

Long-term dynamics of reef crest corals on Heron Island: 1960s to 1990s

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Abstract

Over a 30-year period, the abundance and recruitment of reef-building corals varied drastically, at several scales of space and time, at Heron Island, Great Barrier Reef, Australia. Observations were made at six study areas at spatial scales ranging from one to 1850 m apart, in depth from zero to 14 m, and at temporal scales ranging from one year to three decades.

The abundance of corals declined nearly to zero at some time during the study period at five of the six study areas. Recurrent cyclones (hurricanes, typhoons) were a major cause of coral mortality. In 11 of the 30 years of our study, 17 cyclones passed within 200 km, and in five of these years, at least 40% of the coral cover was killed in one or more study areas. Damage varied considerably among cyclones; the most likely reason for the variability in their effects was a difference in maximum wind speeds at Heron Island. Damage also varied considerably among the different study areas. Cyclones damaged and killed corals and other organisms, and also removed sections of hard substrate and shifted sediments, sometimes altering the pattern of water movement and drainage at low tide. Both the degree of damage caused at different sites, and the rate and extent of recovery thereafter, were influenced by the history of previous damage and recovery.

Recruitment of corals also varied at different spatial and temporal scales. Recruitment rate differed seven-fold among study areas. Years of high input were not consistent among the different study areas. Recruitment rates at two sites declined over the past decade as substrate conditions worsened with increased exposure to air at low tide.

Human impacts at these study sites were relatively small compared to natural changes. Management decisions should be based on a sound knowledge of the mechanisms underlying the dynamics of coral reefs. While long-term monitoring studies are invaluable tools for generating hypotheses, future research will require a much greater focus on experimental manipulations to answer basic and applied questions.

Introduction

A principal goal of ecology is to understand patterns of variation of populations and communities, and the mechanisms that determine them. The present study represents a rare long-term examination of the extent of variation in abundance and recruitment of tropical corals, on a reef that is relatively free of human impacts. In recent years, the effects of human activities on ecosystems has been widely recognised. For example, several reviews (e.g. Rogers 1985; Brown 1987; Grigg and Dollar 1990; Ginsburg 1993; Hughes 1994) have concluded that many coral reefs are endangered by destructive human activities (such as overfishing, dredging, mining, logging, and urban and agricultural pollution). Since anthropogenic effects are superimposed upon natural patterns, an understanding of natural variation in abundances, and

of the mechanisms underlying them, is essential for making rational decisions as to how to manage ecological assemblages.

Studies on coral reef assemblages have been done at several spatial and temporal scales, but few of these extend beyond a single site or last for more than three years (i.e. the approximate duration of a PhD study or research grant). Notable exceptions include studies by Davis (1982), Done (Done 1992) and Hughes (1994). Connell (1996) provides a review of numerous other reef studies that have quantified variations in coral assemblages, and the mechanisms underlying them, over both small and large temporal and spatial scales.

Numerous physical and biotic processes may influence patterns of abundance of corals and associated species on reefs. Reductions in abundance are usually associated with mortality events, which vary hugely in spatial and temporal scale (e.g. from an instantaneous fishbite affecting a portion of a single coral colony to global extinctions of species in geological time). Increasingly, on many reefs significant declines in coral assemblages are being caused by both immediate and cumulative impacts of human activities (e.g. Lessios et al. 1988; Rogers 1985; Brown 1987; Salvat 1987; Grigg and Dollar 1990; d'Elia et al. 1991; Ginsburg 1993; Hughes 1994). Increases in abundance of corals are the results of recruitment and growth. Recruitment in corals has been extensively studied, usually within the first weeks or months after initial settlement from the plankton (reviewed by Harrison and Wallace 1990).

Objectives

The major objective of our studies at Heron Island is to understand the mechanisms of change in assemblages of reef-building corals (rather than simply describing an increase or decline in abundance). This goal is difficult to achieve in species with long life spans and episodic recruitment, such as forest trees and corals, where disturbances may be sudden but recovery is often slow (Connell 1973, 1978; Colgan 1987; Hughes 1994). On the other hand, like most other sessile organisms, corals have the advantage of being relatively open to direct observations of recruitment, growth, and mortality. Therefore, by making frequent censuses of permanently-marked sites, it is possible to identify important mechanisms (such as mortality from cyclones and pulses of recruitment) that cause changes in abundance. By repeating censuses over long time periods, one can document variation in the effects of both relatively rare extreme events, such as violent cyclones, and of very gradual trends and slow changes, undetectable in a short-term study.

