

Ecological Studies of Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands:

**A Quantitative Assessment of Selected Components
of the Coral Reef Ecosystem and
Establishment of Long-Term Monitoring Sites**

Part II

U.S. Department of the Interior, National Park Service

Island Resources Foundation

West Indies Laboratory

**Ecological Studies of
Buck Island Reef National Monument,
St. Croix, U.S. Virgin Islands:**

**A Quantitative Assessment of Selected Components
of the Coral Reef Ecosystem and
Establishment of Long-Term Monitoring Sites**

Part II

John C. Bythell, Elizabeth H. Gladfelter and Mary Bythell

**A Report Prepared for the
U.S. Department of the Interior, National Park Service**

June 1992

**Island Resources Foundation
6296 Estate Nazareth No. 11
St. Thomas, U.S. Virgin Islands 00802-1104**

and

**West Indies Laboratory
Teague Bay, St. Croix
U.S. Virgin Islands 00820**

CONTENTS

Foreword	i
Introduction	ii
Acknowledgements	iv

Chapter 1. Benthic reef community dynamics at selected sites at Buck Island Reef National Monument, 1988-1991: Monitoring fixed linear transects using the chain transect technique. <i>John C. Bythell and Mary Bythell</i>	1
--	---

Chapter 2. Changes in fish assemblage structure at Buck Island, St. Croix, U.S. Virgin Islands from 1980-1990: an indication of predictability in coral reef fish assemblages based on known habitat changes? <i>Elizabeth H. Gladfelter, John C. Bythell and Zandy Hillis</i>	14
--	----

Chapter 3. Coral reef community structure assessment based on planar and three-dimensional area cover: A comparison of techniques. <i>John C. Bythell and Mary Bythell</i>	29
--	----

Chapter 4. Chronic and catastrophic natural impacts on three common Caribbean reef corals: Causes and scale of partial and whole-colony mortality. <i>John C. Bythell, Elizabeth H. Gladfelter and Mary Bythell</i>	40
---	----

Chapter 5. Relative effects of parrotfish grazing, tissue pigment loss and apparent disease on different morphological types of <i>Montastrea annularis</i> Ellis and Solander. <i>John C. Bythell and Mary Bythell</i>	53
---	----

Chapter 6. A record of coral bleaching at Buck Island Reef National Monument between 1989 and 1991: Post-hurricane and seasonal correlates. <i>Mary Bythell and John C. Bythell</i>	62
---	----

FOREWORD

This report forms Part II of a two-volume series, and is submitted to the U.S. Department of Interior, National Park Service in partial fulfillment of Cooperative Agreement No. CA-5000-0-9024, between Island Resources Foundation and the National Park Service, Southeast Region. We present a summary of our findings up to Phase III of the long-term assessment of reef community dynamics at selected sites within Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. This work forms a part of the regional Coral Reef Assessment Program initiated in 1988, with sister studies in Virgin Islands National Park, St. John; Key Biscayne National Park, Florida and Fort Jefferson National Park, Dry Tortugas. Data are included from Phases I and II which were collected under a previous cooperative agreement (CA-5000-8-8010) between the West Indies Laboratory and the National Park Service. Much of the earlier work, including an analysis of the effects of Hurricane Hugo at Buck Island, was described in Part I of this series. All relevant original materials which were generated during this three-year project, including data-sets, maps and photographs, have been deposited in the care of Zandy Hillis, Biological Technician, National Park Service, St. Croix.

John C. Bythell
October 1991

INTRODUCTION

It is now recognized that coral reefs are dynamic systems and not the stable, climax communities they appeared to early reef researchers. Nevertheless, many of the reef's inhabitants are potentially extremely long-lived, and may exhibit sporadic levels of recruitment. Population turnover may therefore take many years and this has hindered our efforts to investigate reef community dynamics.

The need to understand reef community dynamics has never been greater, with worldwide degradation of coral reef structure and function due to coastal development, pollution and over fishing. Without a sound understanding of community dynamics, we can neither determine the long-term effects of a particular environmental disturbance, or predict the likelihood or speed of recovery once impacted. In addition to localized anthropogenic damage to coral reefs, there have also been disturbing signs in recent years of regional impacts such as the mass-mortality of the sea urchin *Diadema antillarum*, loss of much of the once-dominant elkhorn coral *Acropora palmata* and death of corals following bleaching events throughout the Caribbean and Indo-Pacific. At present we do not have sufficient data to tell whether these regional impacts form part of a larger global deterioration in environmental conditions, perhaps linked to the well-documented changes which are occurring (exponentially over time) in the chemical composition of the atmosphere. However, since tropical communities have evolved under relatively stable environmental conditions, there is a convincing argument that these communities will be the first to show deleterious effects of a changing global climate. As stated at a recent workshop on coral reef ecosystems and global change: "There is an immediate and urgent need for ... the coral reef communities of the world to initiate comprehensive, long-term programs of research to consider responses and trends in coral reefs to all aspects of environmental change and anthropogenic influence, both long and short term".

This report summarizes the findings of the initial three-year phase of a long-term marine ecological monitoring program at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. This program, funded by the U.S. Department of Interior, National Park Service, is integrated with other National Park sites throughout the Caribbean and Florida. During this initial period, a wide-scale survey of the Buck Island reef system was conducted and using this information, several sites were selected and semi-permanently marked for repeated surveys of these fixed sites. Baseline surveys were carried out prior to the impact of Hurricane Hugo in September 1989, an extremely severe class V hurricane, and this report is concerned largely with documenting the effects of the hurricane and the two year period of recovery to date. Chapters 1 and 2 address the dynamics of benthic and reef fish communities over the three year study period. At present there are a considerable diversity of methods employed to assess coral community structure, and it is widely recognized that none of these are ideal, but several different techniques may need to be applied in any given situation. In chapter 3 we compare results from three of the techniques we have employed for monitoring benthic communities. Chapter 4 discusses the implications of the chronic and catastrophic

mortality we have witnessed during monthly observations of tagged individual coral heads from various sites around Buck Island. Since the start of the study, it has been suggested that *Montastrea annularis*, arguably the most common coral in the Caribbean, is in fact a family of at least three separate species. In chapter 5, we show some of the marked differences in mortality rates that we have detected between two co-occurring morphs, possibly further evidence that they should be considered separate species. Finally, in chapter 6, we discuss the coral bleaching record at Buck Island over the last three years. We present data to show that chronic levels of bleaching were elevated for six to twelve months following Hurricane Hugo; evidence either of a long-term stress response or of a prolonged period of tissue repair following this major disturbance.

ACKNOWLEDGEMENTS

After the closure of the West Indies Laboratory (WIL), the continuation of this project into its third phase was made possible by the administration of the staff and officers of Island Resources Foundation. We would also particularly like to thank Dr. Caroline Rogers, Head Biologist V.I. National Park, St. John for her efforts and continued support during and after the transition between administrations.

Data are presented from all three phases of the Buck Island monitoring program between 1988 and 1991. We were aided throughout by National Park Service biologist Zandy Hillis and at various times by West Indies Laboratory technicians Kathi French, Michelle Woodbury and Sarah Lewis, and Jeff Miller, the WIL dive supervisor. Jim Beets helped with developing the fish censusing technique and commented on chapter 2, as did Alan Freidlander. Work on this final phase was carried out largely from our own homes on St. Croix and from the Bythells' personal research boat, the "Double Helix". We would also like to thank Dr. Dennis Hubbard and Karla Parsons for use of space and office equipment in their home, the now almost legendary "Cotton Valley Animal Shelter and Home for Frustrated Geoscientists".

Benthic reef community dynamics at selected sites at Buck Island Reef National Monument, 1988-1991: Monitoring fixed linear transects using the chain transect technique

Chapter 1

John C. Bythell and Mary Bythell

Present address: Centre for Tropical Coastal Management, Department of Marine Sciences and Coastal Management, University of Newcastle upon Tyne NE1 7RU, UK.

Introduction

Over the past two decades the paradigm that coral reefs represent stable, climax communities has been overturned in favor of the intermediate disturbance hypothesis (Connell 1978, see review by Brown and Howard 1985). Hughes and Jackson (1985) showed that coral population turnover may be relatively rapid, even when community structure remains apparently stable. These findings will have profound effects on predictions of the effects of natural and man-induced perturbations on reefs and their subsequent recovery (Porter et al. 1982, Dustan and Halas 1987).

Evidence that hurricanes play a key role in shaping coral reef community structure has been growing in recent decades (Stoddart 1974, Highsmith et al. 1980, Woodley et al. 1981, Graus et al. 1984, Hughes 1989). However, the effects of hurricane damage and subsequent processes of recovery have been shown to be highly variable between sites (Porter et al. 1981, Rogers et al. 1982, Knowlton et al. 1990). An extensive database of hurricane impact and subsequent recovery will therefore be needed before we can draw general conclusions about the mechanisms and scale of hurricane impact on reef community structure and determine the relative significance of other, possibly anthropogenic disturbances on reefs. This can be achieved most effectively by establishing long-term monitoring programs to assess community structure before, during and after a given impact (Rogers et al. 1983).

In 1988 the National Park Service initiated a long-term ecological monitoring program at Buck Island which was in place prior to the impact of Hurricane Hugo in 1989 (Rogers 1988, Hubbard et al. 1991, Gladfelter et al. 1991). Damage from the hurricane, easily the worst to impact the site since 1928 was concentrated on the forereef on the south side of the island down to a depth of approximately 7 m. Elsewhere, damage was remarkably light, and differences between pre- and post-hurricane surveys were not statistically significant using visually assessed, haphazard 1 m² quadrats. Fixed linear transects on the north reef did show a significant change when assessed using the chain transect technique (Porter 1972, Rogers et al. 1983), even though the percent surface area loss of live coral was only approximately 2%

Caution must be exercised when interpreting the relative ecological significance of changes in coral cover, however. In studies of individually tagged coral colonies (Bythell et al. in prep and Chapter 4), we have found highly significant differences not only in hurricane-related mortality between species, but also in chronic mortality rates. Relatively small changes in cover of normally resilient species may be the equivalent of several years of mortality under normal conditions, whereas apparently catastrophic mortality of a species with high turnover rates may be equivalent to only a few years routine mortality.

Here we examine in more detail the changes in community structure caused by the hurricane and processes of recovery over the three year period 1988-1991, from repeated surveys of fixed linear transects using the chain transect technique.

Methods

Sampling design. The chain transect technique employs a three-dimensional approach to assessing relative percent cover of benthic organisms, and is compared with other techniques in Chapter 3 of this volume. Cryptic species and vertical or overhanging surfaces will be included using this method which will be omitted when using most benthic assessment techniques which involve planar, two-dimensional cover estimates. Unfortunately, it is time-consuming and sampling could not be accomplished on a scale sufficient to adequately sample independently within and between reef zones. Instead, four fixed 20 m long transects were established at each of three sites, described in detail in (Gladfelter et al. 1991). Briefly, they can be characterized as follows:

- Site 1.* Relatively diverse coral community, with moderately high structural relief produced mainly by live colonies of *Montastrea annularis* and *Porites porites*. Moderate coral cover (13-29% determined by chain transects).
- Site 2.* Less diverse with very low structural relief; a fairly flat coralline pavement with abundant medium to large sized colonies of encrusting *Diploria clivosa* and hemispherical *D. strigosa*. Highest overall coral cover of the three sites (32-40%)

determined by chain transects).

Site 3. Lowest coral diversity and very low coral cover (0.3-3.3% determined by chain transects), but with high structural relief provided by largely dead stands of *Acropora palmata*.

The starting point of each transect within a site was haphazardly placed and transect lines were then run approximately parallel to the reef front. Transects within sites were treated as independent replicates, and changes over time assessed using repeated measures ANOVA. Changes are representative only of the fixed study sites and may or may not reflect general changes in reef community structure in adjacent areas. In order to assess the variability of the technique itself, each transect was repeated within a few weeks of each other in Spring 1989 (Gladfelter et al. 1991; Chapter 7). While no significant differences were detected in total coral cover, rarer species were not consistently included between replicates. All such replicates were included in the repeated measures ANOVA to assess time-dependent changes.

Survey technique. Transects were marked with steel stakes (concrete reinforcing bar) placed at each end and in the center of the transect (0, 10 and 20 m), which were left in place between repeat surveys. During each survey, a fiberglass measuring tape was stretched taut between the markers to establish the line of the transect and horizontal distances along it. A chain with 1.3 cm links was then carefully placed over the surface contour immediately below the tape. For each linear meter, the number of chain links crossing all substrate types were counted, and the substrate type recorded, including scleractinian corals and hydrocorals to species. The methodology employed is compared to two other widely-used coral reef survey techniques in Chapter 3.

Statistical analyses and graphical descriptors. Corals form clonal, variable-sized colonies and surface area cover is therefore a better predictor of relative resource use than number of individuals (Magurran 1988). Each chain-link was therefore treated as an "individual" for the purposes of assessing coral community diversity statistics. Univariate measures (eg. percent

live cover, Shannon diversity H') have been shown to be less sensitive than multi-dimensional scaling (Kruskal and Wish 1978) and certain graphical descriptors (k-dominance curves, Lamshead et. al 1983) in detecting changes in coral community structure over time (Warwick et. al 1990). These multivariate methods were therefore employed to examine the impact from Hurricane Hugo and subsequent recovery over the following two-year period.

K-dominance curves may be used to show differences in species diversity of two or more samples and is independent of any bias towards species richness or evenness, a problem which affects combined indices such as H' . Non-intersecting k-dominance curves indicate a difference in species diversity of two samples, with the upper curve representing a less diverse sample. Multi-dimensional scaling ordination (MDS) was carried out on a matrix of Bray-Curtis similarity indices, derived from square-root transformed species cover data (Warwick et al. 1990). Ordination was carried out in two dimensions, with linear distances between points (samples) being related to the rank order similarities between them. The degree to which these parameters are proportionally related is given as a stress coefficient, with values generally lying between 0.1 and 0.25.

