover and the per capita rate of encounter (Fig. 2). At the two sites showing a strong positive correlation (Exposed Pools and Exposed

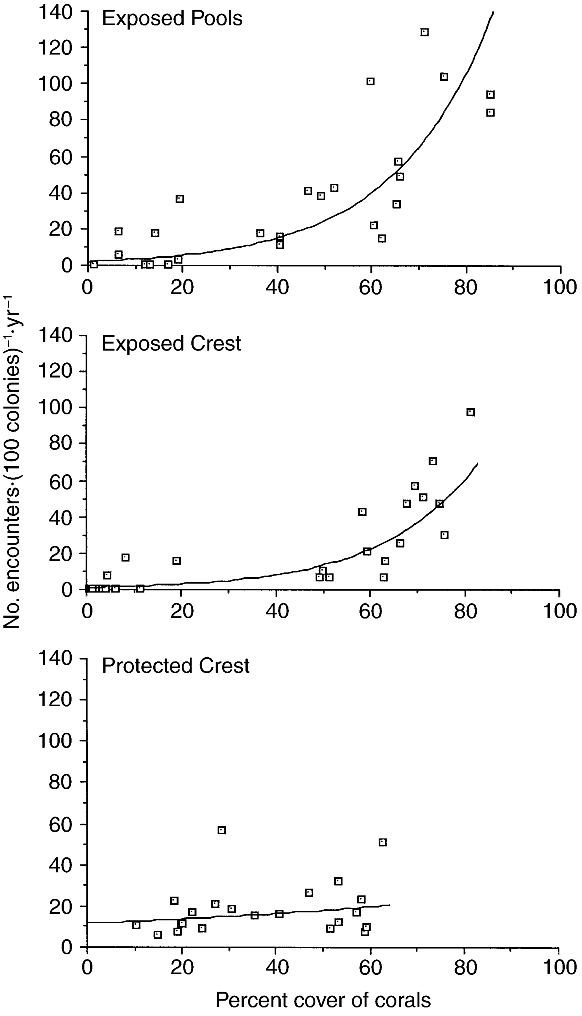

FIG. 2. Number of encounters between different coral colonies during the study period as a function of the percent cover of living corals at the start of each interval.

TABLE 2. Variation in competitive ability of corals among species and locations at Heron Island reef.

	Percentage of wins in interspecific encounters			No. encounters observed			
Species	Exposed Pools	Exposed Crest	Protected Crest	Exposed Pools	Exposed Crest	Protected Crest	χ^2 among sites
A) Species that were consistent in competitive ability among sites ($P > 0.05$, χ^2 among sites)							
Branching *Acropora* species with a high proportion of wins							
A. aspera	···	86	81	···	22	45	0.41
A. hyacinthus	82	86	69	77	37	14	1.57
A. millipora	80	72	64	5	40	32	1.14
A. digitifera	71	84	79	31	32	59	1.75
A. valida	62	80	40	32	5	10	2.57
Branching *Acropora* species with an intermediate proportion of wins							
A. humilis	27	39	33	11	31	15	0.49
A. cuneata	8	31	43	12	45	7	3.28
Species with a low proportion of wins							
Porites spp.	0	0	0	25	49	56	···
Montipora spp.	0	···	23	9	···	44	2.52
Stylophora pistillata	11	0	···	9	4	···	···
Soft corals	12	0	···	8	5	···	···
Unidentified small Scleractinia	0	0	10	39	27	20	···
B) Species that varied significantly in competitive ability among sites ($P \leq 0.05$ in the χ^2 among sites)							
Acropora nasuta	77	65	0	31	23	6	12.35*
Acropora robusta	···	92	57	···	39	7	6.47*
Pocillopora damicornis	5	29	67	59	45	6	19.75***

Note: Only species with ≥ 6 encounters (standoffs not included) at a site were included. Chi-square was calculated only where expected frequencies >1.

* $P < 0.05$; *** $P < 0.001$.

Crest), the per capita numbers of interactions were few until ∼50% cover was reached, and then they increased rapidly. The reason why the Protected Crest did not show a significant correlation was probably because cover there never exceeded 64%. When we used the same range of cover (0–64%) at all sites, only the Exposed Pools showed a significant positive correlation, suggesting that the Protected Crest might also show a correlation if the coral cover ever reached values higher than those found in the 37-year study period. Since cover was often low at all sites, some species never had any encounters with other corals in the quadrats.

In regard to the outcomes of competition, the 15 taxa with ≥ 6 encounters in at least two study sites were analyzed. Of these, 12 either won or lost consistently in competition among the different study sites, thus displaying inherent competitive abilities (Table 2). Five branching species of *Acropora* (*A. aspera*, *A. hyacinthus*, *A. millepora*, *A. digitifera*, and *A. valida*) consistently won the majority of encounters at all sites, although four of the five won least frequently at the Protected Crest (Table 2). Other taxa consistently won less than half of their encounters: *Acropora humilis*, *A. cuneata*, *Stylophora pistillata*, the encrusting *Montipora* species, soft coral species, and small unidentified corals. The sub-massive and encrusting *Porites* spp. lost every encounter at all sites (Table 2). In contrast, three of the species of corals analyzed varied significantly in competitive ability between locations. The branching *Acropora nasuta* and *A. robusta* won fewer encounters at the Protected Crest than elsewhere, whereas *Pocillopora damicornis* won more often there (Table 2).

In nine other species, ≥ 6 encounters were detected at only one site, so spatial variability in their competitive abilities could not be judged. Of these species, all four branching *Acropora* (*A. nobilis*, *A. austera*, *A. formosa*, and *A. tenuis*) won the majority of their encounters, as did the massive species *Plesiastrea versipora* and *Leptoria phrygia*. In contrast, the massive *Favites halicora* won only one of its four interactions. A single genet of the soft coral *Zoanthus vietnamensis* won 38 of 39 encounters, overgrowing the smaller scleractinian colonies encountered. These interactions occurred at the Protected Crest after 1980, when this site had gradually become drier, as described in Connell et al. (1997).

Each species was ranked in competitive ability, using the numbers of wins and losses. Branching *Acropora* species tended to be superior competitors over massive or encrusting species, although low-ranked species could sometimes stand off those ranked higher (Appendices C, D, and E). The frequency of competitive equivalence is an index of the degree of complexity of a web of competitive interactions. The Protected Crest had the most complex web, with about half of all interactions equivalent, i.e., with symmetrical competitive abilities (Table 1). The other two sites had less complex webs, with significantly less than half of the

TABLE 3. Tests of hypotheses concerning abundance and the occurrence of competition.

Site	Period	Dependent variable	Independent variable	Intercept	Slope	r^2	N	P
A) Species with more colonies have more competitive interactions than do rarer species. (Hypothesis not rejected at any site.)								
Exposed Crest	1963–1971	interactions/sp.	log(colonies/sp.)	2.53	17.58	0.472	28	<0.001
Exposed Pools	1969–1974	interactions/sp.	log(colonies/sp.)	−1.14	23.1	0.307	18	<0.02
Protected Crest	1969–1974	interactions/sp.	log(colonies/sp.)	−4.81	16.65	0.615	18	<0.001
B) Species with greater cover have more competitive interactions than do rarer species. (Hypothesis not rejected at any site.)								
Exposed Crest	1963–1971	interactions/sp.	log(cover/sp.)	−30.3	20.65	0.657	17	<0.001
Exposed Pools	1969–1974	interactions/sp.	log(cover/sp.)	−24.42	17.97	0.344	20	<0.01
Protected Crest	1969–1974	interactions/sp.	log(cover/sp.)	−42.08	29.57	0.588	20	<0.001
C) Species that interact more often have a higher proportion of wins in competition. (Hypothesis rejected at the Exposed Crest and Protected Crest, but accepted at the Exposed Pools.)								
Exposed Crest	1963–1971	no. wins − losses	log(interactions/sp.)	−1.92	2.7	0.044	28	>0.05
Exposed Pools	1969–1974	no. wins − losses	log(interactions/sp.)	−5.45	12.08	0.258	18	<0.05
Protected Crest	1969–1974	no. wins − losses	log(interactions/sp.)	−2.17	3.25	0.037	18	>0.10
D) Species that win more often than they lose during competitive encounters are commoner in number of colonies. (Hypothesis rejected at all sites.)								
Exposed Crest	1963–1971	log(colonies/sp.)	no. wins − losses	0.747	−0.02	0.138	17	>0.10
Exposed Pools	1969–1974	log(colonies/sp.)	no. wins − losses	0.573	−0.01	0.045	20	>0.10
Protected Crest	1969–1974	log(colonies/sp.)	no. wins − losses	0.774	0.008	0.027	18	>0.10
E) Species that win more often than they lose during competitive encounters are commoner in area covered. (Hypothesis rejected at all sites.)								
Exposed Crest	1963–1971	log(cover/sp.)	no. wins − losses	2.53	0.015	0.043	17	>0.10
Exposed Pools	1969–1974	log(cover/sp.)	no. wins − losses	1.92	0.004	0.011	20	>0.10
Protected Crest	1969–1974	log(cover/sp.)	no. wins − losses	2.17	0.016	0.037	20	>0.10

encounters equivalent; 30% at the Exposed Crest and 25% at the Exposed Pools were equivalent. The Protected Crest had fewer crevices and hollows, i.e., was more two dimensional than the Exposed Crest, which may account for its higher degree of competitive equivalence. If overgrowth competition is important in determining abundance, species superior in competitive ability should be commoner than those of inferior competitive ability. This was never the case for the three study sites where competition was commonly seen. Judging competitive ability by the difference between the number of encounters won vs. those lost, there was no correlation between this index and the abundance of a species, measured either by number of colonies or area covered (Table 3).

The sizes of competing colonies had an influence on the outcome of the interaction. Winners were larger than losers at the Exposed Pools and larger than non-interactors at all three sites (Table 4). Winning affects survival also; winning colonies survived longer than losers at the Exposed Crest and Exposed Pools and longer than non-interactors, at all three sites (Table 5). Species with more colonies or greater cover engaged in more interactions than more rare ones at all three sites, but more interactions resulted in a higher proportion of wins only at the Exposed Pools (Table 3). The growth of individual coral colonies was sometimes affected by competition. At the Protected Crest, the annual relative growth rate of both the ''winners'' (species that won more often than they lost), and the non-interactors, was faster than that of the ''losers'' (species that lost more often than they won) (Table 6). At the Exposed Crest, winners grew faster than non-interactors, whereas at the Exposed Pools, growth was apparently unaffected by competition (Table 6).

Patterns of abundance and alpha diversity

Abundance.—In this paper we present data on abundance (number of colonies per square meter, or percent cover) from the years 1962–2000, extending the record seven years beyond that described in Connell et al. (1997). Five hurricanes caused damage to corals at some study sites during the study, but the damage varied greatly. On the permanent shallow sites, hurricanes drastically reduced abundance at the Exposed Pools in 1967 and 1992, the Exposed Crest in 1972, the Protected Crest in 1980, and the Inner Flat in 1976. Thus, each hurricane significantly reduced abundance at one and only one of the permanent shallow sites (Figs. 3 and 4). Density and percent cover usually rose after these reductions. At the Exposed Slope subtidal site, the 1992 hurricane drastically damaged corals only at the shallow depths. At both the Exposed and Protected Slope subtidal sites, from 1972 to 1999, the density of colonies was always higher at the shallower depths except just after the 1992 hurricane (Fig. 3). In contrast, percent cover at the shallower depths of the Protected Slope was either lower than or equal to that at the deeper depths. At the Exposed Slope, percent cover at the shallower depths was either higher than or equal to that at the deeper depths, except just after the 1992 hurricane (Fig. 4).