Specifically, we have addressed two general questions based on long-term studies at Heron Island, Australia from 1962 to 1992:

1. What were the patterns of variation in abundance and recruitment of corals, and
2. What were the principal mechanisms underlying these patterns

To address these issues, observations were made over both small and large spatial scales (from cm to km), and over short and long time periods (from annual to multi-decadal). Over the 30-y period of this study, the mean percentage cover of corals in four of six study areas ranged from >50% to <0.1%, revealing the considerable extent of natural variation at several temporal and spatial scales.

This report presents only a brief summary of our findings. Further details are found in Connell et al. 1997.

Methods

To measure changes in distribution and abundance of corals under different environmental conditions, we established permanent study areas in different habitats arrayed across Heron Reef, from the inner reef flat close to the cay, to the reef crest, and beyond to shallow pools isolated from the open water at low tide, and finally to the outer slopes (Fig. 1). There was one or more sites within each study area, each with samples in the form of square meter quadrats, line intercept transects, or belt transects. Detailed site descriptions and methods are provided in Connell et al. (1997).

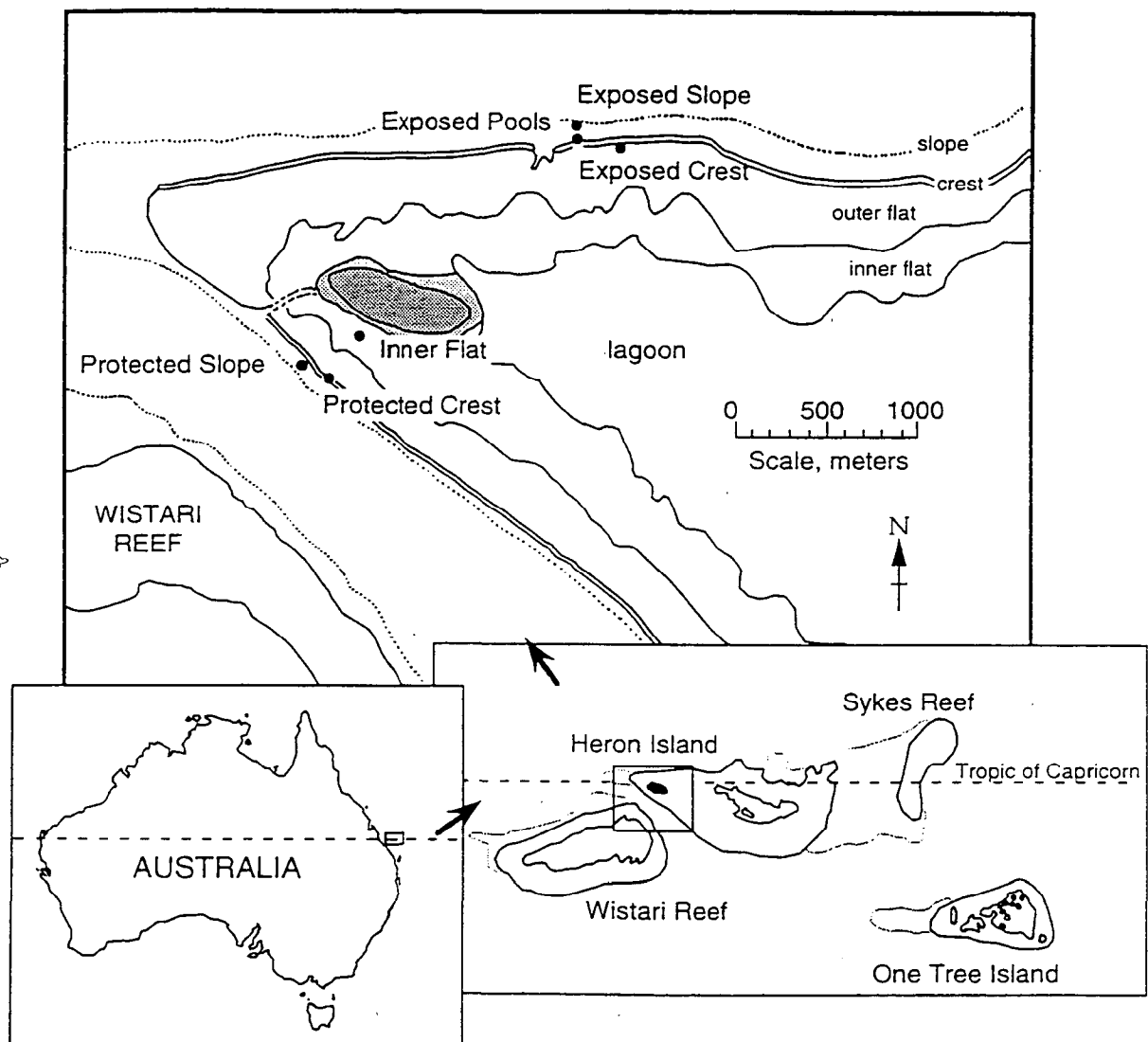


Figure 1. Study sites on Heron Island Reef: 1 = Inner Flat, 2 = Protected Crest, 3 = Exposed Crest, 4 = Exposed Pools, 5 = Protected Slope, 6 = Exposed Slope. Dashed lines to the SW of the island indicate a boat channel first dredged in 1966.

Within each of the study areas, we sampled the abundance and recruitment of corals and macroalgae. The data presented in this report are based on the quadrats only (see Connell et al., 1997 for additional results). The replicate 1 quadrats were established using stakes (reinforcing bars of mild steel, 9 mm diameter) driven in at the four corners. These quadrats were placed in one or more study sites within each study area. At low tide, a colour slide photograph was

taken of each side of these 1 m² quadrats from vertically above, using a 35 mm SLR camera which was mounted on a tripod attached to a 1 m² frame that fitted over the steel stakes; the pair of photographs of a single quadrat overlapped in the middle. Thirty-seven visits to Heron Island were made in 23 different years between 1962 and 1992.

Each colour slide photograph was projected and the boundaries of all coral colonies and clumps of macroalgae were traced to make a map at a scale of one-half the original size. The area of each individual was measured with a digitizer at each census to yield data on cover, population structure, diversity, growth, survival, etc.