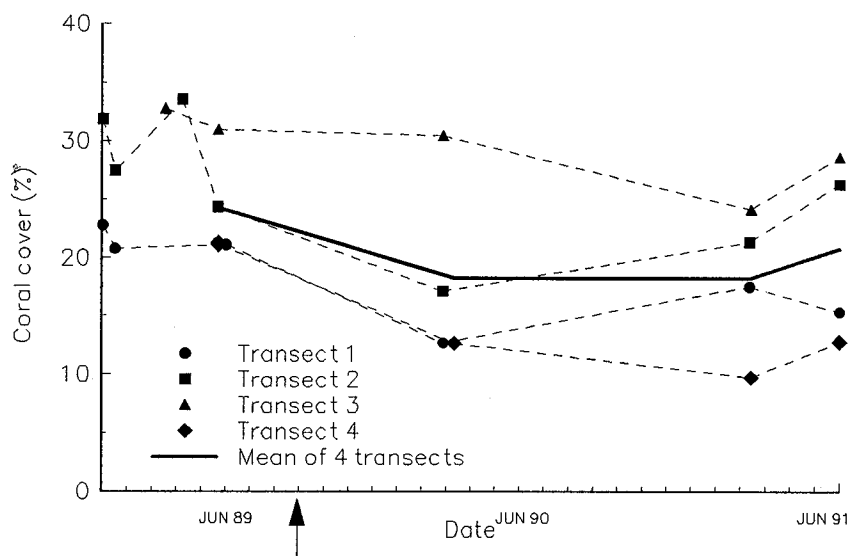
Results

Percent coral cover and species diversity

Percent live coral cover and species diversity (Shannon H') are plotted against date of each survey for the four transects at each of the three sites in Figures 1-3. At the forereef site on the south side of Buck Island (Site 1), three out of four transects showed a marked decline in coral cover after Hurricane Hugo (Fig. 1). This did not result in a significant change over time however (repeated measures ANOVA; $F = 2.2$, $p > 0.1$), unless transect 3 was omitted ($F = 8.4$, $0.05 > p > 0.01$). Reduced coral cover was generally associated with a drop in diversity (Shannon H'), although again no significant time-related changes could be determined ($F = 3.3$, $0.1 > p > 0.05$). All transects had low species diversity, reflecting the dominance in this area of two species, *Montastrea annularis* and *Porites porites* (Appendix 1).

SITE 1

A



B

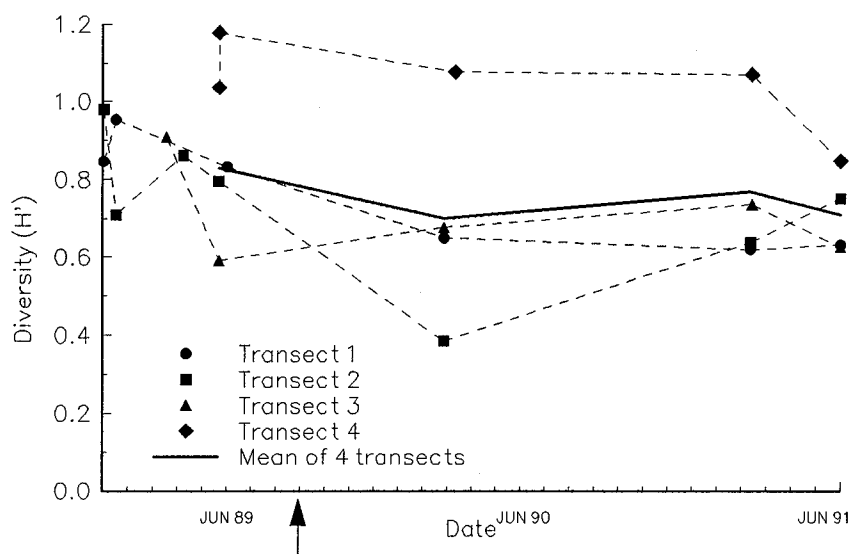
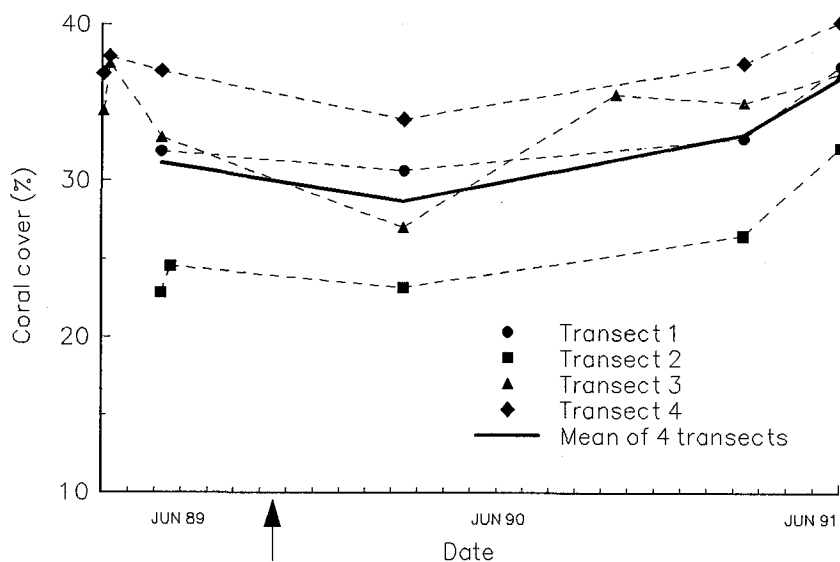


Figure 1. Percent coral cover (a) and Shannon diversity index H' (b) over time for each of the four replicate transects located adjacent to cross-reef transect BI-2 on the south side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

SITE 2

A



B

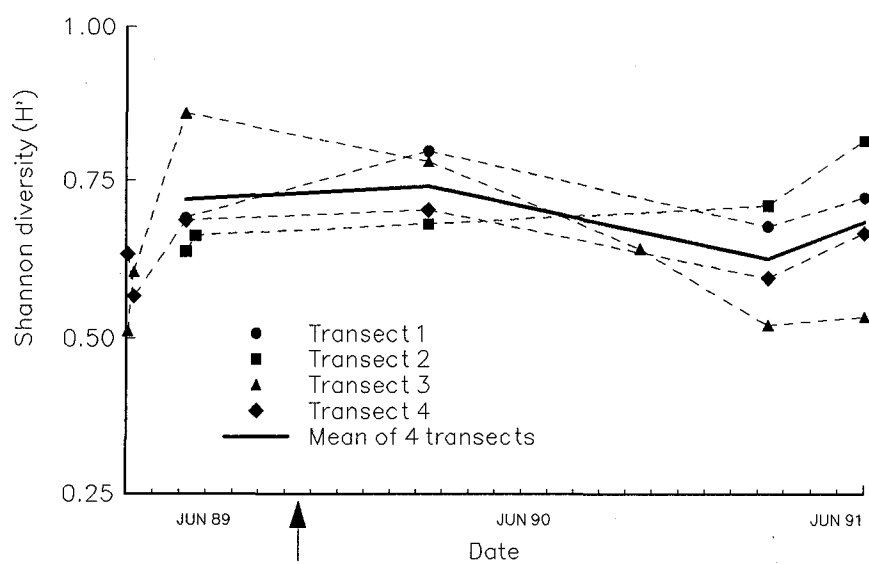
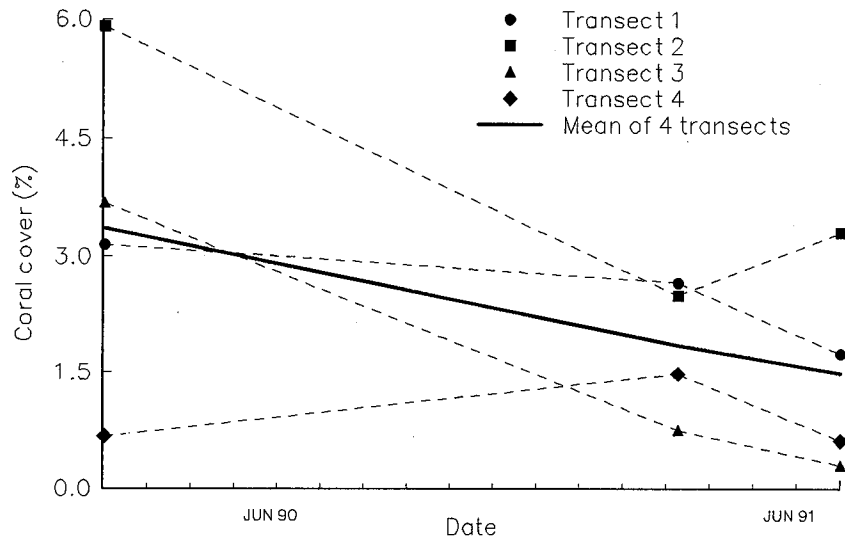


Figure 2. Percent coral cover (a) and Shannon diversity index H' (b) over time for each of the four replicate transects located adjacent to cross-reef transect BI-4 on the north side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

SITE 3

A



B

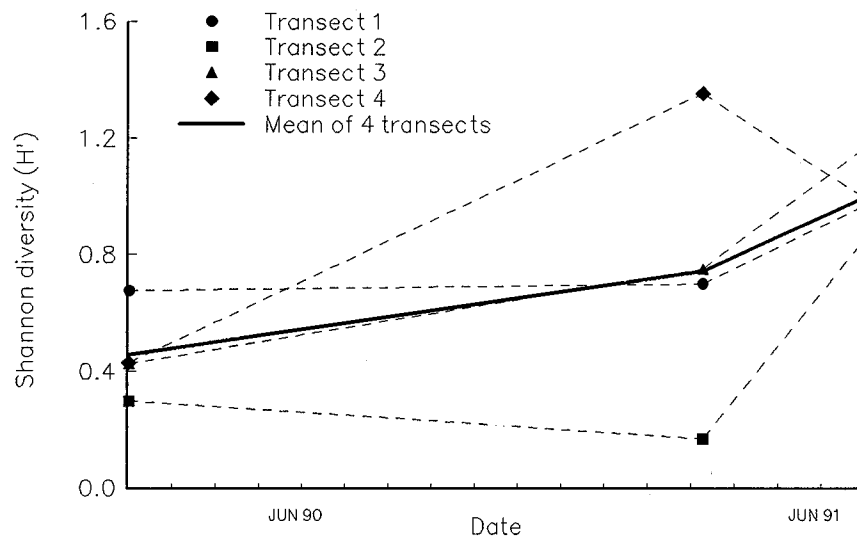


Figure 3. Percent coral cover (a) and Shannon diversity index H' (b) over time for each of the four replicate transects located adjacent to cross-reef transect BI-5 on the north side of Buck Island. No pre-Hurricane Hugo data were collected at this site. The solid line shows mean values where all four transects were surveyed at the same time of year.

No significant differences could be detected between the immediate pre- and post-hurricane percent cover of these dominant species (paired t-test; $t = 0.54$, $p > 0.5$ and $t = 1.46$, $p > 0.2$, respectively). Percent cover of *P. porites* dropped substantially on transects 1, 2 and 4, however. Transect 4 showed consistently higher species diversity than the other transects, coupled with the lowest percent coral cover.

At site 2 (backreef, north Buck Island, adjacent to cross-reef transect BI-4 - see Gladfelter et al. 1991), a significant change in coral cover over time was detected ($F = 19.0$, $p < 0.01$), but not Shannon H' ($F = 1.0$, $p > 0.4$). Coral cover tended to drop slightly following the hurricane, but had risen above pre-hurricane levels on most transects by July 1991. As at site 1, coral diversity was generally low, reflecting dominance by another pair of species, *Diploria clivosa* and *D. strigosa* (Appendix 1). No significant differences were apparent between immediate pre- and post-hurricane percent cover of these species (paired t-test; $t = 0.25$, $p > 0.8$ and $t = 1.48$, $p > 0.2$ for *D. clivosa* and *D. strigosa*, respectively).

At site 3, also on the north backreef (adjacent to cross-reef transect BI-5), no significant trends in coral cover or diversity were detected over time ($F = 3.5$, $0.2 > p > 0.1$ and $F = 3.9$, $0.1 > p > 0.05$, respectively). Only post-hurricane data are available for this site. Both coral cover and diversity were relatively low.

K-dominance curves

K-dominance curves for the three sites are shown in Figures 4-6, with coral cover data combined for all transects within a site. At site 1, species diversity apparently decreased slightly following Hurricane Hugo and had not returned to pre-hurricane levels by July 1991 (Fig. 4). The curves appear to intersect for all surveys carried out at site 2 (Fig. 5), indicating that no unambiguous distinction can be made between pre- and post-hurricane diversity. Species diversity at site 3 apparently increased following the first (post-hurricane) survey in March 1990 (Fig. 6).