TABLE 4. Mean size of colonies (area in cm^2) at three sites that won in competition, lost, or did not interact; and one-way ANOVA results.

Factors	Mean	1 SE	N	df	SS	F
Exposed Crest						
Winners	195.87	81.51	54			
Losers	92.79	87.94	34			
Noninteractors	42.11	21.67	97			
Source						
Among groups				2	2.13×10^8	8.19***
Within groups				182	2.41×10^9	
Total				184	2.62×10^9	
Exposed Pools						
Winners	535.38	373.18	15			
Losers	30.94	11.08	13			
Noninteractors	93.72	52.95	181			
Source						
Among groups				2	5.14×10^8	9.73***
Within groups				206	5.53×10^9	
Total				208	6.04×10^9	
Protected Crest						
Winners	111.05	98.21	99			
Losers	70.15	62.83	27			
Noninteractors	65.44	58.84	372			
Source						
Among groups				2	1.41×10^{18}	3.38*
Within groups				495	1.04×10^{20}	
Total				497	1.05×10^{20}	

Notes: Pairs whose mean sizes were significantly different at $P = 0.05$ (Tukey-Kramer) for Exposed Crest were winners, noninteractors; for Exposed Pools they were winners, losers and winners, noninteractors; and for Protected Crest they were winners, noninteractors.

* $P < 0.05$; *** $P < 0.001$.

Species richness (S).—S is sensitive to the number of individuals (genets) in small samples; this has been demonstrated in many ecological studies (see examples in Peet 1974 and Magurran 1988). This was also found in the present study for the cumulative samples over time from the permanent quadrats, and in the line transects on the subtidal slopes, and over space from the large-scale photographic samples on the reef flat (Fig. 5, Appendix A). In the latter, the Outer Flat had high S, while at the Middle and Inner Flat transects, S was lower (Fig. 5). The only samples that reached an asymptote were those in the Inner Flat. Because S varied with the number of genets, the general patterns of S over time at each site (Fig. 6) were similar to those of the number of genets (Fig. 3), but less similar to those of percent cover (Fig. 4).

Diversity based upon relative abundances of species.—The coral diversity index used here ($D = 1/\Sigma p_i^2$) was affected by variation in sample size, but much less so than was S; the slopes of the regressions of S vs. N (number of genets) were greater than those of D vs. N at all study sites (Appendix A). D varied among the different sites and also over time at all sites, varying least at the Protected Slope (Fig. 7). At the Protected Crest, D based on cover fluctuated around a relatively high level for the first 20 years, then fell from a peak in 1984 to a low level in 1990, and then rose again, before falling to its lowest level by 1999 (Fig. 7). D based on the number of genets showed somewhat less variation, but a similar pattern. At the Exposed Pools, D based on cover recovered almost completely after the crash in the 1967 hurricane, then declined from 1972 to 1991, while cover rose and remained high, and the number of genets fell (Figs. 3 and 4), indicating that a few species had become dominant in cover. Diversity at the Exposed Crest was moderately high until most corals were killed in the 1972 hurricane; over the next 26 years it gradually recovered to nearly its original diversity (Fig. 7). At the Inner Flat, D was low in most years, reflecting the low genet density, cover, and few species there (Figs. 3, 4, and 6); along with abundance, D declined gradually to nearly zero at one point (Fig. 7). The Protected Slope also had low D based on cover, since a few species there had very large colonies, dominating the cover; D based on genets was slightly higher, since no single species dominated in numbers (Fig. 7). Lastly, the Exposed Slope reached the highest S and D of any of the study sites (Figs. 6 and 7). This site had a greater range of habitat heterogeneity than the other sites, being located on a relatively steep slope exposed to storm waves. At both slopes, S and D tended to be slightly greater at shallower depths (Figs. 6 and 7).

TABLE 5. The life spans of colonies that either won in competition, lost, or did not interact (life span in years within the study period).

Factors	Mean	1 SE	N	df	SS	F
Exposed Crest						
Winners	7.3	4.9	54			
Losers	4.3	3.7	34			
Noninteractors	4.2	3.2	97			
Source						
Among groups				2	2.29×10^{8}	19.19***
Within groups				182	1.10×10^{9}	
Total				184	1.33×10^{9}	
Exposed Pools						
Winners	11.4	6.0	15			
Losers	2.2	1.4	13			
Noninteractors	2.9	1.2	181			
Source						
Among groups				2	7.44×10^{4}	41.0***
Within groups				206	1.90×10^{5}	
Total				208	2.64×10^{5}	
Protected Crest						
Winners	13.5	10.6	99			
Losers	13.1	11.7	27			
Noninteractors	8.3	6.0	372			
Source						
Among groups				2	2.40×10^{10}	7.24***
Within groups				495	8.24×10^{11}	
Total				497	8.48×10^{11}	

Notes: Pairs whose mean sizes were significantly different at $P = 0.05$ (Tukey-Kramer) for Exposed Crest were winners, losers and winners, noninteractors; for Exposed Pools they were winners, losers and winners, noninteractors; and for Protected Crest they were winners, noninteractors.

*** $P < 0.001$.

D based on genets was always higher than D based on cover. This is because the percentage abundance of the most common species, when this was based on cover, was always greater than when this percentage was based on number of genets (Appendix A). In other words, the degree of dominance was greater based on cover than on genets. Coral species that have a large range in colony size, such as some *Acropora* species, can reach a very large total cover area, whereas others that often have many colonies but never attain large colony size on our study sites, cannot become as dominant in cover as in numbers of genets. At the four permanent quadrat sites, the species most common in cover were all in the genus *Acropora*, whereas of those most common in genets, it was a species of *Acropora* at one site, but species of *Pocillopora* or *Porites* at the other three sites (Appendix A).

Mechanisms affecting species richness and alpha diversity

The intermediate disturbance model of diversity.—Two hypotheses derived from this model were tested. The first predicts that after a disturbance drastically reduces abundance, S and D first rise and later fall over time, provided that no further disturbance significantly affects abundance. The fall in D is postulated to be due to the competitively superior species increasing in cover at the expense of inferior competitors. If some of the latter are eliminated, S will fall also. We tested this hypothesis by calculating changes in S and D over time at three sites on the exposed side of the reef. (Since the protected side was never as heavily disturbed, sites there did not have sufficient ranges of intensity of disturbance to test this hypothesis.) Coral cover at the Exposed Pools was reduced nearly to zero in the 1967 hurricane, was not significantly reduced in the next three hurricanes, and was then again drastically reduced in the 1992 hurricane (Fig. 4). S rose after 1967 from 0.1 to 12.5 species/m^2, but did not then decline between the 1967 and 1992 hurricanes as predicted (Fig. 6). This was because species were either not eliminated, or if so, were balanced by new recruitment. In contrast, D based on cover rose after 1967 from nearly zero to 6.5, then gradually declined to <2 by 1992, a pattern entirely consistent with the intermediate disturbance hypothesis (Fig. 7). The periodic photographs during this period showed colonies of some species growing over their neighbors, increasing the relative dominance of the former, even when no species were being eliminated.

At the Exposed Crest, cover was drastically reduced by a hurricane in 1972. Recolonization after 1972 was very slow; the patterns of increase in S and D over time are consistent with those predicted by the hy-

TABLE 6. Relative growth rate of colonies that won in competition, lost, or did not interact; rate is [change in size (cm^2)]/[initial size (cm^2)] per year.

Factors	Mean	1 SE	N	df	SS	F
Exposed Crest						
Winners	13.63	81.51	54			
Losers	2.94	87.94	34			
Noninteractors	1.95	21.67	97			
Source						
Among groups				2	5.98×10^5	4.41*
Within groups				182	1.25×10^7	
Total				184	1.31×10^7	
Exposed Pools						
Winners	5.48	7.73	15			
Losers	3.14	2.00	13			
Noninteractors	−35.74	1.65	181			
Source						
Among groups				2	0.00×10^0	0.081 NS
Within groups				206	9.80×10^{-1}	
Total				208	4.70×10^{-3}	
Protected Crest						
Winners	1.56	1.45	99			
Losers	−13.40	5.11	27			
Noninteractors	0.21	0.41	372			
Source						
Among groups				2	1.92×10^0	11.73***
Within groups				495	4.07×10^1	
Total				497	4.26×10^1	

Notes: Pairs whose mean sizes were significantly different at $P = 0.05$ (Tukey-Kramer) for Exposed Crest were winners, noninteractors; for Exposed Pools the pairs did not differ; and for Protected Crest they were winners, losers and losers, noninteractors.

* $P < 0.05$; *** $P < 0.001$; NS, not significant.

pothesis during the early stages of recolonization (Figs. 6 and 7). However, by 1998 the cover had still not reached levels at which interspecific competition was occurring to any degree, so no test of the predictions of this hypothesis for the later stages of colonization is possible as yet. At the Exposed Slope, coral cover was low after the 1972 hurricane had left many corals broken. At shallower depths abundance rose, fell again during the 1992 hurricane, and then rose again (Figs. 3 and 4). At the deeper depths, coral abundance continued to rise after 1985, fluctuating at a moderate level after 1992. S mirrored the number of colonies at both depths, whereas D based on cover fell in the final years, consistent with the intermediate disturbance hypothesis. D based on numbers of colonies was less consistent with the hypothesis (Figs. 6 and 7).

A second hypothesis suggests that species richness and diversity will be highest at intermediate cover of corals, and less at both lower and higher cover. We tested the prediction that S and D would be lower at high than intermediate cover for the five sites where competition was strong. The hypothesis was accepted for S at the Exposed Crest and Protected Slope, but rejected for the other three sites. It was accepted for D at the Exposed Pools, Exposed Slope, and Protected Slope, but rejected at the Protected Crest and Exposed Crest (Table 7).

Compensation among species.—Compensation in recruitment occurred strongly; inferior competitors as a group had significantly higher rates of recruitment per unit area of resident corals at all three sites (Fig. 8). In regard to changes in relative abundance, compensation occurred in over one-third of the intervals between censuses at the Exposed Pools and the Exposed Crest, and in about half at the Protected Crest (Table 8). We also tested the hypothesis that when coral cover was increasing, there would be little compensation, but when coral cover was constant or decreasing, compensation would occur. At the Exposed Pools the hypothesis was rejected, but at the Exposed Crest and Protected Crest, the hypothesis was accepted (Table 8).