Results

In this section we discuss two of the major processes that influence abundance: mortality and recruitment. The principle agents of mortality were storm damage (which caused sudden crashes) and the effects of exposure to air at low tide (which caused gradual declines). Recruitment was significantly influenced by changes in characteristics of the substrate, both physical and biotic.

Patterns of abundance

Sudden declines: mortality in violent storms

Corals exhibited a range of patterns of decline in different areas, showing sudden extreme crashes in cover in some places, and gradual long-term downward trends in others (Fig. 2). Each study area had a characteristic pattern of variation, due to different mechanisms operating (see below).

On the exposed (northern) edge of the reef, declines were abrupt, due to violent tropical cyclones passing close to Heron Island. Photographs of the permanent quadrats in the census after cyclones revealed extensive whole- and partial-mortality of corals: many branches were smashed or sheared off, abraided fragments were common, and many colonies had disappeared entirely. Significant damage to corals occurred in five years (1967, 1972, 1976, 1980 and 1992), and sometimes the physical environment was altered (e.g. sections of hard substrate were broken away, sediments shifted, and the pattern of water movement and drainage at low tide changed).

In contrast, on the protected side of the reef, the only pronounced cyclone damage was at the Protected Crest in 1980 (62% loss of cover), and at the Inner Flat in 1976 (46% loss). Clearly, the effects of each cyclone differed among the study areas. The 1967 cyclone was very damaging to corals at the Exposed Pools, but caused only minor or no damage to the other areas (Fig. 2). Similarly, although the 1972 cyclones killed almost all corals on the Exposed Crest, and caused relatively large reductions in cover at the Exposed Pools, they caused only minor damage to other study areas. The 1976 cyclone caused moderate reductions in cover and density at the Inner Flat, and minor loss of cover at the Protected Crest. The 1980 cyclone caused moderate reductions in cover and density at the Exposed Pools, to cover at the Protected Crest, and to density at the Inner Flat. Finally, the 1992 cyclone caused heavy damage to cover and moderate reduction in density at the Exposed Pools but had little effect at the other areas (Fig. 2). This cyclone removed most of the macroalgae from the Inner Flat; beforehand, in 1991, algae had covered almost all of the hard substrate there that was not occupied by corals; afterwards, algae remained at a low level in annual censuses up to 1995 (unpublished data).