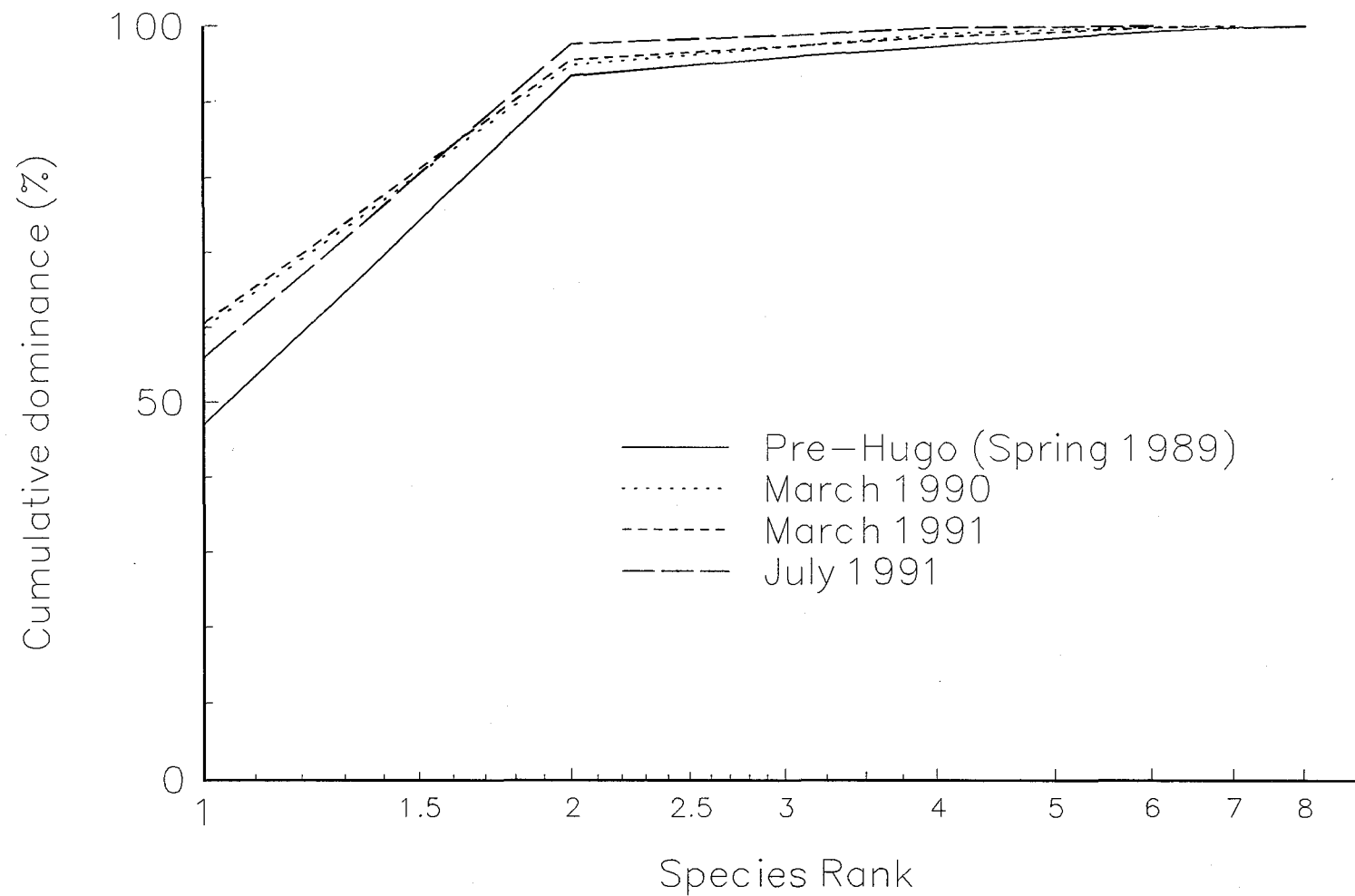


Figure 4. K-dominance curves for different survey dates at site 1 on the south forereef. Data were combined from all four transects to produce the curves, which show cumulative percent dominance of each species against ranked abundance (log scale).

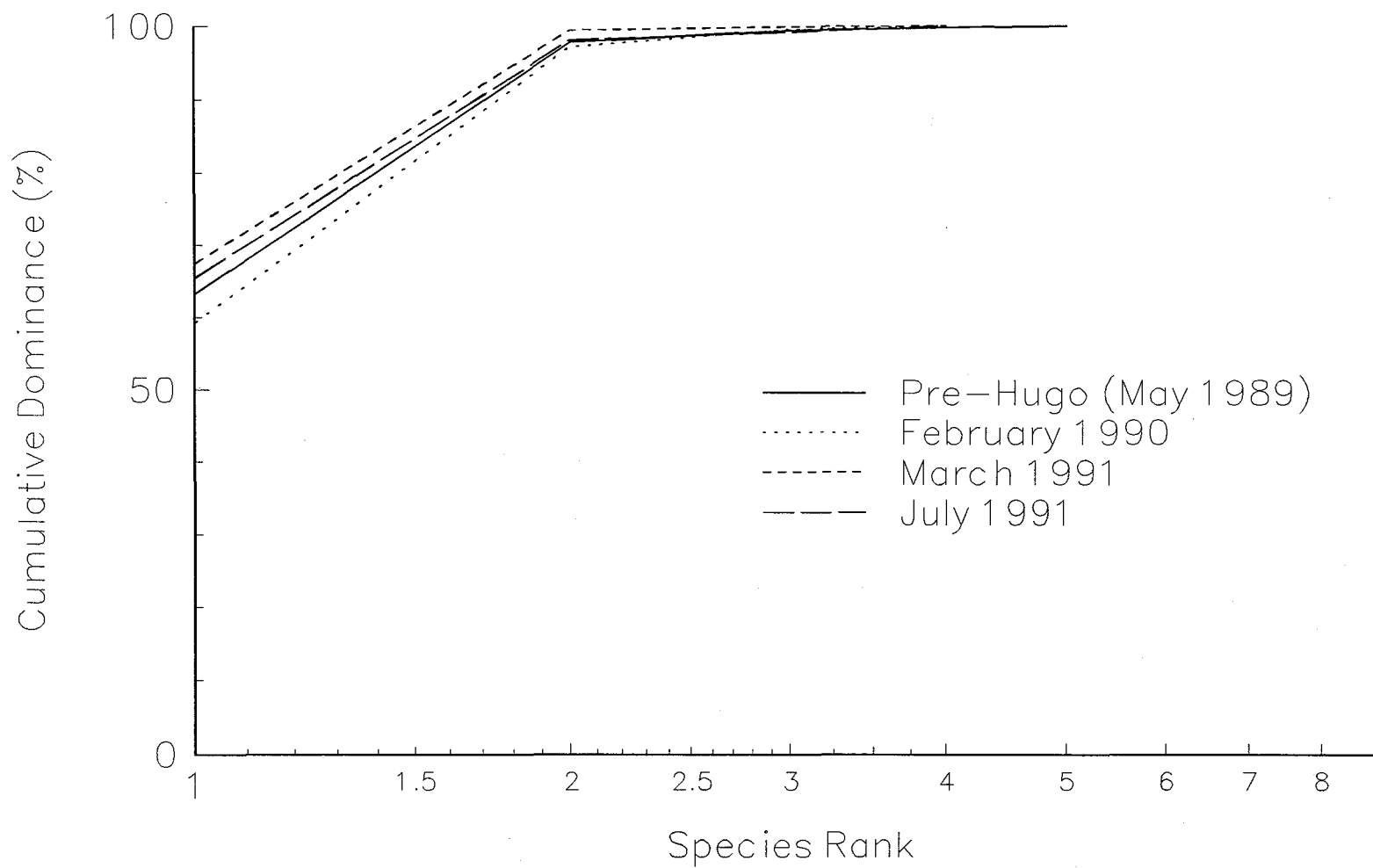


Figure 5. K-dominance curves for different survey dates at site 2 on the north backreef. Data were combined from all four transects to produce the curves, as in Figure 4.

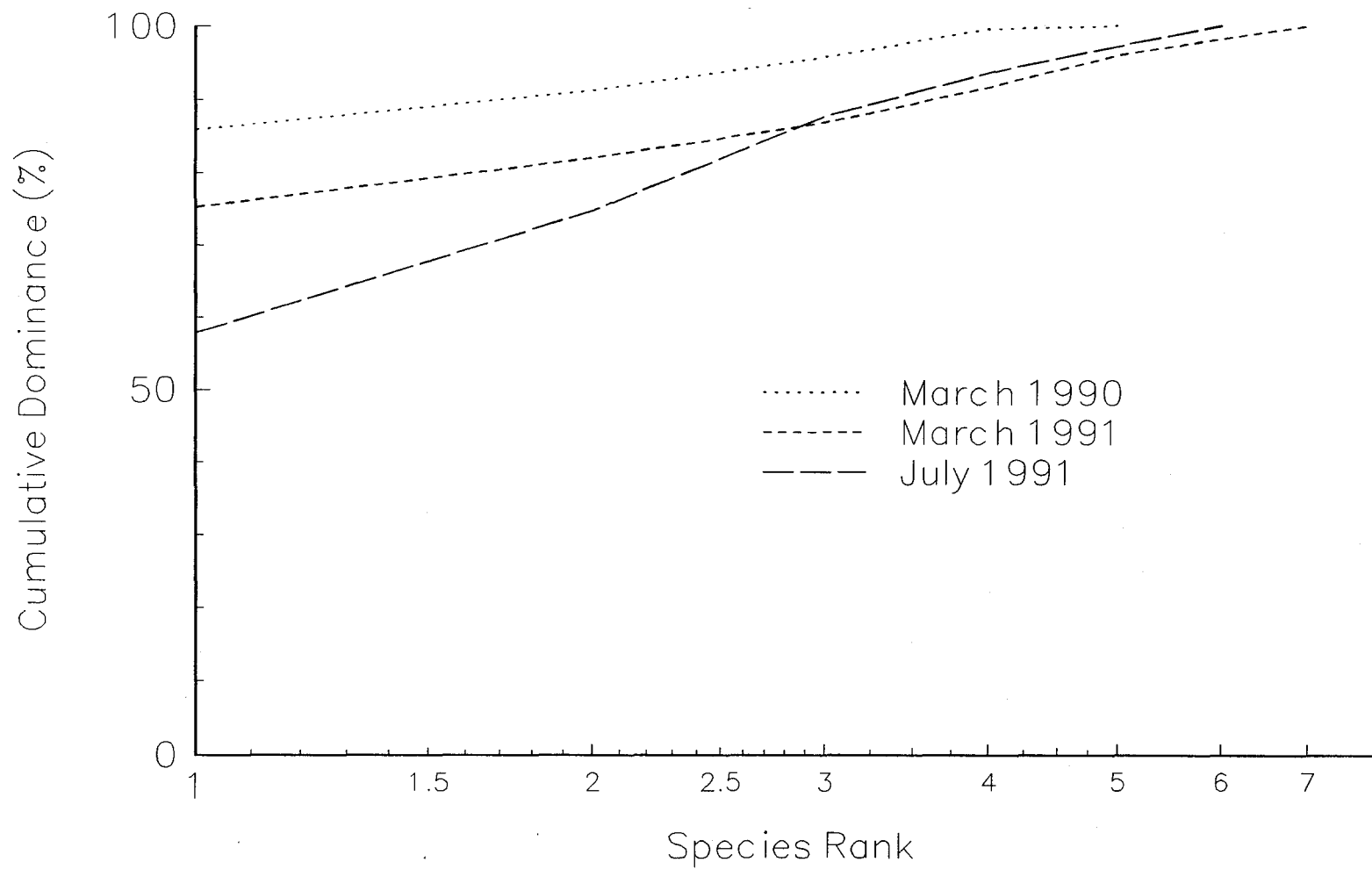


Figure 6. K-dominance curves for different survey dates at site 3 on the north backreef. Data were combined from all four transects, as in Figs. 4 and 5.

Multi-dimensional scaling (MDS)

Multi-dimensional scaling ordinations in two dimensions of Bray-Curtis similarity measures for coral cover are shown in Figures 7-9. At site 1 there is a clear shift in coral composition on transects 1, 2 and 4 following the hurricane. That is, pre-hurricane survey samples cluster independently of those carried out post-hurricane. Interestingly, the direction of shift varies, indicating that the effects of the hurricane were not uniform, but perhaps depended on the original species composition of the transect. The lack of a clear shift on transect 3 supports the findings from coral cover and Shannon diversity data, indicating that no significant changes in community structure occurred on this particular transect due to the hurricane.

At sites 2 and 3 no consistent shifts could be detected in community composition over time. No consistent pre- versus post-hurricane differences could be seen at site 2, a result that contrasts with the significant changes seen in percent coral cover. This suggests that the post-hurricane increase in coral cover (Fig. 2) was a result either of growth of colonies previously present, or (less likely) the recruitment of individuals of similar species composition to that already present on each transect.

Percent cover of macroalgae and sediment

Changes in percent cover over time of macroalgae and sediment (> ca. 1 cm depth) at each of the three sites are shown in Figures 10-12. Although blooms of several species of macroalgae, for example *Liagora* sp., were noted immediately post-hurricane (pers. obs.), overall levels of macroalgal cover decreased in Spring 1990, but increased in Spring/Summer 1991. Significant time-related changes were seen at sites 1 and 2 ($F = 5.1$ and 7.7 , both $0.05 > p > 0.02$), while changes were just not significant at $p = 0.05$ at site 3 ($F = 3.1$, $0.1 > p > 0.05$). Sediment cover did not change consistently at sites 1 and 3 ($p > 0.4$ and $p > 0.8$), but a large increase in Summer 1991 led to significant changes at site 2 ($p < 0.001$).

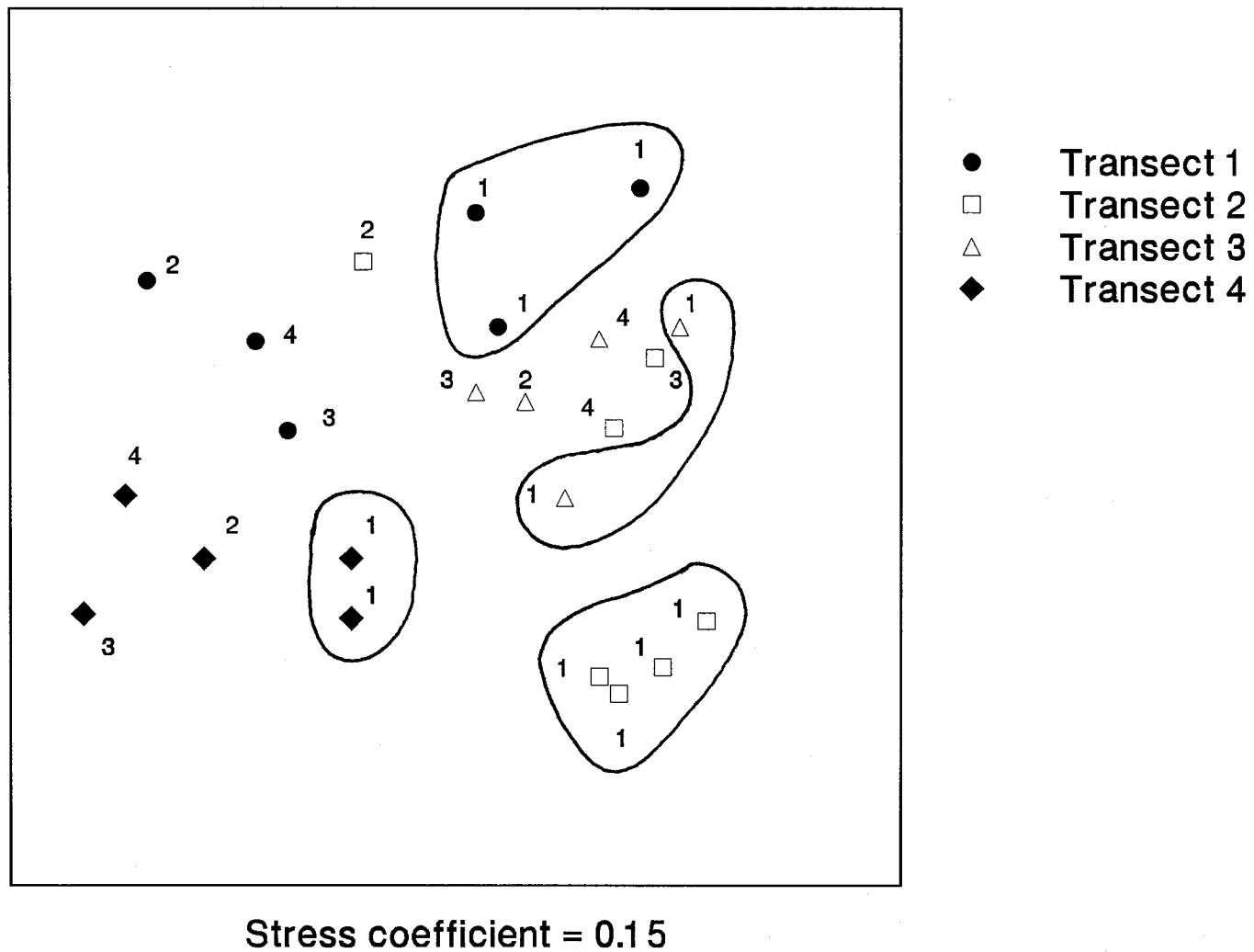


Figure 7. MDS ordination in two dimensions of Bray-Curtis similarity indices for coral species cover at site 1. Repeat surveys are labelled according to survey date: 1 = Spring 1989, 2 = Spring 1990, 3 = Spring 1991, 4 = Summer 1991. Perimeters have been drawn around the pre-hurricane samples of the four transects, which highlights the general leftward trend in post-hurricane samples, although note that individual transects shift in different directions.