Frequency dependence among species.—When abundance was measured as percent cover, negative frequency dependence occurred during 64% of the intervals between censuses at the Exposed Crest, 40% at the Protected Crest, 33% at the Exposed Pools, and 42% at the Inner Flat. When the relative abundance of species was compared between the start and end of the study period as a whole, frequency dependence occurred at the Exposed Crest, but not at the other sites (Table 9). Lastly, frequency dependence was apparently very rare in recruitment, which rarely responded to the cover of conspecific adults. When the number of recruits per species per year per conspecific adult cover

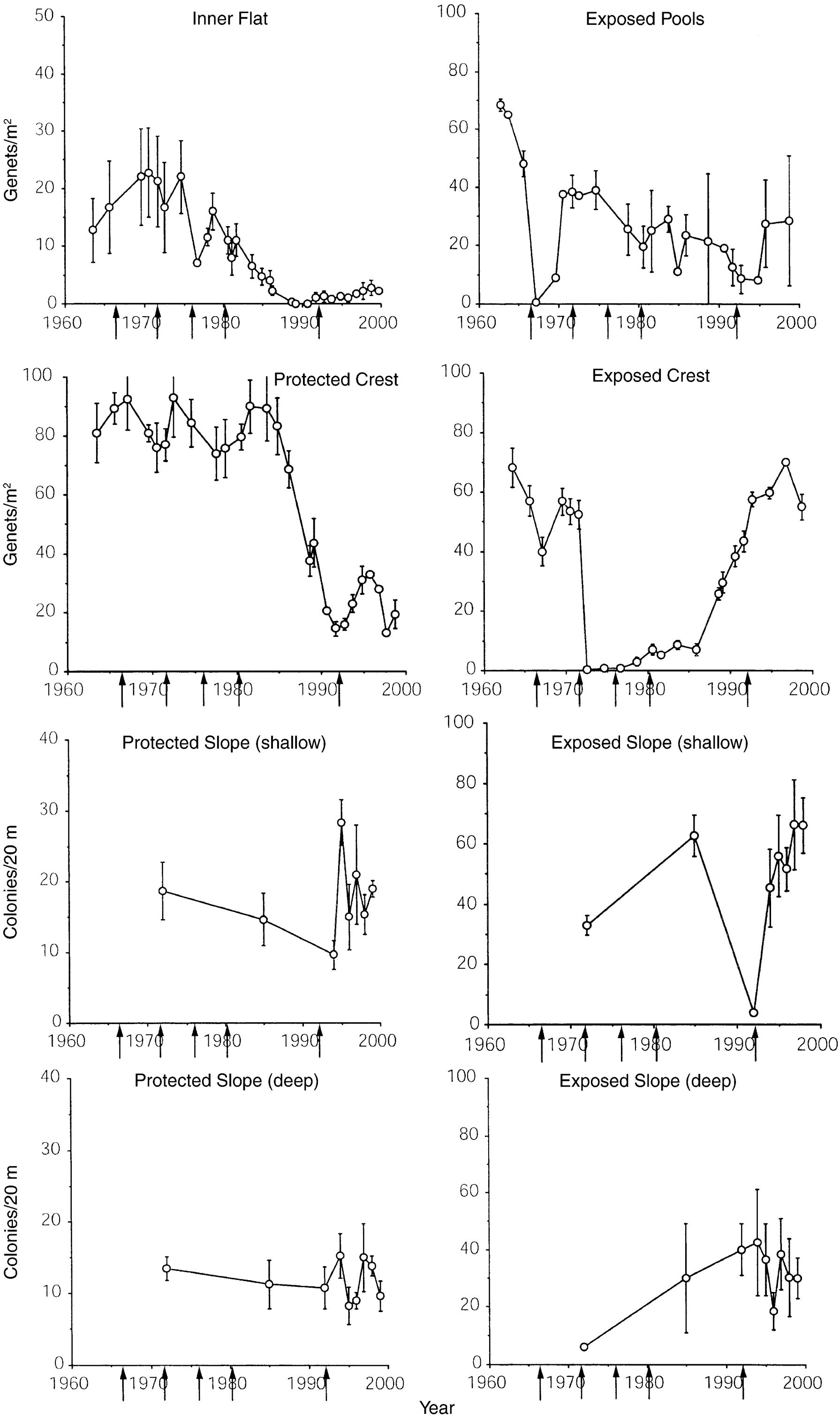

FIG. 3. Number of colonies of living corals at each study area expressed either as the number per square meter at the permanently marked quadrats from 1963 to 1998 or as the number per 20 m of line transect on the outer slope sites from 1972 to 1998. Arrows on the abscissas indicate hurricanes.

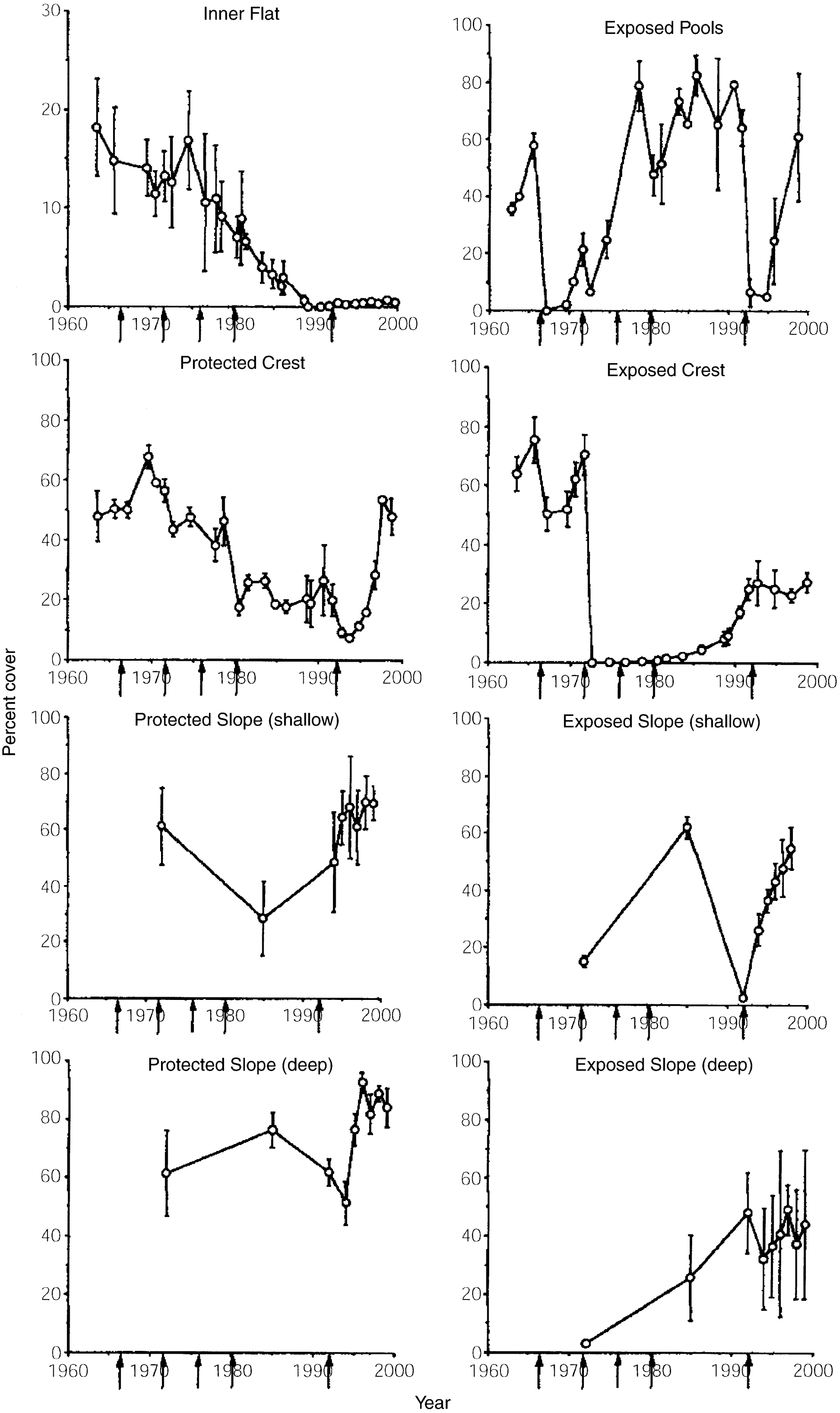

FIG. 4. Percent cover of living corals per square meter at each study area, at the permanently marked quadrats from 1963 to 1998, and on the outer slope sites from 1972 to 1998. Arrows on the abscissas indicate hurricanes.

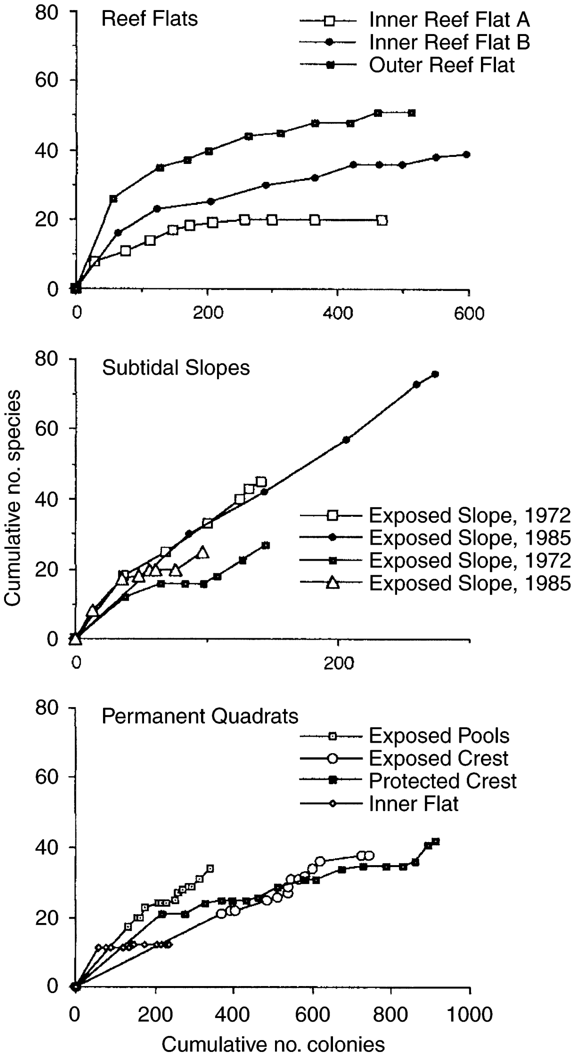

FIG. 5. Cumulative number of species in relation to the cumulative number of colonies in three habitats: (top) on the south reef flat, July 1983; (middle) on the Exposed and Protected subtidal slopes, August 1972; and (bottom) in the series of censuses on the permanently marked quadrats, 1963–1998.

was regressed against the adult cover in the previous census, frequency dependence (i.e., a significant negative slope) never occurred in the 56 comparisons made (Table 9).

Recruitment limitation of diversity.—The pattern of recruitment at the Inner Flat indicates that it had a much smaller species pool of both recruits and resident corals than did the other three study areas. There were only 16 species among the 243 identified recruits at the Inner Flat; in contrast there were 42 species among the 343 identified recruits at the Exposed Pools, and 35 and 47 species among the 561 and 1007 recruits at the two permanent reef crest sites (Table 10). The lower value of *S* among the recruits at the Inner Flat could have been due, in part, to the lower sample size there than at the other three permanent sites. This seems unlikely, however, since the Exposed Crest, with twice the number of recruits as the Inner Flat, had four times the number of new species among its recruits. Also, with the very large number of colonies sampled with the large-scale photographs on the Inner Flat, *S* did not continue to rise after the sample was increased from 260 to 470 colonies (Fig. 5).

The species pool of recruits at the Inner Flat was not only small, but many of these appear to be uniquely adapted for recruiting in the more stressful environment of the Inner Flat. Four of the 16 species (81 of the 243 individuals) recruiting to the Inner Flat (*Goniopora tenuidens*, *Porites cylindrica*, *P. lobata*, and *P. nigrescens*) never occurred among the 1911 identifiable recruits at the three other sites with permanently marked quadrats. Two other species (*Leptastrea purpurea* and *Porites murrayensis*) recruited much more commonly at the Inner Flat, with 58 recruits, as compared to only 10 recruits at the other three sites, despite the fact that the latter sites had a much greater total numbers of recruits. Thus, about one-third of the species recruiting at the Inner Flat seldom or never did so elsewhere. In addition, of the 16 species of identified coral recruits at the Inner Flat site, only five were new, being members of species not present as adults when the quadrats were first mapped.