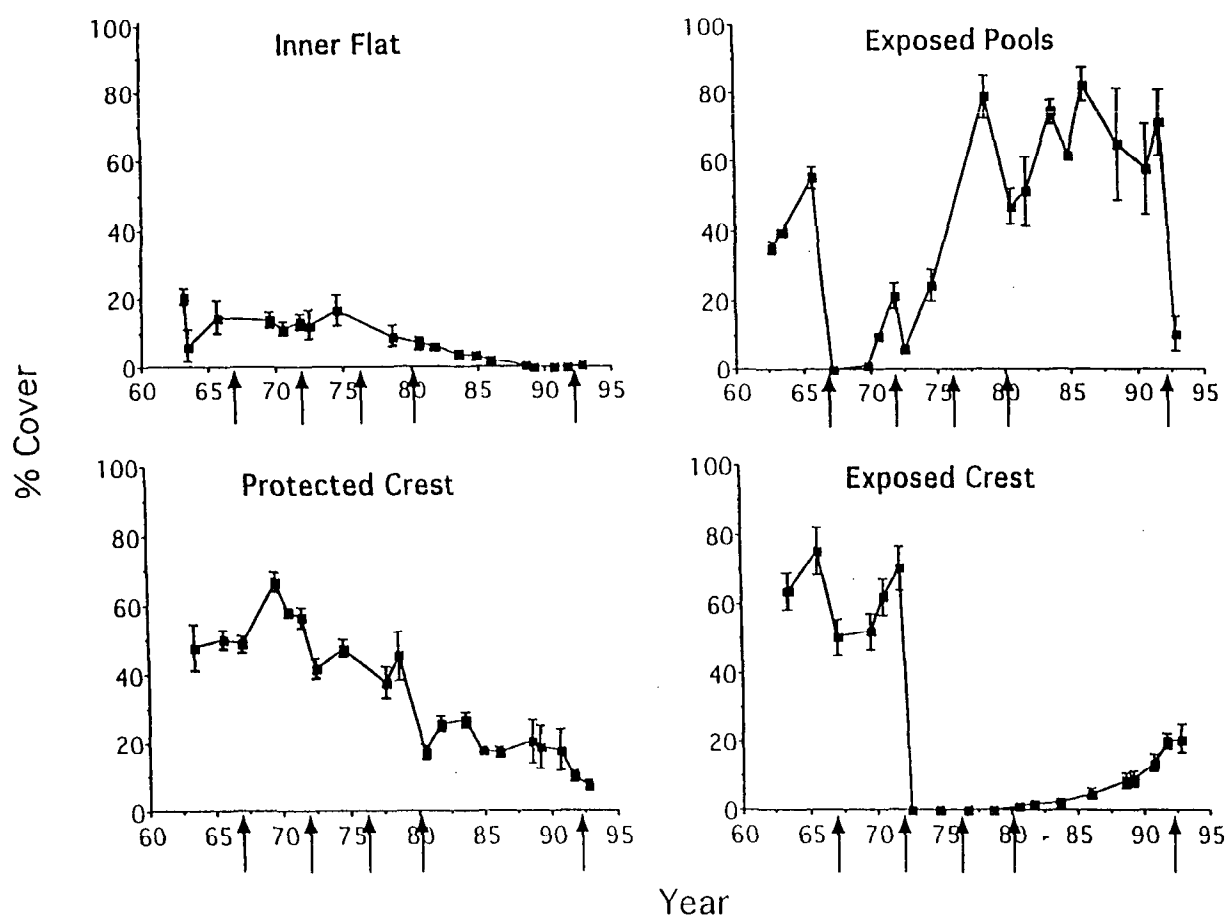


Figure 2. Percentage cover of corals (mean \pm 1 s.e.) on the four shallow sites with permanently marked quadrats. Arrows indicate cyclones.

Gradual declines: mortality from exposure to air at low tide

In contrast to the population crashes at the Exposed Crest and Pools, the long-term patterns of abundance at the Protected Crest and Inner Flats were remarkably different, being characterised by an early period of relative constancy, followed by very gradual declines. At the Protected Crest, coral cover peaked in 1969 (Fig. 2) and thereafter declined irregularly, with little damage (<27% loss of cover) in four of the cyclone years and greater damage (62% loss of cover) in 1980. Some of the decline in cover since 1981 was probably due to the effects of increasing exposure to air as the corals slowly grew upward. The photographic records show extensive in situ mortality of branch tips and tops of massive colonies, which slowly eroded. Basal parts of the colonies survived, but growth was gradually redirected sideways instead of vertically. This process may have been exacerbated when a 13 m launch ran aground on the reef crest in June 1982, eroding a shallow channel across the crest about 50 m east of the Protected Crest study area. As a result, some of the receding tide has continued to flow out this channel, increasing the exposure to air at low tide at this site.