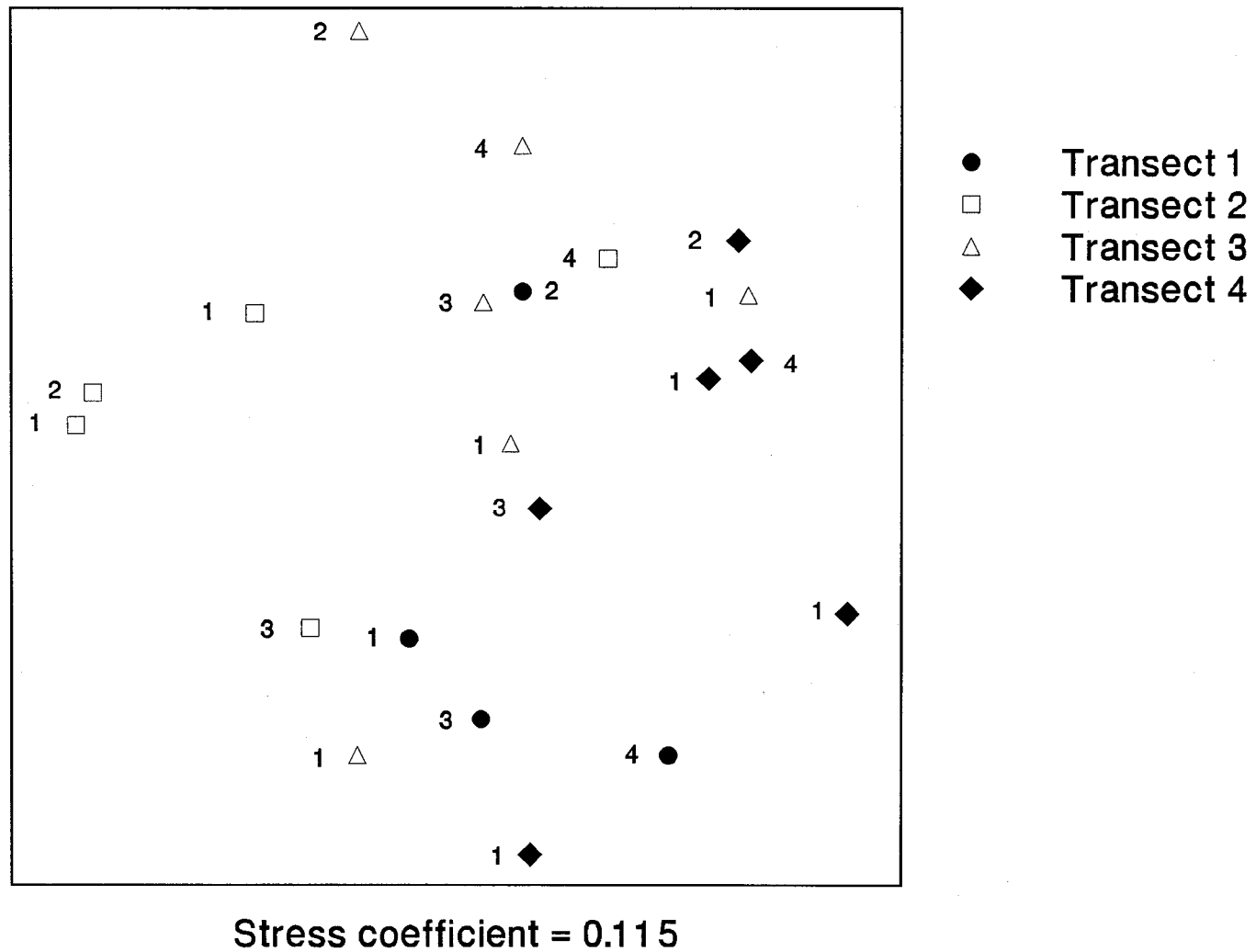


Figure 8. MDS ordination in two dimensions of Bray-Curtis similarity indices for coral species cover at site 2. Repeat surveys are labelled according to survey date: 1 = Spring 1989, 2 = Spring 1990, 3 = Spring 1991, 4 = Summer 1991.

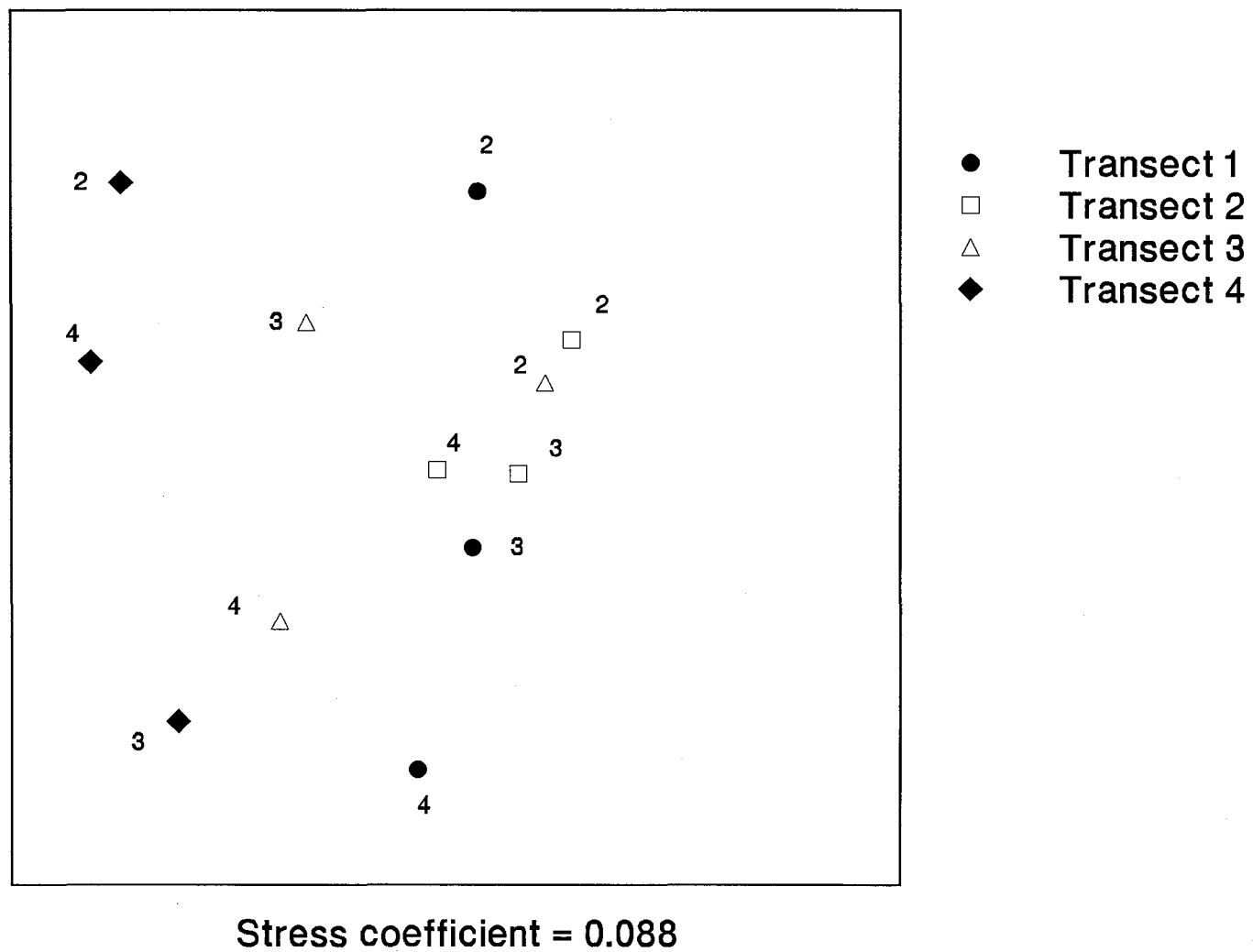
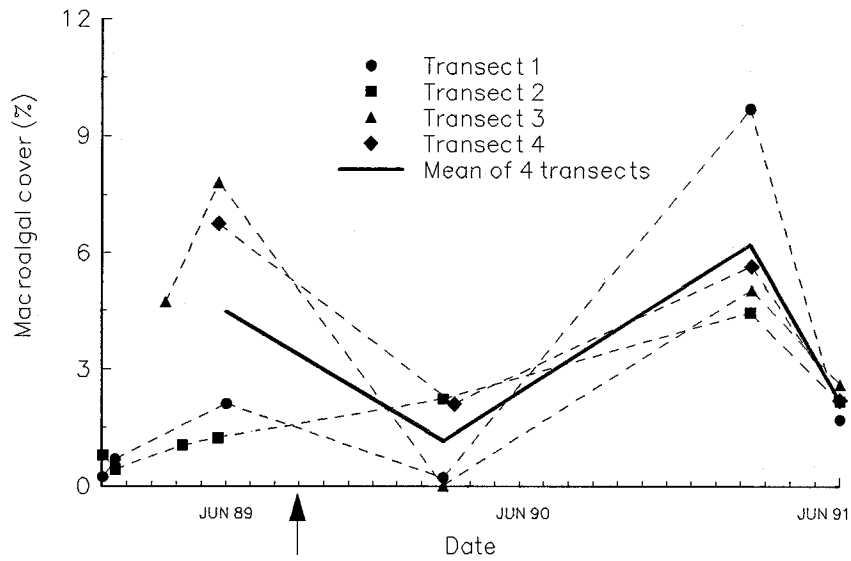


Figure 9. MDS ordination in two dimensions of Bray-Curtis similarity indices for coral species cover at site 2. Repeat surveys are labelled according to survey date: 2 = Spring 1990, 3 = Spring 1991, 4 = Summer 1991 (see also Figs. 7 and 8).

SITE 1

A



B

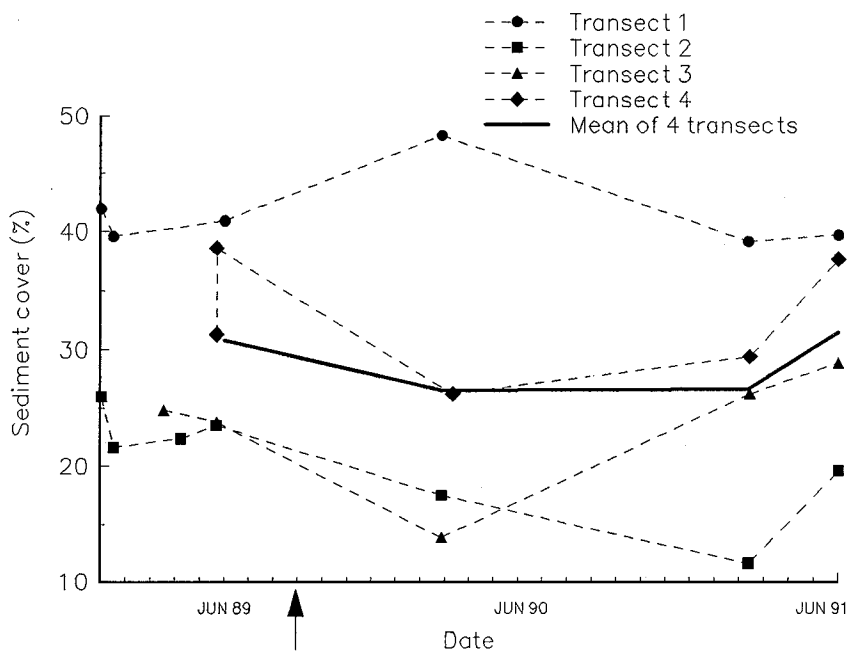
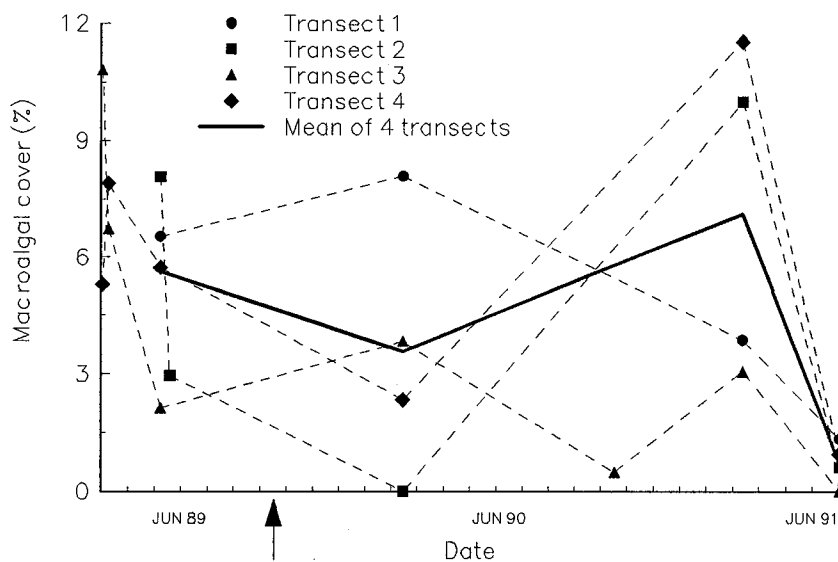