Local recruitment of the resident species can be effective in recovery from disturbance. After coral abundance was heavily reduced by the 1976 hurricane at the Inner Flat site, the original species composition of corals was restored by 1984, via recruitment in five of the seven species (Table 11). After 1986, coral abundance declined almost to zero, and most of the hard substrate became occupied by macroalgae that preempted space (Connell et al. 1997). Then in the hurricane of 1992, almost all macroalgae on the inner flat was torn off. Thereafter, the green alga *Chlorodesmis variegata*, common on the reef crests but rarely seen in the Inner Flat in the previous 29 years, colonized strongly. It persisted for several years, declining only as the species of macroalgae that were present before 1992 gradually recolonized. Very few corals have recruited to the Inner Flat permanent quadrats for the past 14 years (Fig. 3; Connell et al. 1997).

Many other species at the three sites with permanently marked quadrats recruited elsewhere on the reef: 1911 genets of 84 species recruited to these other sites during the study; 1068 of these were members of 70 species that never recruited to the Inner Flat site. In particular, *Acropora* recruits were rare there; of the 243 recruits on the Inner Flat, 32 were *Acropora* recruits of only three species, as compared to 964 recruits of 31 *Acropora* species on the other three permanent sites.

Limitation by mortality.—That the low *S* at the Inner Flat was not due to poorer survival of the more rare species than of the commoner species after both had arrived, is indicated by the transplantation field experiment. When colonies of species both rare and common

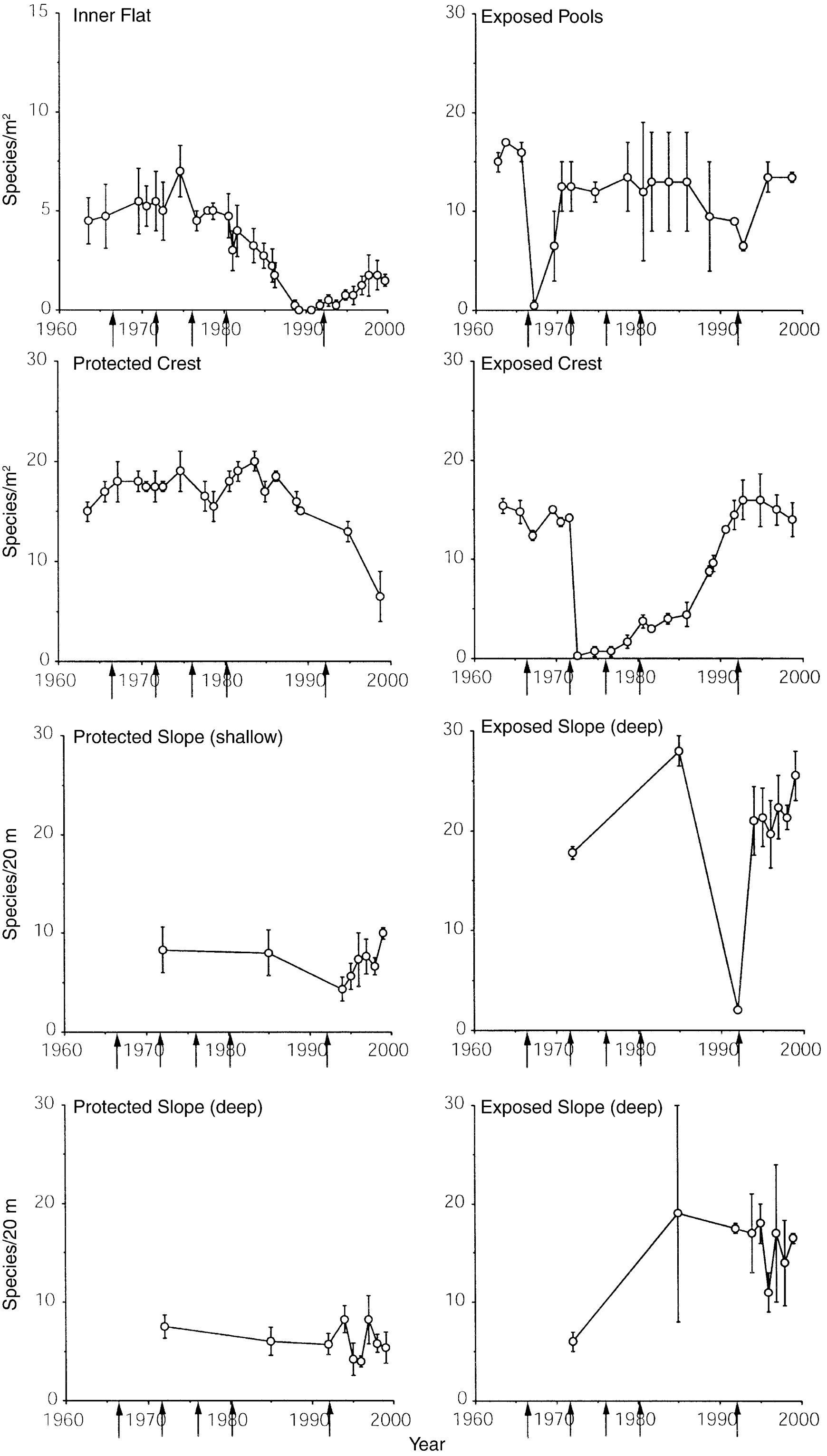

FIG. 6. Number of species of living corals at each census, expressed either as the number of species per square meter on the four permanently marked study areas from 1963 to 1998 or as the number of species per 20 m of line transect on the outer slope sites from 1972 to 1998. Arrows on the abscissas indicate hurricanes.

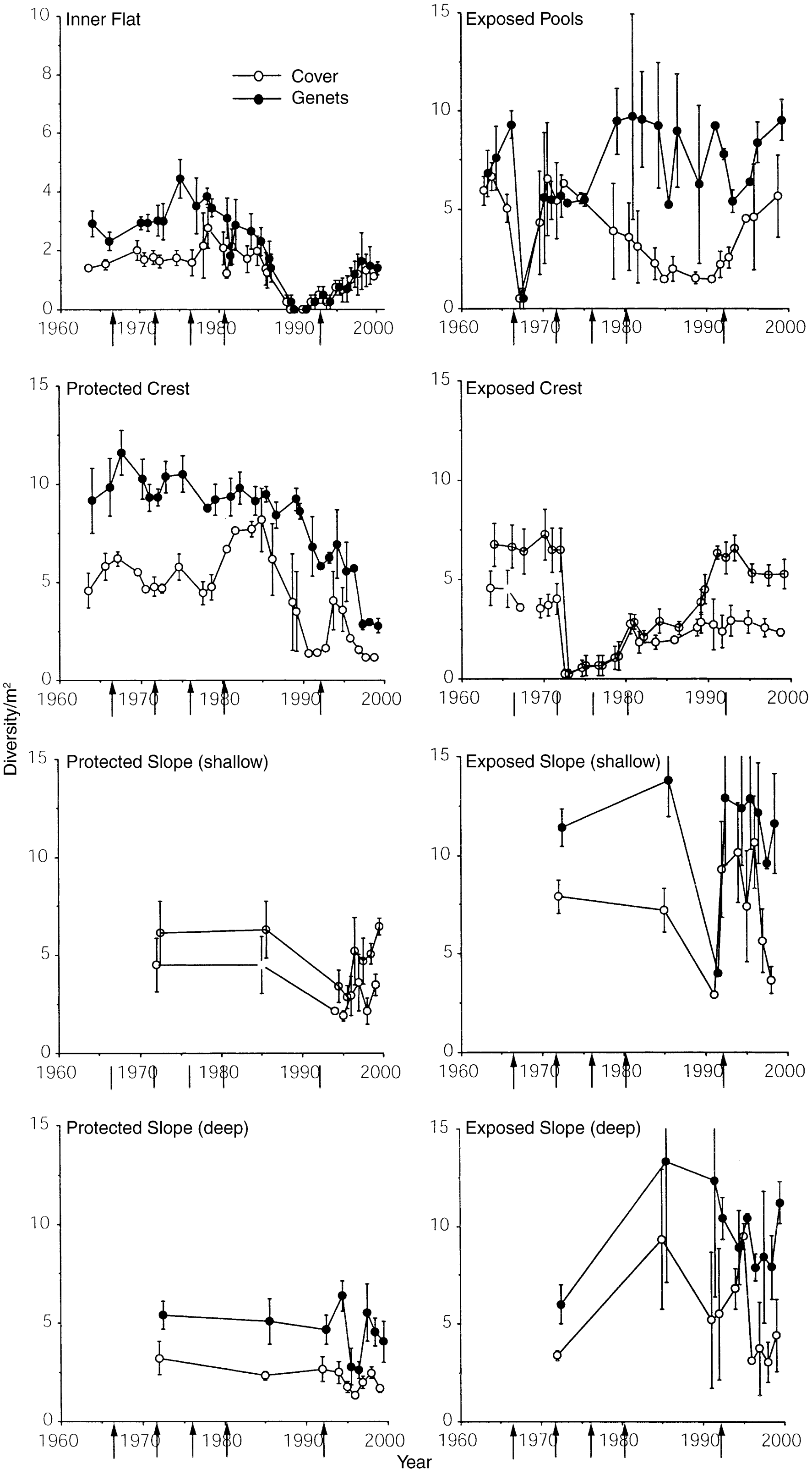

FIG. 7. Species diversity of living corals at each census, expressed either as the diversity per square meter on the four permanently marked study areas from 1963 to 1998 or as the diversity per 20 m of line transect on the outer slope sites from 1972 to 1998. Diversity was calculated using either number of genets per species or percent cover per species. Arrows on the abscissas indicate hurricanes.

TABLE 7. Tests of the intermediate disturbance hypothesis, which states that *S* (species richness) and *D* (diversity) will be higher at intermediate than at high cover. For each site, comparisons between censuses with high vs. intermediate cover are shown for species richness and diversity.

Parameter	Mean	1 SE	*t*	*P*
Protected Crest (N = 24/25, high cover = 45–74%)				
Percent cover				
Intermediate	30.8	1.5		
High	54.7	1.4		
No. species				
Intermediate	14.2	0.7	0.35	0.73
High	14.6	0.9		
Diversity				
Intermediate	4.5	0.5	0.30	0.77
High	4.7	0.3		
Exposed Crest (N = 20/21, high cover = 52–90%)				
Percent cover				
Intermediate	34.6	2.2		
High	70.5	2.3		
No. species				
Intermediate	13.7	0.6	2.47	0.018**
High	12.2	0.2		
Diversity				
Intermediate	4.4	0.6	0.06	0.95
High	4.4	0.3		
Exposed Pools (N = 13/14, high cover = 57–90%)				
Percent cover				
Intermediate	39.3	2.2		
High	74.2	2.7		
No. species				
Intermediate	12.1	1.2	0.77	0.45
High	10.9	1.1		
Diversity				
Intermediate	4.7	0.6	2.91	0.008**
High	2.6	0.4		
Exposed Slope (N = 19/18, high cover = 49–82%)				
Percent cover				
Intermediate	35.9	0.2		
High	0.6	0.0		
No. species				
Intermediate	20.5	1.4	0.41	0.69
High	21.1	1.2		
Diversity				
Intermediate	8.3	1.0	2.18	0.036*
High	5.6	0.7		
Protected Slope (N = 30/30; high cover = 74–100%)				
Percent cover				
Intermediate	58.3	0.3		
High	0.9	0.0		
No. species				
Intermediate	7.6	7.6	2.79	0.007**
High	5.5	5.5		
Diversity				
Intermediate	2.9	0.3	2.89	0.005**
High	2.0	0.1		

Note: N = no. censuses for intermediate/high cover; intermediate cover ranges from 20% to the lower limit of high cover, as shown for each site.

* $P < 0.05$; ** $P < 0.01$.

on the Inner Flat were transplanted there from the Outer Flat, both groups had equal mortality (Table 12). The same applied to the controls, with genetically identical colonies handled the same amount as the experimentals, but not transplanted.