The Inner Reef Flat usually had the lowest abundance of corals of any study area, except when cyclones killed most corals at other sites (Fig. 2). From 1963 to 1981, cover in the permanent quadrats fluctuated between 8% and 18%, then between 1981 and 1989, it declined gradually to nearly zero. This decline occurred over a large region of the inner flat (Connell et al. 1997).

This low average level of abundance on the inner flat in recent years is due to several factors. First, colonies died, partially or completely, from exposure to air as they grew above the low tide level. Second, the area had the lowest rate of recruitment, as described below. Last, some changes were related to the incidence of cyclones; coral cover fell, declining by 46%, in only one cyclone year (1976), and genet density declined between 22% and 32% in the cyclones of 1972, 1976, and 1980. During these cyclones, few colonies were broken, although some were tilted up above the low tide level and died from exposure to air. Cyclones also caused sediments to shift temporarily into groups of colonies, partially burying the larger ones, and completely burying and killing small colonies.

Recoveries in abundance

The rate of recovery of corals differed among study areas and among cyclones. At the Exposed Pools after the 1967 cyclone, which few corals survived, the rates of recovery of coral cover was slow (Fig. 2), because of limited recruitment by larvae and fragments (Fig. 3). In contrast, after the 1972 cyclones, cover recovered rapidly due to regrowth of survivors. In the 1980 cyclone, only a moderate reduction in cover and density occurred at this study area, and both recovered rapidly thereafter.

At the Exposed Crest the rate of recovery after the 1972 cyclone was extremely slow, because storms had caused most of the substrate to dry out at each low tide. Over the 20 years since then, much of the surface has been slowly eroded away in pockets which have vertical or overhanging shaded sides, providing moist spots in which coral recruits are able to survive. By 1992 erosion had removed about 60% of the uninhabitable dry surface and the maximum degree of recovery had reached about 63% of the original number of genets and 29% of the original cover.

On the protected side of the reef, recovery from limited cyclone damage ranged from moderate to nil. At the Protected Crest, the recovery rate of coral cover after the 1980 cyclone, which caused the most damage, was slower than that after other cyclones. At the Inner Reef Flat, the rates of recovery were rapid after the minor damage from the 1972 cyclones, but were nil after the next two cyclones. In both areas, the overall long term trend was a gradual decline (Fig. 2).

Recruitment of corals

Recruitment rates showed considerable temporal variation within each study area. Moreover, the coefficient of variation ranged 7-fold among the study areas; the Protected Crest had the least variation, the Inner Flat the most, with the two other study areas being intermediate (Fig. 3). Recruitment rates also differed significantly among the study areas, the mean values for each area ranging from 1.7 to 12.7 recruits/sq m/year. The Protected Crest was highest, the Inner Flat the least, while the Exposed Pools and Exposed Crest were intermediate. Recruitment rates varied among study areas but not among years, with a significant interaction term (see Connell et al. 1997). This result suggests that years of good (or poor) recruitment were not consistent across all sites.

We tested the hypothesis that recruitment rate could depend on variation in free space, since coral larvae cannot attach to living coral. The recruitment rate increased with the amount of free space available at three of the four study areas (Connell et al. 1997). The exception was the Protected Crest, where free space never fell below 25%, so that the power of the test was low. Free space was preempted mainly by the presence of corals at the two crest sites and the Exposed Pools, since macroalgae never occupied more than 5% of the surface at the crests, or 15% at the Exposed Pools (unpublished data). In contrast, macroalgae were often the main occupiers of space at the Inner Flat site; here coral cover never rose above 35%, whereas

macroalgal cover ranged up to 90%. Therefore we hypothesised that reduction in coral recruitment at the Inner Flat was due mainly to preemption of space by macroalgae rather than by corals. To test this hypothesis we regressed recruitment rate against cover of either algae or corals at the Inner Flat. Recruitment rate fell as algal cover rose ($r^2 = 0.21$, $p < 0.001$, $N = 50$), but showed no significant correlation with coral cover at this study area.