Figure 10. Percent macroalgal cover (A) and sediment cover (B) for each of the four replicate transects located adjacent to cross-reef transect BI-2 on the south side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

SITE 2

A



B

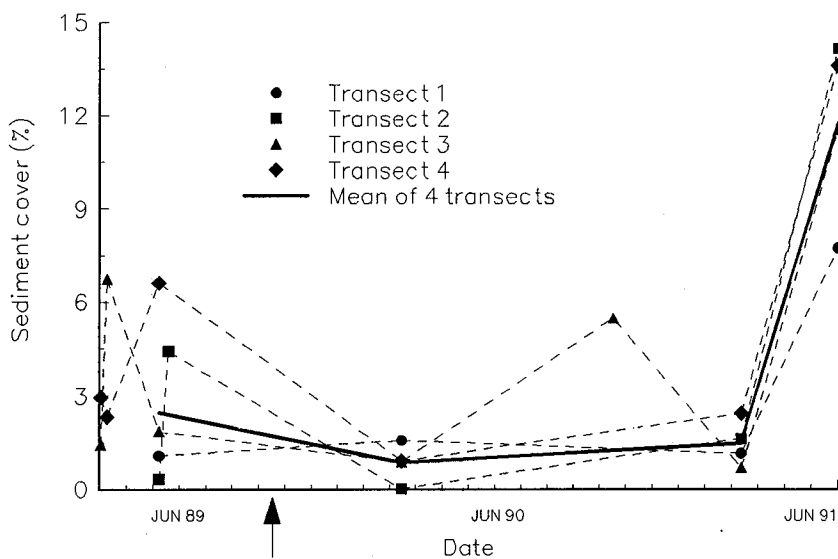
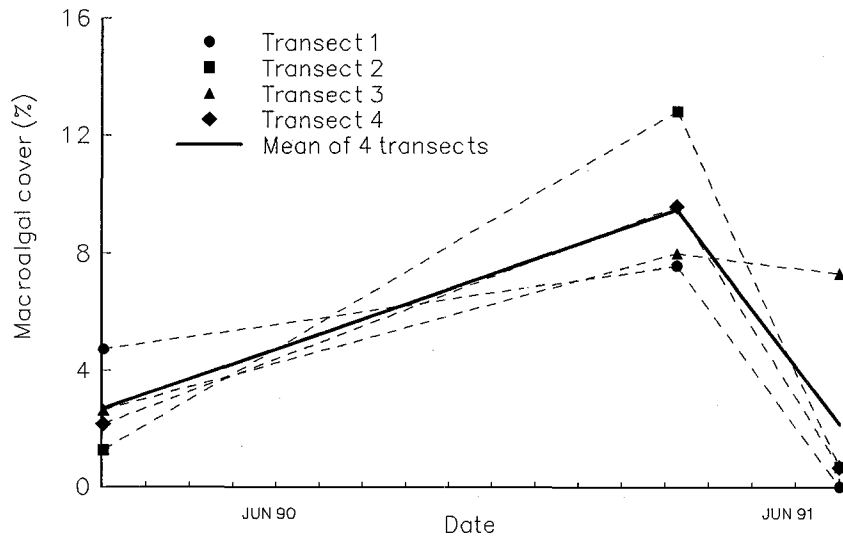


Figure 11. Percent macroalgal cover (A) and sediment cover (B) for each of the four replicate transects located adjacent to cross-reef transect BI-4 on the north side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

SITE 3

A



B

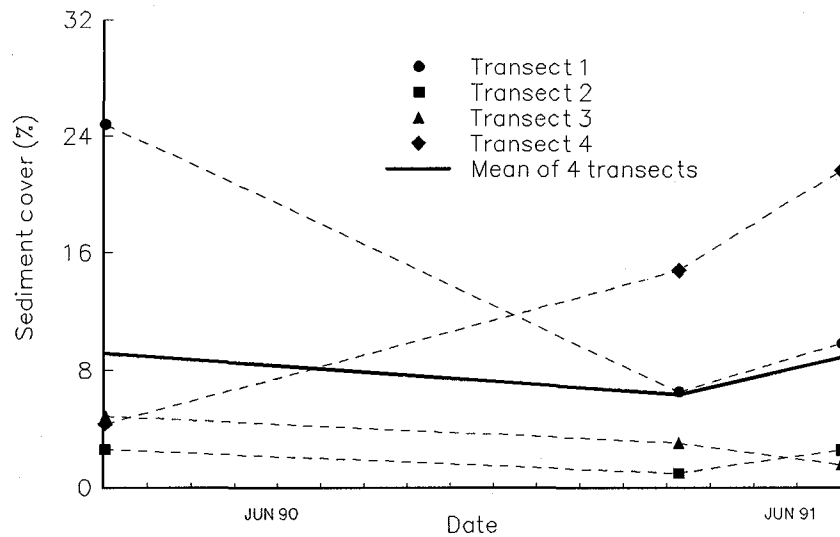


Figure 12. Percent macroalgal cover (A) and sediment cover (B) for each of the four replicate transects located adjacent to cross-reef transect BI-5 on the north side of Buck Island. No pre-hurricane data are available for this site. The solid line shows mean values where all four transects were surveyed at the same time of year.

Spatial indices

Changes in spatial index (surface contour distance/linear distance) over time are shown in Figures 13-15 for each of the three sites. None of the changes were significant (site 1; $F = 0.8$, $p > 0.5$, site 2; $F = 0.3$, $p > 0.7$ and site 3; $F = 2.0$, $p > 0.1$).

Discussion

Spatial patterns

Spatial variability in hurricane impact was seen at two scales: there was a dramatic localization of effects between specific reef zones, and at one site we were also able to detect variability on the scale of one to a few meters. The most seriously impacted reef area was the south reef crest and forereef down to a depth of approximately 7 m (Hubbard et al. 1991, Gladfelter et al. 1991). The shallow forereef was cleared to bare pavement in many areas, with severe destruction along the entire south and east reef front. Small coral fragments (1-5 cm), mostly *Porites porites* and *Millepora complanata*, resulting from this destruction were deposited in a rampart 1 m deep and 10-30 m wide which smothered much of the previous reef crest/backreef community. At the end of this study, two years after the hurricane, the rubble rampart was still intact and forms a physical reef crest 30 m landward of the pre-hurricane crest. Larger coral boulders and dead *Acropora palmata* stands were also flung up onto the rampart and into the backreef, but were more generally deposited down-slope to the base of the steep, shallow forereef at 7-8 m depth. Although the fixed transects in place on the south reef were in 8-10 m depth, outside the region of severe destruction, reductions of 9-14% coral cover occurred on three out of four transects, representing between approximately 40% and 46% of the pre-hurricane coral cover. Hurricane damage on the north of the island was far less severe, and at the one backreef site where pre-hurricane data was available a decrease in coral cover of only approximately 2% was apparent. The north versus south reef differences reflect the direction of approach of the hurricane, from the

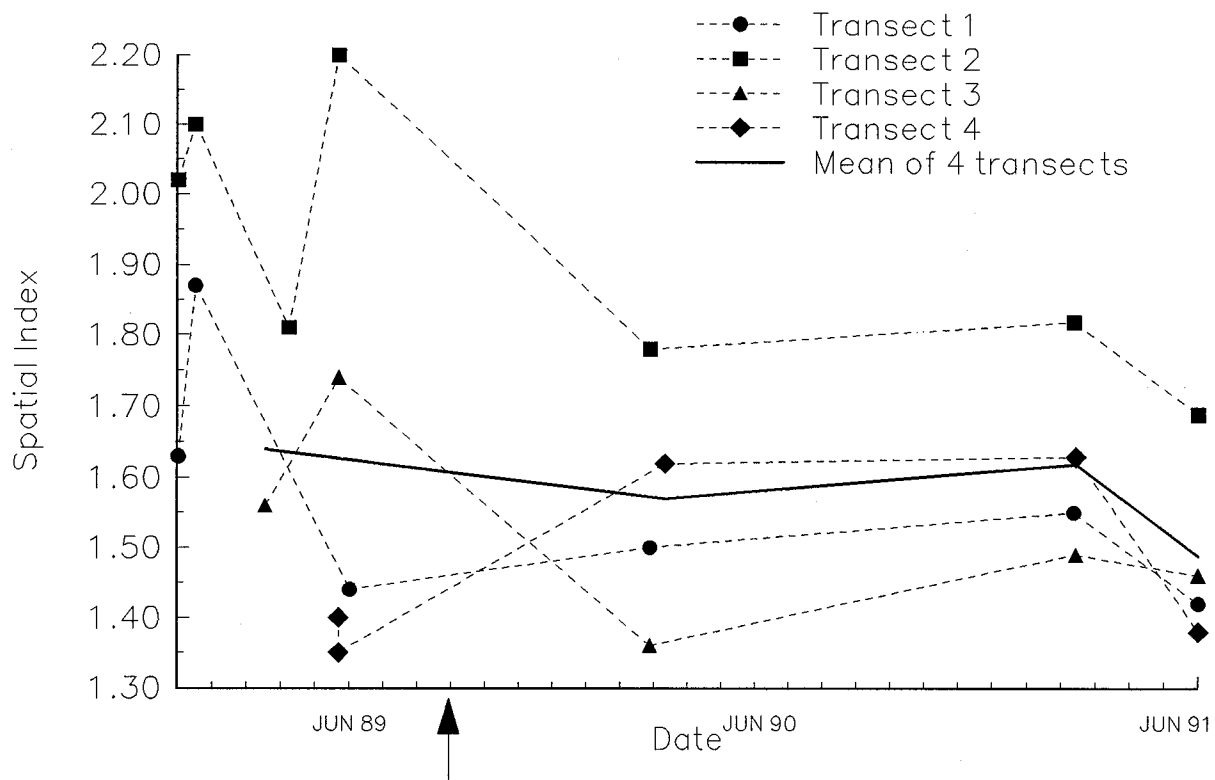


Figure 13. Spatial index (ratio of surface contour distance to linear distance along the transect) over time for each of the four replicate transects at site 1, located adjacent to cross-reef transect BI-2 on the south side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

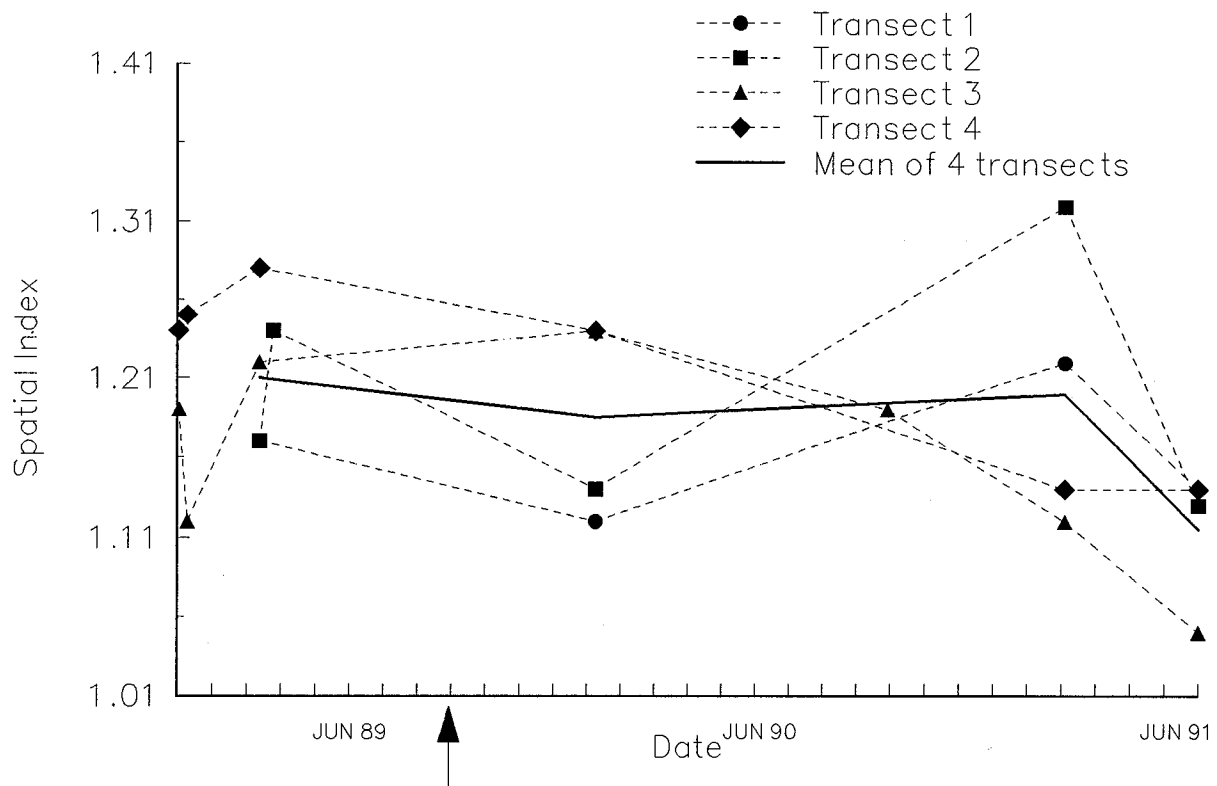


Figure 14. Spatial index (ratio of surface contour distance to linear distance along the transect) over time for each of the four replicate transects at site 2, located adjacent to cross-reef transect BI-4 on the south side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