Variations in species composition

Spatial variation in species composition: beta diversity.—Beta diversity indicates the degree of difference in species composition between sites (Whittaker 1967). Using percent cover as the measure of abundance of each species, the greatest beta diversity occurred when the Inner Flat was compared to other sites (Table 13). Its species composition was clearly different from the others; 4 of its 16 species were never found elsewhere, and many species found elsewhere were missing from the Inner Flat. The transplantation experiment (Table 12) showed that this difference was not due to poorer adult survival, since many adult colonies of species that are seldom if ever found on the Inner Flat survived as well there as did species commonly found there naturally. The two crest sites showed the lowest beta diversity (45%), probably because their habitats were similar (Table 13). The Exposed Pools were more similar to the nearby Exposed Crest and Exposed Slope than to the distant Protected Crest and Protected Slope. The beta diversity between the two slope sites was high, indicating that their species compositions differed greatly. The Exposed Slope was much more similar to the shallow sites with permanent quadrats than was the Protected Slope.

The comparisons based on the number of colonies show similar patterns. The inner and middle flat sites, sampled using the large-scale photographs, were more similar than either was to the outer flat site (Table 14). Comparing these large-scale sites to those sampled with quadrats or line transects, the two inner and middle flat sites were more similar to the Inner Flat quadrats than to any other sites, and least similar to the Protected

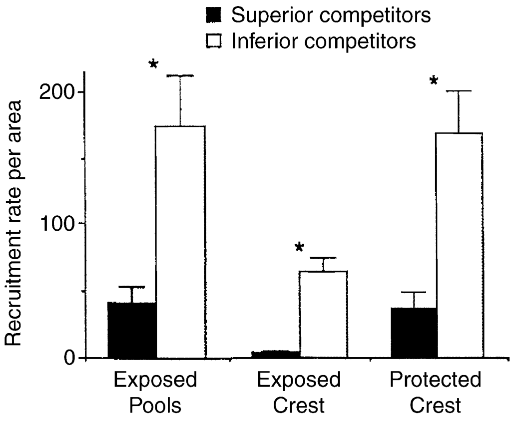

FIG. 8. Compensation: recruitment of superior and inferior competitors at the three study areas where competition was common.

Table 8. Tests of the hypothesis that compensation, defined as the relative abundance of the inferior competitor species increasing while that of the superior competitors decreases, occurs when the total coral cover decreases but does not occur when total cover increases.

	Coral cover†				
	Decreased		Increased		
Site	Compensation occurred	Compensation did not occur	Compensation occurred	Compensation did not occur	χ^2
Exposed Pools	2	2	3	6	0.33
Exposed Crest	2	0	2	7	4.28*
Protected Crest	7	2	1	5	5.40*
All sites	11	4	6	18	8.77**

Note: The last column presents results of χ^2 contingency tests, df = 1.

* $P < 0.05$; ** $P < 0.01$.

† Number of intervals between censuses in which the total cover either decreased or increased.

Slope. In summary, two habitats, the Inner Flat and the Protected Slope, differ most in species composition from all other sites. Beta diversities calculated using relative abundances based on cover were consistently higher than those based on number of genets (Tables 13 and 15). The reasons for this are that the degree of dominance based on cover is always larger than that based on number of genets (Appendix A). As a result, the similarity of species composition will probably be lower, and the beta diversity higher, if it is based on cover than if based on genets.

Temporal variation in species composition: beta diversity in time.—To measure the changes in species composition over time, we calculated the similarity between the relative abundance of species at the initial census and that at each subsequent census. While similarity would be expected to drop over time, it could eventually stabilize at some level, and, if subsequently

Table 9. Frequency dependence, using either (A) changes in the relative abundance of the species or (B) recruits in relation to abundance of adults the previous year.

A) Frequency dependence†

	No. intervals‡				
	Frequency dependence			r^2§	
Site	Occurred	Did not occur	Intervals that were frequency dependent (%)	Percent cover	No. genets
Exposed Pools	4	8	33	0.008	0.129
Exposed Crest‖	7	4	64	0.151*	0.250*
Protected Crest	6	9	40	0.004	0.008
Inner Flat¶	5	7	42	0.584	0.001
All sites	22	28	44		

B) Frequency dependence of recruitment#

	No. recruits·sp.$^{-1}$·yr^{-1}		Cover of adults (%)			
Site	Range	Median	Range	Median	N (yr)	No. significant negative slopes
Exposed Pools	6–59	16	4.5–70.2	44.8	14	0
Exposed Crest	0–189	41	0–73.6	16.7	21	0
Protected Crest	9–91	49	6.2–64.4	24.2	25	0
Inner Flat	0–18	9	0–10.2	0.6	21	0

* $P < 0.05$.

† Frequency dependence is defined as follows: the relative abundance of the rarer species increases, while that of the commoner species decreases.

‡ Number of intervals between censuses when frequency dependency occurred or did not occur as coral cover changed.

§ Relative abundances in 1963 vs. 1998; the coefficient of determination (r^2) is based on either percent cover or number of genets.

‖ For the relative abundance in 1963 vs. 1998 at the Exposed Crest, both comparisons indicated that frequency dependence occurred.

¶ For the Inner Flat, the period was 1963–1981, because few corals were present after 1981.

Frequency dependence of recruitment is defined from regressions of the per capita number of recruits vs. the percent cover of adults/sp. in the previous year. A significant negative slope indicates frequency dependence.

TABLE 10. Recruits from 1965 to 1998, compared to the species and numbers of original residents in 1962–1963.

Site	No. quadrats	Start of study		Whole study period	
		No. species	No. colonies	No. species of recruits	No. recruits
Inner Flat	4	11	50	16	243
Protected Crest	3	19	216	47	1007
Exposed Crest	3	17	183	35	561
Exposed Pools	2	17	129	42	343

† Number of species not present at start of study.

perturbed, might return to that level, providing that no persistent shifts in the environment had taken place. The Protected Crest showed a gradual decline, with similarity in species composition measured as cover (but not as genets), decreasing at a faster rate after 1984 (Fig. 9). At the Inner Flat, the percentage similarity (in cover) fell abruptly from 1974 to 1978, the period that included the 1976 hurricane. It then recovered completely by 1984 (Fig. 9), but fell again, since almost all corals had died by 1988. The recovery in species composition by 1984 was produced entirely by recruitment of new genets in three species, while in two others, it was the result almost entirely of survival of genets (Table 11). Two other species survived the storm, but did not persist until 1984. The Exposed Pools and Exposed Crest were denuded almost completely in the hurricanes of 1967 and 1972, respectively. The pattern of recovery thereafter differed between the sites; the species composition at the Exposed Pools recovered similarity quickly but soon began to decline again, particularly in cover (Fig. 9). In contrast, the Exposed Crest recovered more slowly, though somewhat irregularly, and by 1998 had reached a similarity ranging from 20 to 50% of the initial species composition.

Another measure of change in species composition is the turnover of species. Table 15 shows the proportion of species at each site that either persisted over the whole study period, went extinct, invaded and then persisted, or arrived and then disappeared during the period. Of the four sites, the Inner Flat had the lowest degree of persistence and the highest degree of new invasion. Among the other three sites, the Protected Crest had the lowest fraction of species persisting, and the highest proportion of those going locally extinct. Judging the degree of turnover as the inverse of persistence, the Inner Flat showed the highest turnover, and the Exposed Crest the lowest (Table 15).

The dominant species, that with the highest cover at a site, often maintained this position for many years. Shifts from one coral dominant to another were few, with only 3–4 species of corals ever dominant at any of the study sites during the 36 years of study (Appendix A). Examples are one to three species of *Acropora* at all the study sites, *Pocillopora damicornis* at the Exposed Crest, species of *Montipora* and *Zoanthus* at the Protected Crest, and species of *Porites* at the Inner Flat. Some taxa were seldom common, e.g., massive corals in the families Faviidae and Mussidae. However, they were proportionately more common during recolonization of the Exposed Crest after the 1972 hurricane than in other sites at any time, perhaps indicating a preference for early colonization of free space, and a tolerance of dry conditions. At the Protected Crest in the late 1980s, when many of the corals had fused into a pavement and died (Figs. 3 and 4), the encrusting soft coral *Zoanthus vietnamensis* became the dominant, supplanting the species of *Acropora* and *Montipora* that had dominated the early years. In the late 1990s, after *Zoanthus* died and erosion had corroded the substrate, fragments of *Acropora pulchra* invaded and grew to dominance (Appendix A).

Although the dominant species changed infrequently, other common species shifted significantly. Of the 10 species ranking highest in cover at the start of the study in 1962–1963, 60% at the Exposed Crest, 50% at Exposed Pools, and 50% at the Protected Crest remained as members of the top 10 in 1998. Using numbers of genets as the measure of abundance, of the top ranking group of 10 species in 1962–1963, the percentage still members of this group in 1998 were 60% at the Exposed Crest, 40% at the Exposed Pools, and 30% at the Protected Crest. The Inner Flat had only four species in 1962, one of which was still present among the six species in 1998. In summary, the species at the Exposed Crest remained the most similar over time, even though all corals were killed there in the 1972 hurricane.

The species composition of the new coral recruits showed a similarity to the adult corals present on the study site during the previous census year that ranged from $<5\%$ up to 75% at the different sites (Fig. 10). We also compared the species of recruits that arrived during the study period with those of the original assemblage at each site. Species of recruits at the Inner Flat were more similar to the originals than those at the other three sites. At the Inner Flat, only 31% of all species of recruits were new, i.e., species not present originally, whereas between 57% and 67% of all species of recruits were new at the other three sites (Table 10).

DISCUSSION

Interspecific competition for space among corals

Competition in corals occurs either by preemption of space by residents, or direct aggression between

TABLE 10. Extended.

No. ''new'' species of recruits†	No. recruits of ''new'' species†	Species present at start of study that had recruits thereafter (%)	All species of recruits that were ''new'' (%)	All recruits that were of ''new'' species (%)
5	16	100	31	7
30	194	89	64	19
20	34	88	57	6
28	100	82	67	29

neighboring colonies, by overgrowth, overtopping, or attacks with digestive filaments or tentacles, which may result in partial or complete death of the neighbor. When one species of corals consistently wins over another, this asymmetrical competition implies that the winner is inherently superior in competitive ability. In contrast, if neither species wins consistently, this symmetrical competition could be a result of either (1) a ''standoff'' with one or both species able to defend itself against this direct aggression, (2) equivalent competitive abilities, or (3) the outcome being contingent on local environmental conditions or individual traits, such as size. Several workers have suggested that when a single mechanism of interaction is involved, competition will be asymmetrical, but when several mechanisms come into play, it is more likely to be symmetrical (Chornesky 1989, Lang and Chornesky 1990, Tanner 1993, Chadwick-Furman and Rinkevich 1994). Our present results indicate that the type of competition may also be a function of the local environment, being more symmetrical on the Protected Crest, and more asymmetrical on the Exposed Pools and Exposed Crest.

Asymmetrical interspecific competition, by increasing mortality, would be expected to alter *S*, *D*, and the relative abundance of species in a community. In contrast, symmetrical competitive interactions might be expected to maintain, rather than alter, these community attributes. Therefore, since both the absolute rate of competition and the proportion of asymmetrical interactions were greater at the Exposed Pools and Exposed Crest than at the Protected Crest, interspecific competition would be expected to change community structure more strongly at the exposed than at the protected sites. Species that are consistent winners in competition should be more likely to have high inherent competitive ability. In contrast, species that are inconsistent winners probably do sometimes win because, although they may have a poor inherent competitive ability, they are favored by the particular environmental conditions at the time.