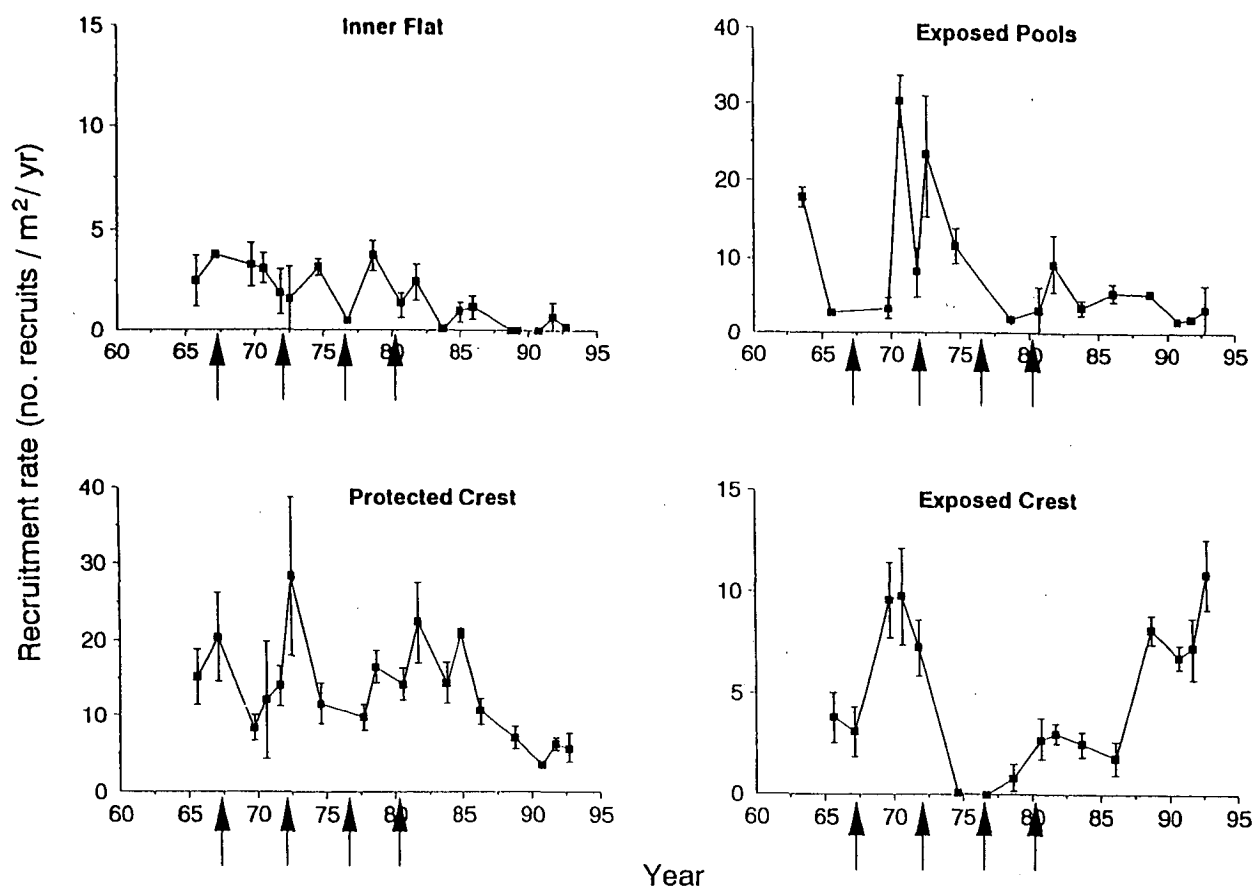


Figure 3. Coral recruitment (no./m²/year, mean \pm 1 s.e.) over time on the four shallow sites with permanently-marked quadrats. Arrows indicate cyclones.

Discussion

Mechanisms affecting the abundance of corals

The two principal mechanisms associated with significant mortality in this study were natural rather than anthropogenic: cyclones and exposure to air. Recurrent cyclones produced sharp declines at most study areas at least once, but their effects were extremely patchy and they never impacted on all sites simultaneously. For example, although the Protected Crest study area is usually sheltered by nearby Wistari reef, it was the only location which suffered heavy damage in the 1980 cyclone. Similarly, the Exposed Pools and Exposed Crest, within 20 m of each other, suffered > 60% mortality in 1972, while other intertidal study areas were virtually unaffected. Therefore, we conclude that the spatial scale of cyclone damage was relatively small, usually affecting adjacent areas differently at a scale of a few 10s of metres or larger. Similar patchiness in damage from cyclones has been described elsewhere from subtidal sites, especially in relation to attenuation of wave damage in deeper water (e.g. Woodley et al. 1981; Porter et al. 1981; Blythell 1993; Hughes 1994).