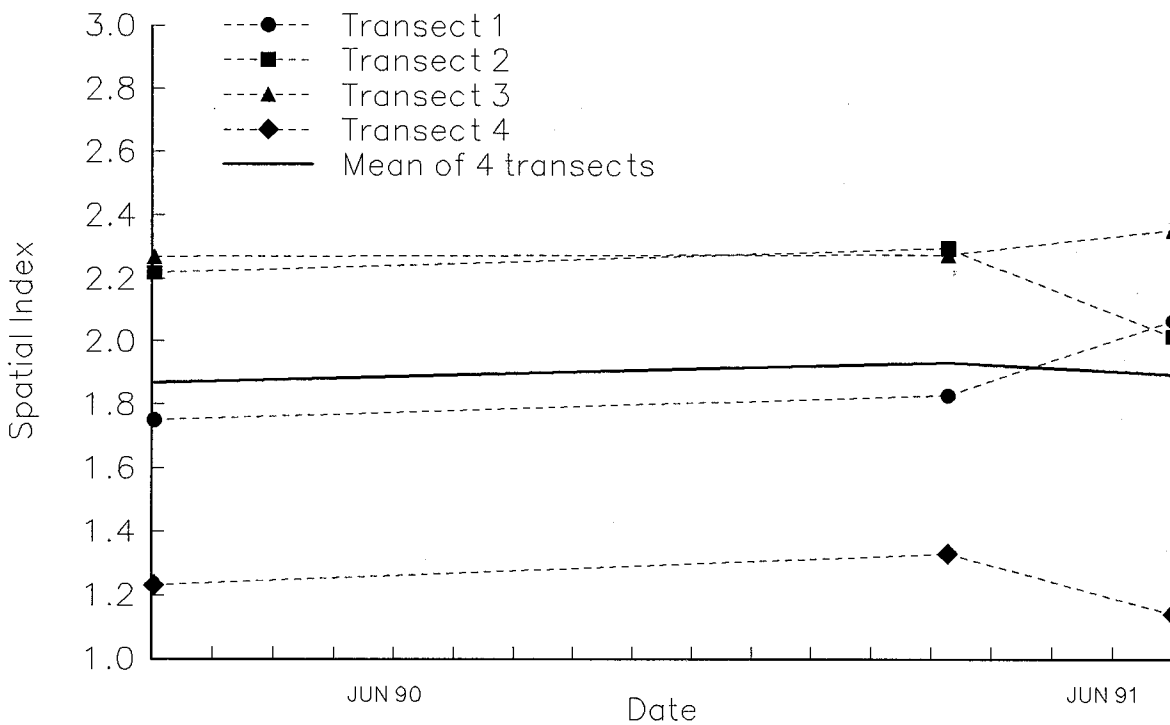


Figure 15. Spatial index (ratio of surface contour distance to linear distance along the transect) over time for each of the four replicate transects at site 3, located adjacent to cross-reef transect BI-5 on the south side of Buck Island. Arrow shows the time of impact of Hurricane Hugo. The solid line shows mean values where all four transects were surveyed at the same time of year.

southeast (Case and Mayfield 1990). However, the depth to which extensive damage occurred was shallow compared with previous reports of severe storm impact (Highsmith et al. 1980, Woodley et al. 1981, Laboute 1985). Although Hurricane Hugo made direct landfall on St. Croix and the period of exposure to hurricane force winds was prolonged (8 h), it appears that average wave height was lower than expected (Hubbard et al. 1991), which may explain the relatively shallow zone of destruction.

All transects were separated by less than 1 m depth of water and adjacent parallel transects were only a few meters apart. Even so, one of the four transects at the south reef site showed no significant hurricane damage. Similar patchiness has recently been reported for Hurricane Hugo damage in St. John (Rogers et al. in press). At this scale, it seems unlikely that bathymetric or topographic variation in reef structure would have influenced wave action sufficiently to cause the differences observed (Kjerfve et al. 1986). Woodley et al. (1981) have shown that coral species may have different susceptibilities to storm damage. However, populations of the relatively fragile finger coral *Porites porites* survived intact on the single undamaged transect, a species which was severely impacted on the other transects. The results may therefore support the idea that damage was caused mainly by impact from loose debris rather than direct wave-action effects. The one transect could have escaped damage either by chance, or due to a lack of suitable debris-forming substrate in the immediate surrounding area. Smaller-scale variability or patchiness in hurricane impact may have important consequences for post-impact recovery of community structure. Pockets of relatively undisturbed benthos may provide "seed populations" for recolonization of the surrounding area, either through fragment dispersal and propagation (Loya 1976, Highsmith et al 1980, Pearson 1981) or via local dispersal and settlement of planula larvae (Gerrodette 1981).

Sampling methods

This study reinforces the need to work at several spatial scales when monitoring reef coral community structure, employing various techniques as suggested by Rogers (1988). Using haphazardly placed 1 m² quadrats, we were able to show quantitatively the between-

zone differences discussed above (Gladfelter et al. 1991). The present analysis shows that monitoring fixed transects using the chain transect technique allows a more precise measurement of community structure to be made. Thus we were able to detect small changes in community structure which we were unable to do using haphazardly placed quadrats in the same area. In Chapter 4 we have shown how even very small reductions in projected surface area of live tissues may represent a significant degree of mortality, particularly in long-lived, resilient corals such as *Diploria strigosa*. In addition, the higher precision of the technique enabled us to define the smaller-scale variability in hurricane impact discussed above. Although the technique offers greater precision, the sampling design was necessarily restricted because of the lengthy time requirements (up to 3 h per 20 m transect). Complementary data were therefore collected using both haphazard quadrats (low precision, high efficiency) and fixed chain transects (high precision, low efficiency). A further comparison of these techniques is carried out in Chapter 3.

Methods of analysis

Univariate and multivariate measures of community structure often gave different results for changes over time. Multivariate measures may be considered inherently more sensitive at detecting differences between samples since they simultaneously compare data for all species within the community, rather than a composite value for the whole community (Magurran 1988). Surprisingly, changes at one site (site 2) were detected using percent coral cover where multivariate analysis showed no consistent shifts between transects or over time. We have interpreted this as a small but real change in coral cover while overall species composition remained stable, rather than a Type 1 error (Sokal and Rohlf 1981) in percent cover estimates. Multivariate measures have proved extremely useful for detecting changes and recovery of pre-hurricane community structure at site 1, where recovery of the pre-hurricane condition appears to be continuing, but is not complete.

Synopsis - Short-term (2 y) recovery of the coral community

Those transects on the south forereef which showed severe damage tended towards recovery of the pre-hurricane condition in subsequent months, as measured by both univariate measures (benthic cover, Shannon H') and multi-dimensional scaling (MDS) ordinations of species composition similarities. However, k-dominance curves and MDS ordinations suggest that complete recovery of species composition and abundance had not taken place by summer 1991, two years after the hurricane. On the north backreef (site 2) there was a slight drop in coral cover following the storm, but no apparent change in univariate or multivariate measures of species diversity. These results are therefore consistent with our preliminary observations that the drop in coral cover resulted mainly from scouring and partial mortality of the dominant species *Diploria clivosa* and *D. strigosa* (Gladfelter et al. 1991). These losses have apparently been more than compensated for since the hurricane.

Results of only two years post-hurricane monitoring must be considered preliminary in long-lived coral populations (Rylaarsdam 1983, Babcock 1988, Hughes and Jackson 1980). However, the hurricane did not appear to lead to an increase in coral species diversity, for example by the mechanism of opening space for coral recruitment (Connell 1978, Hughes 1989), as has been described elsewhere following hurricane impact (Porter et al. 1981, Woodley et al. 1981). The data suggest that although populations of the dominant corals were reduced by the hurricane, these species recovered relatively rapidly during the ensuing months. Conversely, rarer species were also affected, and have not recovered as rapidly and overall species richness was reduced, although this did not appear to significantly affect species diversity (Shannon H').

References

- Babcock RC (1988) Age-structure, survivorship and fecundity in populations of massive corals. Proc 6th Int Coral Reef Symp, Townsville 2:625-633
- Brown BE, Howard LS (1985) Assessing the effects of "stress" in reef corals. Adv Mar Sci 22:1-63

- Case RA, Mayfield M (1990) Annual summaries. Atlantic hurricane season of 1989. *Mon Weather Rev* 118:1165-1177
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Dustan P, Halas JC (1987) Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* 6:91-106
- Gerrodette T (1981) Dispersal of the solitary coral *Balanophyllia elegans* by demersal planulae larvae. *Ecology* 62:611-619
- Gladfelter EH, Bythell JC, Gladfelter WB, Lewis SK, Woodbury M (1991) Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites. Part 1. U.S. Dept. Interior, National Park Service, Spec. Rept.
- Graus RR, MacIntyre IG, Herchenroder BE (1984) Computer simulation of the reef zonation at Discovery Bay, Jamaica: Hurricane disruption and long-term physical oceanographic controls. *Coral Reefs* 3:59-68
- Highsmith RC, Riggs AC, D'Antonio CM (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* 46:322-329
- Hubbard DK, Parsons KM, Bythell JC, Walker ND (1991) The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, U.S. Virgin Islands - a preliminary assessment. *J Coastal Res*:33-48
- Hughes TP (1989) Community structure and diversity of coral reefs: The role of history. *Ecology* 70:275-279
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141-166
- Kjerfve B, Magill KE, Porter JW, Woodley JD (1986) Hindcasting of hurricane characteristics and observed storm damage on a fringing reef, Jamaica, West Indies. *J Mar Res* 44:119-148
- Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. *Smithsonian Contrib Mar Sci* 31:1-25
- Kruskal JB, Wish M (1978) Multidimensional scaling. Sage, Beverley Hills
- Laboute P (1985) Evaluation of damage done by the cyclones of 1982-1983 to the outer slopes of the Tikehau and Takapoto Atolls (Tuamotu Archipelago). *Proc 5th Int Coral Reef Congr, Tahiti* 3:323-329
- Lambshead PJD, Platt HM, Shaw KM (1983) The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *J Nat*

- Loya Y (1976) Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57:278-289
- Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton
- Pearson RG (1981) Recovery and recolonization of coral reefs. *Mar Ecol Prog Ser* 4:105-122
- Porter JW (1972) Patterns of species diversity in Caribbean reef corals. *Ecology* 53:745-748
- Porter JW, Woodley JD, Smith GJ, Neigel JE, Battey JF, Dallmeyer DG (1981) Population trends among Jamaican reef corals. *Nature* 294:249-250
- Porter JW, Battey JF, Smith GJ (1982) Perturbation and change in coral reef communities. *Proc Natl Acad Sci, USA* 79:1678-1681
- Rogers CS (1988) Recommendations for long-term assessment of coral reefs: U.S. National Park Service initiates regional program. *Proc 6th Int Coral Reef Symp, Townsville* 2:399-404
- Rogers CS, Suchanek TH, Pecora FA (1982) Effects of hurricanes David and Frederick (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bull Mar Sci* 32:532-548
- Rogers CS, Gilnack M, Fitz CH III (1983) Monitoring of coral reefs with linear transects: A study of storm damage. *J Exp Mar Biol Ecol* 66:285-300
- Rogers CS, McLain LN, Tobias CR (in press) Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Mar Ecol Prog Ser*
- Rylaarsdam KW (1983) Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar Ecol Prog Ser* 13:249-260
- Sokal RR, Rohlf FJ (1981) Biometry: the principals and practice of statistics in biological research, 2nd edn. Freeman and Co., New York
- Stoddart DR (1974) Post-hurricane changes on the British Honduras reefs: re-survey of 1972. *Proc 2nd Int Symp Corals and Coral Reefs, Brisbane* 2:49-63
- Warwick RM, Clarke KR, Suharsono (1990) A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8:171-179
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755