Competition by preemption of space occurs when corals either prevent larval settlement or defend themselves against aggressive attacks by neighbors. Massive species in the Faviidae and Mussidae often exhibit defensive behavior, using digestive filaments that keep the superior branching *Acropora* species from overgrowing them in shallow sites (Lang 1973). Also, *Pocillopora damicornis* and *Agaricia agaricites* defend themselves by developing sweeper tentacles that fend off normally superior species (Wellington 1980, Chornesky 1989). Species may be poor competitors because of inherent traits such as small polyps, small size, and short life span, or because of local environmental constraints (Romano 1990). At deeper sites, corals can interact in three dimensions, overtopping neighbors above and beyond the reach of filaments or tentacles. At the shallow crests, corals interact mainly in two dimensions, attacking and killing the tissues on the periphery of a neighbor with filaments or tentacles, or overgrowing directly on top of it, as well as defending

TABLE 11. Recovery of species composition after an abrupt decline during the 1976 hurricane at the Inner Flat. For each species, the table shows the proportion of recovery by 1984 from recruitment of new genets after the storm vs. from survival of genets present before the storm.

		Relative abundance of each species (percent total cover)					
Year	Percent cover, all species	*Porites cylindrica*	*Acropora millepora*	*Porites annae*	*Porites nigrescens*	*Leptastrea purpurea, Pocillopora damicornis, Porites murrayensis*	*Acropora formosa, Porites lichen*
1974: just before the hurricane	16.7	50	31	7	1	6	5
1978: just after the hurricane	9.26	10	58	8	9	11	4
1984: eight years after the hurricane	3.2	56	24	13	1	6	0
1984: percent cover represented by genets that recruited after the storm	···	100	0	6	100	100	···

TABLE 12. Mortality of corals from the outer reef flat that were transplanted to sites on the Inner Flat (experimentals) vs. control colonies, handled equally and genetically identical to the experimental colonies, but not transplanted and replaced at the Outer Flat. The table shows the overall effect of the handling done during the process of transplanting itself.

	Experimentals				Controls			
Site and treatment	No. live	No. dead	Dead (%)	χ^2	No. live	No. dead	Dead (%)	χ^2
A) Mortality after two years, 1969–1971								
South				0.184				0.457
Rare species on Inner Flat	13	8	38		10	11	52	
Common species on Inner Flat	1	1	50		1	1	50	
North				0.008				0.265
Rare species on Inner Flat	6	6	50		10	2	17	
Common species on Inner Flat	3	5	62		6	1	14	
Both sites				0.377				0.314
Rare species on Inner Flat	19	14	42		20	13	39	
Common species on Inner Flat	4	6	60		7	2	22	
B) Mortality after five years, 1969–1974								
North				0.278				0.001
Rare species on Inner Flat	4	8	67		10	2	17	
Common species on Inner Flat	1	7	87		5	2	29	

Notes: None of the chi-squared contingency tests showed a significant difference between the mortality of species that were rare on the Inner Flat vs. those that were common there, after both were transplanted either to sites on the Inner Flat, or to control sites on the Outer Flat.

against such attacks and overgrowth. As a consequence of the presence of effective defenses in shallow sites and their absence in deeper sites, species were more often equivalent in competitive ability in the former. Thus, as cover increased after disturbance, some species overtopped others in deeper sites, so reducing diversity, whereas on the shallow crests, this happened less often. As a consequence, the intermediate disturbance hypothesis (Horn 1975, Connell 1978) would be more likely to apply at deeper sites than on the shallow crests, which is what we found.

Alpha diversity of corals

Effects of recruitment, growth and mortality on alpha diversity.—*S* is a function of the numbers of genets in the small sample sizes taken in most ecological studies. Therefore, since recruitment increases genet density, it would be expected to increase *S*, while mortality would have the opposite effect. In recovery of *S* following a disturbance, local recruitment of the resident species can be effective, as we found after the 1976 hurricane at the Inner Flat site. Changes in recruitment, growth and mortality may also alter the relative abundances of the species, but these could either increase or decrease *D*. If the numbers or cover of the more common species were decreased proportionately more than that of the more rare species by recruitment, growth, or mortality, *D* would be increased. If the opposite occurred, *D* would obviously be decreased.

Effects of disturbances on alpha diversity.—In storms, particularly hurricanes, severe damage almost invariably reduces the numbers of genets, and so directly reduces *S*. However, the direct effects of mortality by disturbance on *D* are less predictable than they are on *S*, for the reasons described. The ‘‘intermediate disturbance’’ hypothesis of Horn (1975) and Connell (1978) predicts that coexistence of species will be promoted if the process of asymmetrical competition is interrupted by a disturbance before some superior competitors increase at the expense of inferior competitors. If recolonization by both these species types then follows, alpha diversity may be restored. Evidence indicates that this process has occurred during our study. Of particular interest is the fact that, even though hur-

TABLE 13. Beta diversity values (= 100 − percentage of similarity between sites), based on percent cover of corals, at the study sites at Heron Island reef.

	Small-scale, permanent quadrats at four sites				Intermediate scale, using line transects	
Site	Inner Flat	Protected Crest	Exposed Crest	Exposed Pools	Exposed Slope	Protected Slope
Protected Crest	87					
Exposed Crest	91	45				
Exposed Pools	95	75	65			
Exposed Slope	94	71	69	62		
Protected Slope	92	91	93	88	85	
Mean	70.5	75.7	75.0	85	74.2	89.8
CV	76.6	83.2	80.6	96.6	21.7	3.6

TABLE 14. Beta diversity between different sites, based on the number of genets (or colonies for line transects and large-scale photographs).

	Small-scale, permanent 1-m² quadrats				Intermediate-scale line transects		Large-scale photographs		
Site	Inner Flat	Protected Crest	Exposed Crest	Exposed Pools	Exposed Slope	Protected Slope	Inner Flat A	Inner Flat B	Outer Flat C
Protected Crest	73								
Exposed Crest	82	44							
Exposed Pools	78	58	41						
Exposed Slope	87	67	67	58					
Protected Slope	90	78	83	78	61				
Inner Flat A	63	77	81	76	83	94			
Inner Flat B	68	78	76	76	82	93	24		
Outer Flat C	89	70	77	80	71	81	57	54	
Mean	78.8	68.1	68.9	68.1	72.0	82.3	69.4	68.9	72.4
CV	12.8	17.4	24.8	20.8	15.0	13.0	31.2	30.9	16.6
Total no. genets or colonies	244	909	746	344	409	296	467	595	507
Total no. species	12	37	37	33	90	43	20	39	51

ricanes are usually very large storms, their effects on the Heron Island reef were always very localized. None of the individual hurricanes that damaged corals during the present 37-year study affected more than one of the study sites, yet all the sites were damaged once by a hurricane.

Other workers have also seen spatial variation in effects of successive hurricanes. Witman's (1992) explanation for why two hurricanes a year apart damaged different locations on a reef at the U.S. Virgin Islands, was that: ''there wasn't much left that was vulnerable to dislodgement'' at the site that had been damaged most in the first storm. The same explanation was offered for spatial variation in coral damage by two intense storms two years apart on reefs in Florida (Lirman and Fong 1995, 1996). These examples illustrate the role of the history of disturbance in explaining spatial variation in damage by successive intense storms (Hughes 1989).

Similarly, a historical explanation applies to some, but not all, of the effects of the five hurricanes that caused some coral destruction in the present study. After the 1967 hurricane removed all corals at the Exposed Pools (Fig. 4), the next hurricanes in 1972, 1976, and 1980 had little appreciable effect, since the corals apparently had had too little time to grow large enough to be vulnerable to breakage or dislodgement by storm waves. In contrast, by 1992, they had grown large, and so were apparently more vulnerable, since most were killed in that hurricane. Likewise, on the Exposed Crest, the lack of effect of the 1976, 1980, and 1992 hurricanes is probably due to the fact that the habitat had been destroyed in the 1972 hurricane, and was only very slowly becoming suitable for coral recruitment, so again the corals were small.

In contrast, disturbance history does not explain why the 1967 hurricane caused much less damage than the 1972 one on the Exposed Crest, given that the corals were very similar in both instances. Likewise, the corals on the Protected Crest did not vary appreciably in percent cover from 1963 to 1978, and so were little affected by the hurricanes of 1967, 1972, and 1976, but were reduced by more than half during the 1980 storm (see Fig. 4). In these latter instances, spatial var-

TABLE 15. Species turnover: changes in species presence/absence during the study period (total time of 21 years for Inner Flat and 26 years for all other sites); in all cases, genets had a 100% turnover in that time.

		Total species (%)				
Sites, years of observation	Total species ever observed	Persisted	Extinct	Invaded	Transient	Turnover (%)
Inner Flat, 1963–1984†	13	46‡	38	0	15	54
Protected Crest, 1963–1989	42	31	19	21	28	69
Exposed Crest, 1963–1989	35	37	23	17	23	63
Exposed Pools, 1962–1988	33	24	27	18	30	76
All four sites, 1963–1989	71	37	20	18	25	63

Notes: Definitions are: Persisted, species present from start to end; Extinct, species present at start only; Invaded, species present at end only; Transient, species present in the middle only. Percentage of turnover was calculated as 100 − percentage that persisted.

† Persistence was due to replacement by new recruits, rather than by survival of original colonies.

‡ For the Inner Flat, only one colony persisted to 1989; by 1989, there was 92% turnover.

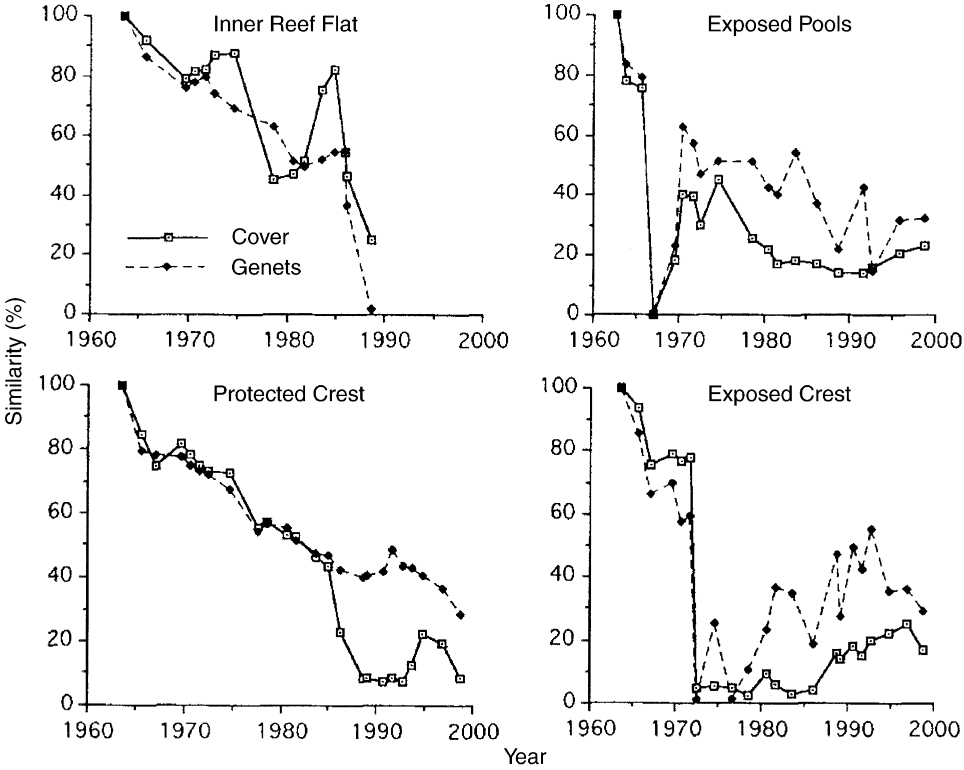

FIG. 9. Percentage similarity of species composition of corals at each census, 1965–1998, to that at the initial census in 1963. The similarity was calculated using either number of genets per species or percent cover per species. At the Inner Flat site, corals had almost disappeared by 1989, so calculations were not continued thereafter.

iations in winds or tides during the current storm seems more likely to account for the damage patterns, rather than variation in the condition of the corals caused by historical events.