Exposure to air as corals grew above the low tide levels was associated with more gradual declines in abundance. In larger colonies, damage from aerial exposure often began as partial loss of tissue, gradually increasing over several years as the colony grew upward. While this slow process occurred to some extent at all of the intertidal areas, its effects were strongest at the Protected Crest and Inner Flat, where coral cover gradually declined during the last 20 years of the study period. This slow decline in abundance occurred concordantly in both these study areas, and in study sites up to 350 m apart within each habitat. We conclude that mortality from exposure to air on Heron Island operates at a relatively large spatial scale of 100s of metres. Elsewhere, widespread mortality of corals from desiccation has been reported following unusually low tides (e.g. Loya 1990) and tectonic uplifting (e.g. Cortez 1993).

Mechanisms affecting recruitment of corals

Recruitment in marine organisms is notoriously variable in space and time (e.g. Coe 1957; Caffey 1985; Milicich and Doherty 1994). The causes of spatial variation in recruitment rates could include differences among study areas in: 1) supply of larvae from the plankton, 2) suitability of the substratum for settlement, and 3) mortality during the period between settlement and the time they were first censused.

Spatial variations in water circulation are probably more likely to supply similar numbers of larvae to adjacent quadrats than to widely separated sites in different habitats, which could produce the observed spatial pattern of variation in recruitment (see also Steele 1978, 1989; Caffey 1985; Babcock 1988; Harrison and Wallace 1990; Milicich and Doherty 1994). The swift currents channelled between Wistari and Heron reefs could explain, in part, the significantly faster rates of recruitment at the Protected Crest than at other areas. Similarly, sluggish water movement at the Inner Flats may have contributed to the very low rates of recruitment there (Fig. 3).

We documented evidence for two mechanisms which are likely to have affected the rates of settlement; inhibition by the established benthos and harsh physical conditions on the substrate. Firstly, recruitment rate per year was positively correlated with the amount of free space available at Heron Island, indicating that resident corals and/or algae preempt space sought by settling larvae (or subsequently smother newly settled juveniles). This relationship has been confirmed experimentally at Rio Bueno, Jamaica (Hughes 1986), where annual recruitment over six years was much higher on plots cleared of all corals than on undisturbed plots. Secondly, spatial and temporal patterns of recruitment may have reflected variation in the suitability of the substrate. For example, settlement is likely to have been inhibited by desiccation at the Exposed Crest after the 1972 cyclone up to 1986, and at the Protected Crest since 1985. Rates of recruitment at other periods at these two study areas were much higher (Fig. 3).

Conclusions

We measured a very wide range of community dynamics on Heron Reef, in part because we studied these assemblages for a relatively long period compared to most ecological investigations, and because the spatial scale of the study was sufficiently large to include a variety of habitats. The present study emphasises that there is considerable spatial and temporal variation in the effects of rare events such as cyclones. The dramatic differences in damage to corals at different sites and times at Heron Island caused by five different cyclones (Fig. 2), emphasises the difficulty in drawing general inferences from observations of a single event in isolation. Long-term studies are required to fully understand the full range of dynamic responses of coral reefs.

Anthropogenic changes had only minor impacts at our sites. However, we stress that this study was not designed to examine human impacts (e.g. with quadrats established close to areas of impact together with comparable controls further removed from human influence). To detect the effects of dredging, anchor damage, fishing, reef walking and nutrient additions on Heron Reef would require appropriate sampling designs and experimental tests.