Site 1							
Transect 1	Jan-89	Jan-89	Jun-89	Mar-90	Mar-91	Jul-91	
Acropora cervicornis	0.34%	0.30%	0.48%				
Agaricia agaricites	0.15%			0.59%	0.73%	0.31%	
Eusmilia fastigiata	0.38%	0.51%	0.26%				
Millipora alaicornis	0.11%	0.17%	0.18%	0.42%			
Millipora complanata		0.41%					
Montastraea annularis	14.30%	11.96%	13.40%	10.38%	13.95%	11.51%	
Porites furcata					0.04%		
Porites porites	7.47%	7.40%	6.75%	1.27%	2.77%	3.51%	
Sediment (>1cm deep)	41.91%	39.59%	40.87%	48.31%	39.17%	39.73%	
Dead coral w/ turf algae	32.68%	38.41%	34.78%	38.65%	32.27%	41.47%	
Macro algae (>2cm)	0.23%	0.68%	2.10%	0.21%	9.71%	1.69%	
Sponges	1.46%	0.14%	0.74%			0.80%	
Gorgonians	0.53%	0.41%	0.22%	0.17%	0.12%	0.53%	
Zoanthus	0.19%	0.03%					
True anemones (Actinaria)	0.26%						
Crustose coralline algae			0.22%				
Other					1.22%	0.44%	
TOTAL CORAL COVER	22.74%	20.74%	21.07%	12.66%	17.50%	15.33%	
TOTAL OTHER	77.26%	79.26%	78.93%	87.34%	82.50%	84.67%	
SPATIAL INDEX	1.63	1.87	1.44	1.50	1.55	1.42	
Site 1							
Transect 2	Jan-89	Jan-89	Mar-89	Apr-89	Mar-90	Mar-91	Jul-91
Acropora cervicornis	0.22%	0.12%	0.42%				
Agaricia agaricites	0.13%	0.84%		0.49%			0.56%
Colpophyllia natans	3.19%	1.80%	1.25%	0.69%	0.25%	0.42%	0.11%
Millipora alaicornis				0.06%			
Millipora squarrosa		0.09%	0.07%				
Montastraea annularis	17.94%	15.61%	18.77%	19.22%	15.27%	16.53%	17.60%
Porites astreoides						0.21%	0.07%
Porites furcata	0.06%	0.39%	0.17%	0.14%			
Porites porites	10.33%	8.60%	12.09%	12.94%	1.59%	4.16%	7.96%
Sediment (>1cm deep)	25.95%	21.62%	22.36%	23.47%	17.50%	11.57%	19.62%
Dead coral w/ turf algae	40.73%	50.20%	43.75%	41.11%	60.54%	61.99%	48.58%
Dead coral (bare skeleton)						0.24%	
Macro algae (>2cm)	0.78%	0.42%	1.04%	1.23%	2.23%	4.54%	2.17%
Sponges	0.09%	0.03%			0.39%		0.04%
Gorgonians	0.38%	0.21%	0.07%	0.37%	0.46%	0.35%	0.15%
Zoanthus							0.15%
Crustose coralline algae				0.29%			
Other	0.19%	0.06%			1.77%		2.99%
TOTAL CORAL COVER	31.87%	27.46%	32.78%	33.53%	17.11%	21.31%	26.31%
TOTAL OTHER	68.13%	72.54%	67.22%	66.47%	82.89%	78.69%	73.69%
SPATIAL INDEX	2.02	2.10	1.81	2.20	1.78	1.82	1.69
Site 1							
Transect 3	May-89	May-89	Mar-90	Mar-91	Jul-91		
Agaricia agaricites			0.46%	0.64%			
Millipora alaicornis	0.60%	0.33%					
Montastraea annularis	6.13%	6.79%	8.89%	7.66%	9.13%		
Porites furcata		0.84%					
Porites porites	24.23%	16.38%	21.13%	15.83%	19.57%		
Sediment (>1cm deep)	24.80%	23.78%	13.82%	26.71%	28.83%		
Dead coral w/ turf algae	39.03%	43.61%	54.79%	44.07%	39.65%		
Macro algae (>2cm)	4.72%	7.81%		5.04%	2.60%		
Gorgonians	0.48%	0.25%		0.04%			
Zoanthus		0.11%	0.92%		0.22%		
Other		0.11%					
TOTAL CORAL COVER	30.97%	24.33%	30.47%	24.13%	28.70%		
TOTAL OTHER	69.03%	75.67%	69.53%	75.87%	71.30%		
SPATIAL INDEX	1.56	1.74	1.36	1.49	1.46		
Site 1							
Transect 4	May-89	May-89	Mar-90	Mar-91	Jul-91		
Acropora cervicornis	0.72%	0.93%	0.06%	0.15%			
Agaricia agaricites	0.50%	1.03%	0.66%				
Millipora alaicornis	0.05%						
Montastraea annularis	5.04%	5.83%	7.34%	5.03%	7.89%		
Porites astreoides				0.19%			
Porites furcata	1.53%	1.77%	1.20%	0.89%	0.91%		
Porites porites	13.42%	11.53%	3.34%	3.44%	3.97%		
Sediment (>1cm deep)	31.29%	38.59%	26.17%	29.41%	37.71%		
Dead coral w/ turf algae	40.25%	37.98%	59.03%	55.22%	46.15%		
Macro algae (>2cm)	6.75%	1.82%	2.10%	5.65%	2.19%		
Sponges	0.09%	0.23%	0.08%		0.23%		
Gorgonians		0.05%					
Corallimorph anemones	0.36%	0.23%					
Other					0.96%		
TOTAL CORAL COVER	21.25%	21.09%	12.62%	9.71%	12.77%		
TOTAL OTHER	78.75%	78.91%	87.38%	90.29%	87.23%		
SPATIAL INDEX	1.40	1.35	1.62	1.63	1.38		

Site 2							
Transect 1		May-89	Feb-90	Mar-91	Jul-91		
Diploria clivosa		17.06%	16.69%	19.21%	21.67%		
Diploria strigosa		14.79%	13.04%	13.53%	15.41%		
Porites astreoides			0.90%				
Siderastrea radians					0.33%		
Sediment (>1 cm deep)		1.08%	1.57%	1.14%	7.76%		
Dead coral w/ turf algae		59.45%	49.92%	57.33%	36.14%		
Macro algae (> 2cm)		6.53%	8.09%	3.87%	1.33%		
Gorgonians			0.45%	1.96%	1.55%		
Zoanthus		1.03%	9.33%	2.74%	15.80%		
Palythoa				0.21%			
Corallimorph anemones		0.05%					
TOTAL CORAL COVER		31.86%	30.64%	32.75%	37.42%		
TOTAL OTHER		68.14%	69.36%	67.25%	62.58%		
SPATIAL INDEX		1.17	1.12	1.22	1.14		
Site 2							
Transect 2		May-89	Jun-89	Feb-90	Mar-91	Jul-91	
Agaricia agaricites					0.10%		
Diploria clivosa		15.18%	15.85%	13.35%	14.35%	14.57%	
Diploria strigosa		7.64%	8.64%	9.81%	12.06%	16.69%	
Porites astreoides			0.05%			0.61%	
Siderastrea radians						0.28%	
Sediment (> 1 cm deep)		0.32%	4.42%		1.62%	14.18%	
Dead coral w/ turf algae		68.25%	65.70%	73.57%	55.96%	41.82%	
Macro algae (> 2cm)		8.07%	2.95%		10.01%	0.61%	
Gorgonians		0.11%	0.25%		0.43%	0.11%	
Zoanthus		0.43%	1.47%	3.27%	5.48%	11.12%	
Corallimorph anemones			0.25%				
Crustose coralline algae			0.41%				
TOTAL CORAL COVER		22.82%	24.54%	23.16%	26.50%	32.15%	
TOTAL OTHER		77.18%	75.46%	76.84%	73.50%	67.85%	
SPATIAL INDEX		1.17	1.24	1.139	1.32	1.13	
Site 2							
Transect 3		Mar-89	Mar-89	May-89	Feb-90	Nov-90	Mar-91 Jul-91
Diploria clivosa		27.94%	29.02%	18.88%	25.65%	25.60%	28.81% 30.34%
Diploria strigosa		6.28%	7.86%	12.31%	6.54%	9.54%	5.65% 6.00%
Isophyllastrea rigida		0.21%	0.28%				
Porites astreoides			0.34%	1.03%	1.42%	0.42%	0.56% 0.30%
Siderastrea radians				0.52%	0.30%		0.30%
Sediment (>1 cm deep)		1.44%	6.73%	1.86%	0.91%	5.46%	0.68% 11.57%
Dead coral w/ turf algae		48.46%	42.85%	61.56%	60.77%	48.70%	56.44% 39.21%
Macro algae (> 2cm)		10.80%	6.73%	2.12%	2.33%	0.48%	3.05%
Sponges			0.40%				0.17%
Gorgonians		0.11%	0.11%	0.57%	0.96%	0.26%	
Zoanthus		6.44%	5.37%	0.88%	1.12%	9.43%	4.01% 11.57%
Palythoa		0.32%	0.34%				0.40% 0.36%
Crustose coralline algae				0.26%			
Corallimorph anemones			0.17%				
Other						0.11%	0.23% 0.36%
TOTAL CORAL COVER		34.43%	37.50%	32.75%	33.91%	35.56%	35.03% 36.93%
TOTAL OTHER		65.57%	62.50%	67.25%	66.09%	64.44%	64.97% 63.07%
SPATIAL INDEX		1.19	1.12	1.22	1.24	1.19	1.12 1.05
Site 2							
Transect 4		Mar-89	Mar-89	May-89	Feb-90	Mar-91	Jul-91
Agaricia agaricites				0.25%			
Diploria clivosa		27.95%	28.29%	27.28%	25.65%	27.56%	29.88%
Diploria strigosa		8.13%	9.67%	8.58%	6.54%	9.94%	9.37%
Porites astreoides		0.61%		0.89%	1.42%	0.11%	0.33%
Siderastrea radians		0.15%			0.30%		0.66%
Sediment (> 1 cm deep)		2.95%	2.33%	6.61%	0.91%	2.44%	13.62%
Dead coral w/ turf algae		43.50%	47.67%	46.82%	60.77%	40.83%	26.68%
Macro algae (> 2cm)		5.28%	7.89%	5.72%	2.33%	11.56%	0.94%
Sponges		0.10%					
Gorgonians		6.30%	1.52%	1.43%	0.96%	0.89%	2.65%
Zoanthus		4.88%	2.53%		1.12%	6.67%	15.55%
Crustose coralline algae				0.49%			
Corallimorph anemones		0.10%	0.10%				
Other		0.05%					0.33%
TOTAL CORAL COVER		36.84%	37.96%	37.00%	33.91%	37.61%	40.24%
TOTAL OTHER		63.16%	62.04%	63.00%	66.09%	62.39%	59.76%
SPATIAL INDEX		1.24	1.25	1.279	1.24	1.14	1.14

Site 3			
Transect 1	Feb-90	Mar-91	Jul-91
Acropora palmata	2.46%	2.14%	0.76%
Agaricia agaricites		0.24%	0.03%
Favia fragum	0.36%	0.14%	0.03%
Isophyllastrea rigida			0.06%
Porites astreoides	0.33%		
Siderastrea radians		0.14%	0.85%
Sediment (>1cm deep)	6.94%	6.52%	9.83%
Dead coral with turf algae	84.67%	75.98%	65.70%
Macro algae (>2cm)	0.07%	7.59%	
Sponges		0.69%	
Gorgonians		1.17%	0.46%
Zoanthus	5.17%	2.62%	22.28%
Other		2.76%	
TOTAL CORAL COVER	3.15%	2.66%	1.73%
TOTAL OTHER	96.85%	97.34%	98.27%
SPATIAL INDEX	1.75	1.83	2.07
Site 3			
Transect 2	Feb-90	Mar-91	Jul-91
Acropora palmata	5.48%	2.41%	2.37%
Agaricia agaricites	0.34%	0.05%	0.65%
Favia fragum	0.09%	0.03%	0.12%
Porites astreoides			0.06%
Siderastrea radians			0.09%
Sediment (>1cm deep)	2.58%	0.96%	2.56%
Dead coral w/ turf algae	81.15%	75.05%	77.71%
Macro algae (>2cm)	1.26%	12.86%	0.69%
Sponges			0.03%
Gorgonians	1.52%	0.41%	0.87%
Zoanthus	5.82%	5.73%	13.53%
Palythoa	1.75%	1.15%	1.31%
Other		1.34%	
TOTAL CORAL COVER	5.91%	2.50%	3.31%
TOTAL OTHER	94.09%	97.50%	96.69%
SPATIAL INDEX	2.20	2.30	2.02
Site 3			
Transect 3	Feb-90	Mar-91	Jul-91
Acropora palmata	3.26%		0.16%
Agaricia agaricites	0.14%	0.55%	0.05%
Favia fragum	0.28%		
Porites astreoides		0.11%	0.03%
Siderastrea radians		0.08%	0.05%
Sediment (>1cm deep)	4.87%	3.04%	1.55%
Dead coral w/ turf algae	86.53%	76.44%	71.91%
Macro algae (>2cm)	2.64%	8.01%	7.34%
Sponges			
Gorgonians	0.28%		0.64%
Zoanthus	1.95%	11.63%	17.40%
Palythoa	0.06%		0.86%
True anemones (Actinaria)		0.14%	
TOTAL CORAL COVER	3.67%	0.75%	0.29%
TOTAL OTHER	96.33%	99.25%	99.71%
SPATIAL INDEX	2.27	2.28	2.36
Site 3			
Transect 4	Feb-90	Mar-91	Jul-91
Agaricia agaricites		0.29%	
Diploria clivosa		0.52%	
Isophyllastrea rigida			0.11%
Porites astreoides	0.56%	0.38%	0.33%
Siderastrea radians	0.10%	0.29%	0.17%
Sediment (>1cm deep)	4.35%	14.80%	21.59%
Dead coral w/ turf algae	83.94%	51.52%	42.19%
Macro algae (>2cm)	2.15%	9.61%	0.86%
Gorgonians		0.67%	3.04%
Zoanthus	8.90%	21.93%	31.75%
Corallimorph anemones			0.17%
TOTAL CORAL COVER	0.66%	1.47%	0.61%
TOTAL OTHER	99.34%	98.53%	99.39%
SPATIAL INDEX	1.23	1.33	1.14

Changes in fish assemblage structure at Buck Island, St. Croix, U.S. Virgin Islands from 1980-1990: an indication of predictability in coral reef fish assemblages based on known habitat changes?

Chapter 2

Elizabeth H. Gladfelter¹, John C. Bythell² and Zandy M. Hillis³

Present address: ¹P.O. Box 26472, Gallows Bay, St. Croix 00824, U.S. Virgin Islands. ²Centre for Tropical Coastal Management, Department of Marine Sciences and Coastal Management, University of Newcastle upon Tyne NE1 7RU, UK. ³National Park Service, Christiansted National Historic Site, Christiansted, St. Croix 00820, U.S. Virgin Islands.

Introduction

Studies of long term dynamics of fish communities are complicated by physical factors (e.g. seasonal variability; storms), biological factors (e.g. predation, competition, recruitment processes) and exploitation of the resource by man's fishing activities. At Buck Island Reef National Monument (BIRNM), a large portion of the reef that encircles the northern, eastern and southeastern portions of the island has been designated as a "Marine Garden" since 1961. Within the designated area there are bans on spear fishing, but the protective legislation only extends to the "fringes of the reef". Traps, spear and line fishing all occur within 50 feet of the reef itself on the bank seaward of the reef. The National Park Service continues to actively enforce fishing restrictions, but lack of manpower prevents total success and illegal spear fishing can and does occur. Fishing pressure outside the protected areas also affects fish populations within BIRNM, because some of the populations are targeted when they aggregate for reproduction at sites outside the monument boundaries.

The reefs of BIRNM, relatively protected from fishing pressure, have been used for several investigations to determine the effect of fish predators on species populations or behavior (Carpenter 1984, Wolf 1985). The fish community structure of Buck Island reef has been described several times in the past fifteen years (cf. Gladfelter et al. 1977, Gladfelter 1980, Simpson 1979, Tobias et al. 1987), providing initial baseline data for present studies.

Various factors including competition for space and/or food, predation and chance have been cited as influencing fish community structure. In the early 1980's proponents of stability (predicted by reef structural complexity; Gladfelter and Gladfelter 1978, Gladfelter et al. 1980) seemed to be at conflict with proponents of the lottery hypothesis (first arrival establishes its space; Sale 1980). When spatial and temporal scales were more fully considered (Ogden and Ebersole 1981, Clarke 1988) these contrasting views were discussed as components of the whole process of community dynamics. Recently, research emphasis has shifted to the role of recruitment and density independent mortality in

structuring communities (cf. Doherty and Williams 1988). Nevertheless, long term monitoring of fish communities continues to provide important data for an understanding of the dynamics of these communities. The frequency of monitoring will determine whether short term changes can be detected (Bohnsack 1983), yet even infrequent monitoring (annual or at greater periods) will provide an indication of long term stability (or lack of it), even in the absence of detailed knowledge of the population dynamics of individual species. Furthermore, it provides information to protected area resource managers and to fisheries personnel about long term trends in reef fish populations, which can assist them in management strategies.