Since recruitment rates are higher with more free space, (Hughes 1985, Connell et al. 1997), disturbances indirectly increase recruitment by opening up space, which should usually increase genet density and so *S*. Increased recruitment at low density may correspond to the "storage effect" (Chesson and Warner 1981), in which stochastic environmental variation, e.g., disturbance, acts so that "all species have positive average growth rates at low density" (Chesson 1986:255). However a disturbance may or may not result in an increase in *D*.

Interspecific competition intense, effectively reducing S and D.—Interspecific competition reduced *S* and *D* at the Exposed Pools. Strong competition also occurred when the physical environment changed at the Protected Crest between 1981 and 1990, when upward growth and a partial diversion of tidal flow resulted in the surface of the crest gradually becoming drier at low tide. With this change, *Zoanthus vietnamensis* invaded, gradually dominating the cover and eliminating many small colonies of Scleractinia. Later still, as erosion lowered the surface and added pits and crevices, so that drying during low tide was reduced, *Zoanthus* cover fell and hard corals reinvaded.

An example of both direct elimination and preemption of space occurred at the Protected Crest. In 1990–1998, the majority of coral recruits were fragments of a single species, *Acropora pulchra*, broken off from a very large colony on the nearby outer reef flat. These fragments quickly became established and either grew to overtop the resident corals or preempted space and prevented further recruitment of other species. In that eight-year period, both the degree of competitive asymmetry and the dominance by a single species gradually increased, and as a consequence, *S* and *D* fell.

Interspecific competition intense, but ineffective in reducing S and D.—Interspecific competition may be intense, but need not lead to elimination of species if the winning colony causes only partial mortality of the losing colony, or if the two species are equivalent in competitive ability. The extent to which this latter situation applies to corals on Heron reef seems to be a function of environmental conditions. It applies most in very shallow water on the reef crests. Here, the upward growth that is required to overtop a neighbor is limited by aerial exposure at low tide, so that colonies encounter each other principally on the same horizontal level. As a result, standoffs are common and elimi-

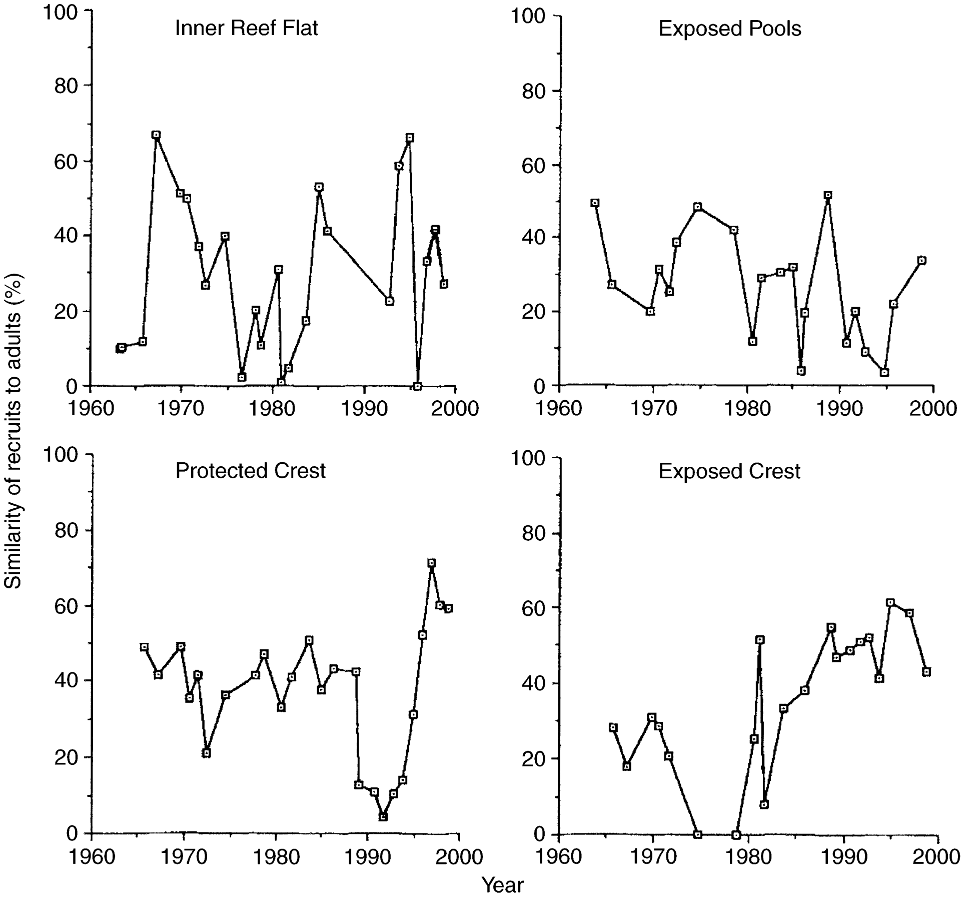

FIG. 10. Percentage similarity of the species composition of recruits to that of adults at each census from 1965 to 1998.

nation is less common. An example of this was the Protected Crest, which had the lowest rate of competitive overgrowth of any site. It suffered little damage from hurricanes, and for the first 20 years of the study, *S* and *D* remained high. It also had the highest rate of recruitment (Connell et al. 1997), which tended to maintain high genet density and so high *S*.

Compensation.—Compensation is defined as the tendency for the per capita recruitment of the inferior competitor to be higher, or its relative abundance to increase over time, compared to superior species. It could counter asymmetrical interspecific competition and help maintain *S* and *D*. The hypothesis that this occurs during periods when total coral cover declines, but not when it increases, was confirmed at two of the study sites, Protected Crest and Exposed Crest, but not at the Exposed Pools (Table 8). A possible explanation for this pattern is linked to colony morphology at the different sites. The morphology of many of the inferior species (e.g., encrusting species of *Acropora, Montipora,* and *Porites*, thick-branched *A. humilis* and *A. palifera*, and mound-like *Porites*), should be less vulnerable to breakage by storm waves than superior competitors such as bushy or aborescent forms of many *Acropora* species. The former morphology is more characteristic of the intertidal crest sites than of the deeper pools and reef slopes. This is also generally true in other reefs (Woodley et al. 1981, Hughes 1989). However, some species do not fit this morphological hypothesis: The bushy Pocilloporids are inferior competitors but vulnerable to breakage, whereas massive species in the Faviidae and Mussidae are superior in defending space, but less vulnerable. Moderate disturbance was also indirectly compensatory as it affected recruitment rates. Since inferior competitors tend to have faster rates of recruitment than superior competitors (Fig. 8), disturbance, by opening up space, augmented recruitment of inferior competitors and thus tended to maintain or increase *S* and *D*.

The precise mechanisms producing these compensatory trends are related to morphological, behavioral, and life history traits. In regard to recruitment, many of the commoner inferior competitors (*Porites* spp., *Pocillopora damicornis, Montipora* spp., and two brooding species of *Acropora* in the subgenus *Isopora*) tend to release gametes or larvae at intervals throughout the year. In contrast, most of the superior competitors, e.g., non-brooding *Acropora* species, spawn in a short period in late spring (see review by Harrison and Wallace 1990). On average, this behavior of the former ''spreads the risk'' (den Boer 1968), reducing the probability of a complete failure of recruitment in a given year, as compared to the ''all eggs in one basket'' tactic of the latter (although the risk is reduced because these perennial corals are iteroparous). In addition, many of these inferior competitors release relatively large brooded larvae, which probably have a higher survival in both the water column and after settlement, whereas most of the superior competitor species release gametes that probably have lower survival at these times (Harrison and Wallace 1990). Both traits apparently result in an average higher rate of recruitment for inferior competitors than superior ones at Heron Island (Dunstan and Johnson 1998).

In summary, the reason for these compensatory trends lies, in part, in the morphology of the corals. When hurricanes damage corals and reduce cover, the superior competitors, e.g. the large and widely branching *Acropora*, are often badly broken (Woodley et al. 1981). In contrast, the inferior competitors, e.g., the smaller encrusting, bushy, and massive species, are much less vulnerable to such breakage. In contrast, when cover is increasing markedly, the branching *Acropora* grow quickly, overtopping or overgrowing these inferior species that are thus eliminated or reduced in cover.

Frequency dependence.—We found that recruitment was not frequency dependent, in that recruitment of more rare species was never greater than more common ones. Frequency dependence sometimes did occur during changes in relative abundances, which tends to equalize them, so increasing diversity. It occurred at the Exposed Crest, but not at the Exposed Pools, Inner Flats, and Protected Crest. The mechanisms producing such frequency-dependent trends are probably the same as those for compensatory trends, because the inferior competitor species also tend to be more rare. Superior competitors had higher cover than inferior ones because the faster growth of the superior branching *Acropora* in the intervals between disturbances was apparently not offset by the higher recruitment of the inferior species.

Species composition and beta diversity of corals

The species composition of corals differed greatly among the study sites, and within sites, it was extremely dynamic over time. Fluctuations in three factors were likely causes of variation in species composition: population dynamics, the physical environment, and interspecific competition.

Population dynamics.—Chance variations in recruitment, growth, and mortality among species will tend to cause the relative abundance of species to change gradually over time at the same site. Such variations probably account for the gradual reduction of similarity over the study period. Also, recruitment limitation produced differences at the Inner Flat, where the species assemblage consists of a few species that all recruit successfully, but with relatively few other recruits. A large number of species that recruited elsewhere did not do so at the Inner Flat. What constrains the species pool at the inner reef flat? Hypotheses involving larval transport and early survival seem more likely than those involving adult survival. The transplantation experiment showed that adults of many species that are seldom, if ever, found on the inner flat survive as well there as do species commonly found there naturally.

The following five hypotheses involve larval survival, dispersal, and settlement, and early mortality thereafter. Planktonic larval dispersal may be poor in the inner flat region, so that (1) locally produced larvae are retained in the region, and (2) those produced in the outer reef are seldom carried to the inner flat. Hypothesis 1 is likely since some of the most common species on the inner flat brood and release larvae (e.g., *Acropora palifera*, *A. cuneata*, *Porites* spp.; Harrison and Wallace 1990), and in one, *Acropora palifera*, the larvae seldom disperse more than a few meters (Best and Resing 1987). However, the pattern of currents in the region of the inner flat makes hypothesis 2 unlikely. Tidal currents move very large volumes of water from the outer reef crest to the inner flat within a short period. Thus, the current pattern would probably not completely prevent transport of larvae produced on the outer reef to the inner flat. (3) A third hypothesis is that currents do carry larvae toward the inner flat, but predation in the plankton is so intense that no larvae survive the passage. This hypothesis seems unlikely since the incoming tide floods the inner flats within two to three hours, so that complete mortality in this short period is unlikely. Some larvae of the 70 species that recruited at the outer reef but not at the Inner Flat would probably escape such predation over the 35 years of study.