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References

- Babcock, R.C. 1988. Fine-scale spatial and temporal patterns in coral settlement. *Proceedings of the Sixth International Coral Reef Symposium* 2: 635-639.
- Blythell, J.C., E.H. Gladfelter and M. Blythell 1993. Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12: 143-152.
- Brown, B.E. 1987. Worldwide death of corals - natural cyclical events or man-made pollution? *Marine Pollution Bulletin* 18: 9-13.
- Caffey, H.M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55: 313-332.
- Coe, W.R. 1957. Fluctuations in littoral populations, *Geological Society of America Memoir* 67 1: 935-940.
- Colgan, M.W. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci* *Ecology* 68: 1592-1605.
- Connell, J.H. 1973. Population ecology of reef-building corals, pp. 205-245. *In* O.A. Jones and R. Endean (eds). *Biology and Geology of Coral Reefs*. Academic Press, New York.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Connell, J.H. 1996. Long term studies of coral reefs: A review. *Proceedings 8th International Coral Reef Symposium*, Panama.
- Connell, J.H., T.P. Hughes and C.C. Wallace 1997. Scale of space and time in the abundance and recruitment of corals. *Ecological Monographs* (in review).
- Cortés, J. 1993. Recently uplifted Caribbean Reef. *Coral Reefs* 12: 76.
- d'Elia, C.F., R.W. Buddemeier and S.V. Smith (ed.) 1991. Workshop on coral bleaching, coral reef ecosystems and global change: Report of proceedings. Maryland Sea Grant College, College Park.
- Davis, G.E. 1982. A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bulletin of Marine Science* 32: 608-623.
- Done, T.J. 1992. Constancy and change in some Great Barrier Reef coral communities: 1980-1990. *American Zoologist* 32: 665-662.
- Fisk, D.A. and V.J. Harriot 1992. Are understorey coral communities recruitment limited? *Proceedings of the Seventh International Coral Reef Symposium (Guam)* 1: 517-520.

- Ginsburg, R.N. (ed.) 1993. Global aspects of coral reefs: health, hazards and history. Colloquium at the Rosenstiel School of Marine and Atmospheric Sciences. University of Miami, Florida.
- Grigg, R.W. and S.J. Dollar 1990. Natural and anthropogenic disturbance on coral reefs, pp. 439-452. *In* Z. Dubinsky (ed.). *Ecosystems of the World: Coral Reefs*. Elsevier Press, Amsterdam.
- Harrison, P. and C.C. Wallace 1990. Reproduction, dispersal and recruitment of scleractinian corals, pp. 133-207. *In* Z. Dubinsky (ed.). *Ecosystems of the World: Coral Reefs*. Elsevier Press, Amsterdam.
- Hughes TP, 1986. Life histories and population dynamics of early successional corals, in *Proceedings of the 5th International Coral Reef Congress, Tahiti, Vol. 4*, pp. 101-106.
- Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.
- Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review of Ecology and Systematics* 19: 371-393.
- Loya, Y. 1990. Changes in a Red Sea coral community structure: a long-term case history study, pp. 369-384. *In* G.M. Woodwell (ed.). *The earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, Cambridge, England.
- Milicich, M.J. and P.J. Doherty 1994. Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. *Marine Ecology Progress Series* 110: 121-134.
- Porter, J.W., J.D. Woodley, G.J. Smith, J.E. Neigel, J.F. Battey and D.G. Dallmeyer 1981. Population trends among Jamaican reef corals. *Nature* 294: 249-250.
- Rogers, C.S. 1985. Degradation of Caribbean and western Atlantic coral reefs and decline of associated fisheries. *Proceedings of the 5th International Coral Reef Symposium, Tahiti*. 6: 491-496.
- Salvat, B. (ed) 1987. Human impacts on coral reefs: facts and recommendations. Antenne Museum Ecole Pratique des Hautes Etudes, French Polynesia.
- Steele, J.H. 1978. Some comments on plankton patches, pp. 1-20. *In* J.H. Steele (ed.). *Spatial pattern in plankton communities*. Plenum, New York.
- Steele, J.H. 1989. Scale and coupling in ecological systems, pp. 177-180. *In* J. Roughgarden, R.M. May and S. Levin (eds). *Perspectives in ecological theory*. Princeton University Press, Princeton, NJ, United States of America.
- Woodley, J.D., E.A. Chornesky, P.A. Clifford, J.B.C. Jackson, L.S. Kaufman, N. Knowlton, J.C. Lang, M.P. Pearson, J.W. Porter, M.C. Rooney, K.W. Rylaarsdam, V.T. Tunnicliffe, C.M. Wahle, J.L. Wulff, A.S.G. Curtis, M.D. Dallmeyer, B.P. Jupp, M.A.R. Koehl, J. Neigel and E.M. Sides 1981. Hurricane Allen's impact on Jamaican reefs. *Science* 214: 749-755.