Other hypotheses of recruitment limitation suggest either that (4) larvae arrive at the inner flat, but do not choose to establish themselves, or that (5) they do establish, but the environmental conditions at the inner flat are so stressful that they exceed the tolerance limits of the newly recruited young corals of species found almost exclusively on the outer reef. Hypotheses 4 and 5 are difficult to test, since most newly settled recruits cannot yet be identified to species in the field. Laboratory and field experiments with larvae produced from known species could probably test hypotheses 4 and 5.

Variation in the physical environment

Local environmental characteristics.—The environment characteristics of each study site account for some of the differences between sites in species composition. As described earlier, the physical environment of the Inner Flat was the least similar to that of other sites, and is likely to be harsher for corals. Thus, the distinct species composition of the Inner Flat may be maintained both by their adaptation to its particular environment, as well as by the sorts of recruitment limitation.

Gradual shifts in the physical environment.—The species composition of the coral assemblage can be expected to shift if the average physical environment changes over time. Such a change occurred at the Protected Crest when a small launch ran aground in 1982, eroding a shallow channel that reduced the normal tidal water flow across the crest, causing increased drying out of the surface at low tide, with a concomitant increase in coral mortality. The dead coral surface then gradually eroded to become a smooth pavement of ‘‘coral rock.’’ With the diminishing cover of corals, a species of soft coral, *Zoanthus vietnamensis*, invaded and overgrew many of the smaller scleractinian corals. This new species composition persisted until erosion gradually produced pits and crevices in the surface, changing the originally smooth substratum into one more suitable for scleractinian coral recruitment.

Abrupt changes in the physical environment.—Storms that remove or break corals may result in changes in species composition, some of which may be long lasting. On the Inner Flat, coral cover was nearly halved between 1974 and 1978, the period that included the 1976 hurricane. The species composition also changed as the most common species, *Porites cylindrica*, suffered a relatively greater loss of cover than any of the other species. By 1984, the species composition had almost recovered to its original value, although the coral cover continued to decline after 1978. The nearly complete recovery by 1984 was due to recruitment of *P. cylindrica* and four other species, and in two others, the persistence of colonies present before the decline. These changes refer to species composition based on cover, which was affected more than the number of genets by the hurricane. Genet number was reduced only 22% in that period, and the species composition based on genet numbers changed much less than that based on cover.

After hurricanes destroyed almost all corals at the Exposed Pools in 1967 and 1992, and at the Exposed Crest in 1972, the species composition during recolonization recovered toward that of the original, but in different patterns (Fig. 9). The composition based on genets recovered more than that based on cover, and the crest recovered more slowly than the pools. Corals at neither site had recovered by 1998 to the degree shown by the Inner Flat between 1978 and 1984, probably because the species pool of recruits on the Inner Flat is small and quite similar to that of the adult population, in contrast to that at the two exposed reef sites, where the species pool of recruits is much larger. As a consequence, recruits at the latter sites are more likely to have a species composition that is different from that of the adult population than at the Inner Flat (Table 10). In contrast, one site, the Protected Slope, showed no drastic effects of disturbance from any of the hurricanes that damaged other sites during the study period, and, judging from the very large sizes of some of the staghorn *Acropora* colonies there (ranging up to 5.5 m diameter), had not been significantly disturbed for many years.

Effects of competition on species composition

Asymmetrical competitive interactions could alter species composition. When species of high competitive ability eliminate neighbors or reduce their size, relative abundances will be altered. Winning species tended to live longer and sometimes to grow faster than losers or those that did not interact. The fact that those that did not interact did not grow faster than those that did interact, implies that relatively little energy is used in competition. A great deal of such space competition occurred at the Exposed Pools from 1974 to 1988, because coral cover rose rapidly after 1974, and remained high until 1988, with one brief drop in cover after the 1980 hurricane. By 1990, D had declined to less than one-third of its 1974 value. Species composition had also changed, as indicated by the percent similarity index that was more than halved in the same period. Since competitive interactions affected life span at the Exposed Pools, this suggests that interspecific competition contributed to these changes in species composition. Likewise, at the Protected Crest, the soft coral *Zoanthus vietnamensis* increased in cover almost 10-fold between 1983 and 1990, overgrowing many smaller hard corals; the number of coral genets fell rapidly during this period. The percentage similarity index also fell more rapidly in this period than prior to 1983, indicating that competitive interactions, by affecting the relative growth rates among the winners and losers, were in large part responsible for this change in species composition (see also Grigg and Maragos 1974, Grigg 1983).

General conclusions about coral diversity

Variations in alpha and beta diversities of corals at the different localities on Heron reef can be produced by several factors. For example, there were differences in the direct effects of storm damage, and in the mechanisms influencing recovery thereafter, principally the differences in the size of the species pools of recruits, and in the contrasting competitive processes due to the disparate local environments at the various sites (Fig. 11). Soon after a major disturbance, such as a severe hurricane that removes most corals and algae, diversity is low because abundance is low. With time, recolonization occurs and diversity rises. In some places, such as the Inner Flat, the species pool of coral larval recruits that were available, competent to settle, and able to survive, is apparently very low, so S and D never reach high levels. At the other study sites, this species pool of recruits was much higher, and S and D soon rise to high levels.

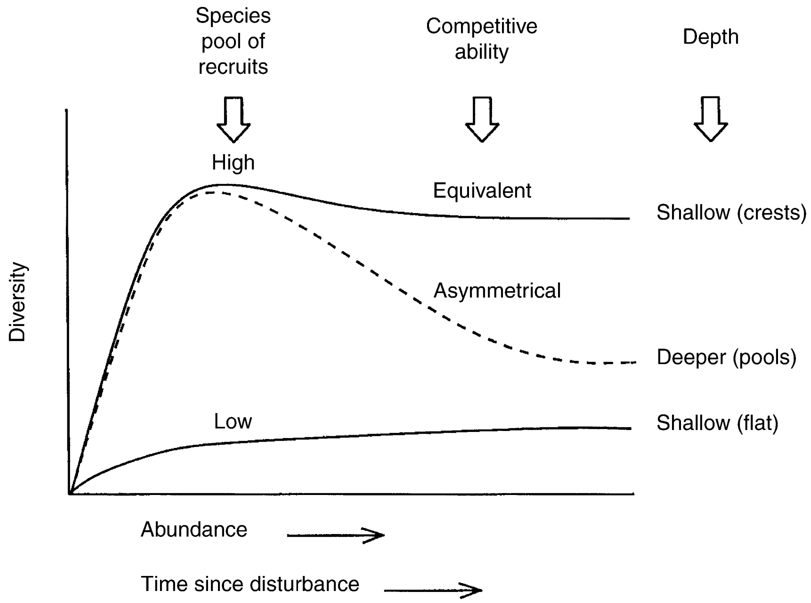

FIG. 11. Hypotheses of the relationship of species diversity to variation in abundance in different environments, either in a series of samples or during recovery of abundance following a drastic disturbance.

On the exposed side of the reef, after hurricanes caused heavy destruction of corals, abundance, *S*, and *D* recovered and reached their peaks in periods ranging from 3 to 25 years. One reason for the long recovery times is that the physical environment is sometimes changed so drastically during a hurricane that a long period is required for it to again become suitable as a habitat for corals. For example, at the Exposed Crest site, the habitat was changed during the 1972 hurricane from one almost continually bathed in water to one that dried out every low tide. A channel had been broken through the crest during the storm, diverting most of the tidal outflow into it, so instead of the previous broad sheet of water draining over the entire crest, a section of the Exposed Crest within ~250 m of the channel (including the permanent study quadrats) was left high and dry at low tide. Gradual breakdown of this intertidal substrate was still continuing 28 years after the hurricane. In contrast, at the Exposed Pools after the 1967 and 1972 hurricanes, abundance, *S*, and *D* recovered rapidly, since the physical environment was not changed appreciably.

An environmental shift similar to that at the Exposed Crest occurred on the Protected Crest; in 1983, a launch was washed up on the crest, where its rocking motion overnight cut a narrow channel across the crest. This produced an effect on tidal drainage similar to, but not as drastic, as that caused by the 1972 hurricane at the Exposed Crest site, causing adjacent sections of that crest, including the study quadrats, to become drier at low tide. Soon thereafter, the soft coral *Zoanthus vietnamensis* invaded and increased in cover almost 10-fold, overgrowing many smaller hard corals; probably as a consequence, *D* fell steeply over the next few years (Fig. 7). *Zoanthus* is apparently more tolerant of drier conditions than the hard corals.

Once *S* and *D* have peaked during recolonization after a disturbance, they may fluctuate around a high level or decline to a much lower level, depending upon several factors. At the Exposed Pools, *D* based on cover declined gradually between 1972 and 1990, similar to the pattern of number of genets but not to that of percent cover, which remained high. This decline in *D* was due to a few competitively superior species increasing to dominate the cover at the expense of others, some of which disappeared, presumably being overtopped by the dominants. At the Exposed Crest site, *D* did not decline over time, in part because the superior competitors could not overtop or overgrow inferior competitors without exposing themselves to increased mortality from deleterious exposure at low tide (Fig. 7).

In the study sites on the protected side of the reef, *S* and *D* have also gradually declined over time. One cause of the decline is a reduction in abundance in the 1980s, due to a gradual deterioration of the physical environment, as a consequence of upward coral growth into the intertidal region. Within branching colonies, the stunted adjacent branches fused as they grew, gradually coming to resemble encrusting colonies in completely covering the substrate with living tissue. As they grew upward into the intertidal zone, the higher portions died, presumably from conditions related to aerial exposure. Eventually, the entire fused upper surface died, and with erosion, formed a solid substrate with few crevices. Thereafter, surface erosion and boring organisms gradually broke down the solid substrate. This cycle of recruitment, growth, death, and erosion on the crests and inner flat produces a patchwork of living and dead surfaces.

The decline in coral diversity at the Inner Flat sites in the 1980s was due mainly to upward growth, but may have been hastened or protracted by competition with algae. At the Inner Flat, macroalgal cover of hard substrate fluctuated between 15% and 85% in the years between 1962 and 1983, rising to above 95% by 1989 (J. H. Connell, *unpublished data*). These fluctuations suggest that some environmental change allowed algae to increase in the early 1980s and to remain high in the late 1980s. The causes of this increase are unclear, but may be associated with (1) increases in tourism at the resort, which may have increased the seeping of sewage into areas close to the cay, and (2) dredging activity in the harbor, which may have caused increased sedimentation in nearby sites (Staunton Smith and Johnson 1995).

At some deeper sites, some reductions in *S* and *D* seem to be caused by interspecific competition at the Exposed Pools. At the Protected Slope, those transects with low *S* and *D* had high coral cover dominated by very large colonies of staghorn *Acropora* species, which are capable of overtopping massive, encrusting species and the smaller branching species. Likewise, at shallow depths on the Exposed Slope, after the 1992 hurricane caused heavy damage, cover and diversity rose rapidly. Thereafter, cover remained high, but diversity plummeted, presumably as a result of strong interspecific competition.

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APPENDIX A

Descriptions of the sampling design and dates are available in ESA's Electronic Data Archive: *Ecological Archives* M074-003-A1.

APPENDIX B

A table of the sampled species is available in ESA's Electronic Data Archive: *Ecological Archives* M074-003-A2.

APPENDIX C

Results of the encounters between neighboring corals at the Exposed N. Crest, 1963–1989, are available in ESA's Electronic Data Archive: *Ecological Archives* M074-003-A3.

APPENDIX D

Results of the encounters between neighboring corals at the Exposed Pools, 1962–1989, are available in ESA's Electronic Data Archive: *Ecological Archives* M074-003-A4.

APPENDIX E

Results of the encounters between neighboring corals at the Protected S. Crest, 1963–1989, are available in ESA's Electronic Data Archive: *Ecological Archives* M074-003-A5.