In the present study, the fish community at BIRNM was monitored approximately every three months from 1989 through 1991, including two census periods before the reef was hit by Hurricane Hugo (17/18 September 1989) and for two years (six census periods) after the hurricane. Presence and abundance of species was determined for six reef sites. Results of this study are compared to previous studies of the fishes at BIRNM. Finally, an analysis of trends in abundance of selected taxa (families and species), begun in Gladfelter et al. 1991b, is continued.

Methods and Materials

This report forms part 2 of the study first described in Gladfelter et al. (1991b). Details of sites and census techniques are found in that report.

Sites. The six sites used in this study comprised three sets, a forereef site (FR) and a backreef site (BR), along three transects located on the southern portion (BI-2; sites FR2 and BR2), the eastern portion (BI-3; sites FR3 and UWT) and the northern portion (BI-4; sites FR4 and BR4) of the reef encircling the eastern and northern portion of Buck Island. Characteristics of these sites and maps showing their location are found in Gladfelter et al. (1991a,b).

Census Methods. Fishes were censused using a modification of the method described by Bohnsack and Bannerot (1986); details are found in Gladfelter et al. (1991b). At each site, during each census period (2-4 days) each of two observers would make 5 five-minute long censuses per morning (am) and 5 five-minute long censuses per afternoon for a total of 20 censuses per site per census period (census date). One observer was the same person (Z. Hillis) during the 3 years of the study, while the other observer changed each year (K. French 1989, M. Woodbury 1990, and J. Bythell 1991). Censuses were conducted in January, April and July of each year (plus or minus one week) starting in April 1989 and concluding in July 1991, for a total of 8 census dates. To determine whether abundance of fishes were different by site, by census date, by time of day (am or pm) or by observer, an analysis of variance was made on the numbers of fishes observed in the individual five-minute censuses by both observers, and a second ANOVA on those data collected by Hillis alone.

For most analyses however the total abundance of each species seen at each site during the total censusing period (20 five-minute long point counts; $t = 100$ min) were compiled into species lists for the entire reef (App. I) and by site (App. II). It should be noted that censuses were conducted in morning and afternoon periods; thus, no censuses were conducted at night and the abundance and presence of nocturnal species will be underestimated in these data. This method also underestimates the presence and abundance of cryptic species. Field guides by Stokes (1980) and Chaplin (1972) and the annotated fish list of St. Croix (Clavijo 1980) were used in compiling the species list.

Results

Species number, fish abundance and distribution

A total of 113 species of fishes were recorded at BIRNM during this study (Table 1, App. I). Total abundance of fishes per site per census period is found in Table 2. The greatest abundance of fishes were consistently found at FR2 (largely due to the high

Table 1. Master list of all fish species seen during censuses from April 1989 through July 1991 at Buck Island. Acronyms in parentheses are used in following tables.

ACANTHURIDAE

Acanthurus bahianus (ACBA) - Surgeonfish
A. chirurgus (ACCH) - Doctorfish
A. coeruleus (ACCO) - Blue tang

APOGONIDAE

Apogon binotatus (APBI) - Barred cardinalfish

ATHERINIDAE

Allanetta harringtonensis (ALHA) - Reef silversides

AULOSTOMIDAE

Aulostomus maculatus (AUMA) - Trumpetfish

BALISTIDAE

Aluterus scriptus (ALSC) - Scrawled filefish
Balistes vetula (BAVE) - Queen triggerfish
Cantherhinespullus (CAPU) - Orangespotted filefish
Melichthys niger (MENI) - Black durgon

BELONIDAE

Strongylura timucu (STTI) - Needlefish
Tylosurus crocodilus (TYCR) - Houndfish

BLENNIES

Malacoctenus triangulatus (MATR) - Saddledblenny
Ophioblennius atlanticus (OPAT) - Redlipped blenny

BOTHIDAE

Bothus lunatus (BOLU) - Peacock flounder

CANTHIGASTRIDAE

Canthigaster rostrata (CARO) - Sharpnose puffer

CARANGIDAE

Caranx latus (CALA) - Horse-eye jack
C. ruber (CARU) - Bar jack

CHAETODONTIDAE

Chaetodon capistratus (CHCA) - Four eye butterflyfish
C. striatus (CHST) - Banded butterfly

DASYATIDAE

Dasyatis americana (DAAM) - Southern stingray

ECHENEIDAE

Echeneis naucratus (ECNA) - Sharksucker

FISTULARIIDAE

Fistularia tabacaria (FITA) - Cornetfish

GERREIDAE

Eucinostomus lefroyi (EULE) - Mottled mojarra
Gerres cinereus (GECI) - yellowfin mojarra

Gobiidae

Coryphopterus glaucofraenum (COGL) - Bridled goby
Gobiosoma spp. (GOOC)
G. evelynae (GOEV) - Sharknose goby?

GRAMMIDAE

Gramma loreto (GRLO) - Fairy basslet

GRAMMISTIDAE

Rypticus saponaceus (RYSA) - Greater soapfish

HAEMULONIDAE

Anisotremus virginicus (ANVI) - Porkfish
Haemulon album (HAAL) - Margate
H. aurolineatum (HAAU) - Tomtate
H. carbonarium (HACA) - Caesar grunt
H. chrysargyreum (HACH) - Smallmouth grunt
H. flavolineatum (HAFL) - French grunt
H. plumieri (HAPL) - White grunt
H. sciurus (HASC) - Blue striped grunt
Grunt juveniles (HAJU)

HEMIRAMPHIDAE

Hemiramphus brasiliensis (HEBR) - Ballyhoo

HOLOCENTRIDAE

H. ascensionis (HOAS) - Longjaw squirrelfish
Holocentrus rufus (HORU) - Squirrelfish
Myripristis jacobus (MYJA) - Blackbar soldierfish

INERMIDAE

Inermia vitatta (INVI) - Boga
Emmelichthyops atlanticus (EMAT) - Bonnetmouth
Malacanthus plumieri (MAPL) - Sand tilefish

KYPHOSIDAE

Kyphosus sectatrix (KYSE) - Bermuda chub

LABRIDAE

Bodianus rufus (BORU) - Spanish hogfish
Clepticus parrai (CLPA) - Creole wrasse
Halichoeres bivittatus (HABI) - Slippery dick
H. garnoti (HAGA) - Yellowhead wrasse
H. maculipinna (HAMA) - Clown wrasse
H. pictus (HAPI) - Rainbow wrasse
H. poeyi (HAPO) - Blackear wrasse
H. radiatus (HARA) - Puddingwife

Thalassoma bifasciatum (THBI) - Bluehead wrasse

LUTJANIDAE

Lutjanus analis (LUAN) - Mutton snapper
L. apodus (LUAP) - Schoolmaster
L. griseus (LUGR) - Grey snapper
L. jocu (LUJO) - Dog snapper
L. mahogoni (LUMA) - Mahogany snapper
Ocyurus chrysurus - Yellowtail snapper

MULLIDAE

Mulloidichthys martinicus (MUMA) - Yellow goatfish
Pseudupeneus maculatus (PSMA) - Spotted goatfish

MURAENIDAE

Gymnothorax moringa (GYMO) - Spotted morayeel

MYLOBATIDAE

Aetobatus narinari (AENA) - Spotted eagle ray

OSTRACIIDAE

Lactophrys polygonia (LAPO) - Honeycomb cowfish
L. quadricornis (LAQU) - Scrawled cowfish
L. triqueter (LATR) - Smooth trunkfish

POMACANTHIDAE

Holacanthus tricolor (HOTR) - Rock beauty
Pomacanthus arcuatus (POAR) - Gray angelfish
P. paru (POPA) - French angelfish

POMACENTRIDAE

Abudefduf saxatilis (ABSA) - Sergeant major
A. taurus (ABTA) - Night sergeant
Chromis cyanea (CHCY) - Blue chromis
C. multilineatus (CHMU) - Brown chromis
Microspathodon chrysurus (MICH) - Yellowtail damselfish
Stegastes dorsopunicans (+*S. dienaesus*) (STDO) - Dusky dameselfish
S. leucostictus (STLE) - Beaugregory
S. partitus (STPA) - Bicolor damselfish
S. planifrons (STPL) - Threespot damselfish
S. variabilis (STVA) - Cocoa dameselfish

SCARIDAE

Scarus coeruleus (SCCO) - Midnight parrotfish
S. croicensis (SCCR) - Striped parrotfish
S. guacamaia (SCGU) - Rainbow parrotfish
S. taeniopterus (SCTA) - Princess parrotfish
S. vetula (SCVE) - Queen parrotfish
Sparisoma aurofrenatum (SPAU) - Redband parrotfish
S. chysopteron (SPCH) - Redtail parrotfish
S. rubripinne (SPRU) - Yellowtail parrotfish
S. viride (SPVI) - Stoplight parrotfish

Scarid juveniles (SPJU)

SCOMBRIDAE

Scomberomorus maculatus (SCMA) - Spanish mackerel
S. regalis (SCRE) - Cero mackerel

SERRANIDAE

Epinephelus adscensionis (EPAD) - Rock hind
E. cruentatus (EPCR) - Graysby
E. (cephalopholis) fulva (EPFU) - Coney
E. guttatus (EPGU) - Red hind
E. striatus (EPST) - Nassau grouper
Hypoplectrus chlorurus (HYCH) - Yellowtail hamlet
H. guttavarius (HYGU) - Shy hamlet
H. nigricans (HYNI) - Black hamlet
H. puella (HYPU) - Barred hamlet
H. unicolor (HYUN) - Butter hamlet
Mycteroperca bonaci (MYBO) - Black grouper
M. tigris (MYTI) - Tiger grouper
M. venenosa (MYVE) - Yellowfin grouper
Serranus tabacarius (SETA) - Tobaccofish
S. tigrinus (SETI) - Harlequin bass

SPARIDAE

Calamus bajonado (CABA) - Jolthead porgy

SPHYRAENIDAE

Sphyræna barracuda (SPBA) - Great barracuda
S. picudilla (SPPI) - Southern sennet

SYNODONTIDAE

Synodus intermedius (SYIN) - Sand diver lizardfish

TETRAODONTIDAE

Sphoeroides spengleri (SPSP) - Bandtail puffer

Table 2. Abundance of fishes censused (minus juvenile grunts, parrotfishes and atherinids, needlefishes and halfbeaks).

A. Fishes censused per site per census period and total species seen at that site during 1989-1991.

	#Spp	4/89	7/89	1/90	4/90	7/90	1/91	4/91	7/91	Mean(s.d.)
FR2	89	3932	4179	2393	2651	3273	3365	2502	3598	3236(667)
FR3	75	1903	2313	1339	1911	1749	1451	2041	1853	1820(311)
FR4	74	1128	1159	900	723	1316	909	1288	2059	1185(408)
BR2	70	987	1554	1152	848	1201	1629	952	1452	1221(293)
UWT	74	2123	2313	1723	1270	1735	2968	2052	3142	2165(634)
BR4	69	1966	2007	1289	992	1140	1177	1390	1657	1452(383)
MEAN (s.d.)		2006 (1053)	2254 (1045)	1466 (527)	1399 (744)	1735 (797)	1916 (1006)	1704 (584)	2293 (869)	

Average number of fishes per five minute census period compared by site and by census date for both observers (B) and for the one constant observer (C).

Total average	B 93.6	C 87.2
(greater or less than average)		
FR2	+68.9	+77.2
FR3	-2.6	+10.9
FR4	-32.9	-32.2
BR2	-30.4	-29.6
UWT	+17.3	+2.7
BR4	-20.2	-28.9
4/89	+8.8	+3.0
7/89	+21.6	+6.0
1/90	-20.5	-5.1
4/90	-22.5	-6.7
7/90	-5.2	+14.0
1/91	+2.7	-6.1
4/91	-7.2	-7.0
7/91	+22.3	+2.1

number of planktivores; cf. App. IIa) and the most abundant site in the backreef was the UWT (Fig. 1; Table 2). FR2 had the highest species count, 89, while the UWT had the greatest number of species seen in the backreef, 74.

An analysis of variance of the abundance of fishes by site, by census date and time of day indicated that there was a significant difference due to site, no difference due to time of day, and equivocal results due to census date. In these ANOVAs the contribution by juveniles, atherinids, halfbeaks and needlefishes were subtracted because these groups occasionally occur in large numbers, sometimes seasonally, and inclusion in analysis may obscure important trends. However an additional ANOVA with all fishes except atherinids resulted in similar results.

The first ANOVA used data from both observers for each census date. It showed highly significant differences by site ($p < 0.001$; $df = 5$; $F\text{-ratio} = 84.551$) and census date ($p < 0.001$; $df = 7$; $F\text{-ratio} = 12.449$), with no significant difference by time of day ($p = .833$; $df = 1$; $F\text{-ratio} = 0.044$). Table 2b shows that the FR2 and UWT averaged the greatest number of fish among the forereef and backreef sites (68.9 and 17.3 greater than the average per site), while BR2 and FR4 had the least number of fishes (-32.9 and -30.4 less than average). In comparing the average abundances per census date, the 1990 censuses were always lower than average, and each period censused in 1990 was lower than the respective census dates in 1989 or 1991.

However for the second ANOVA, only those data compiled by the one constant observer were analyzed. While differences by site were highly significant ($p < 0.001$; $df = 5$; $F\text{-ratio} = 54.224$), differences due to census date were not significant ($p = 0.238$; $df = 7$; $F\text{-ratio} = 1.321$). Differences in fish abundance due to time of day were also not significant ($p = 0.308$; $df = 1$; $F\text{-ratio} = 1.043$). The relative number of fishes per site was the same as when data from both observers were compiled (Table 2c) with FR2 and UWT having the greatest average abundance of fishes for the forereef and backreef (77.2 and 2.7 above average for all sites), while FR4 and BR2 had the lowest averages (-32.2 and -29.6 less than total average, respectively). In this second ANOVA, there was no distinct trend in the abundance of fishes by census date, except that the July census for each year always had a greater abundance of fishes than the January or April censuses; the greatest

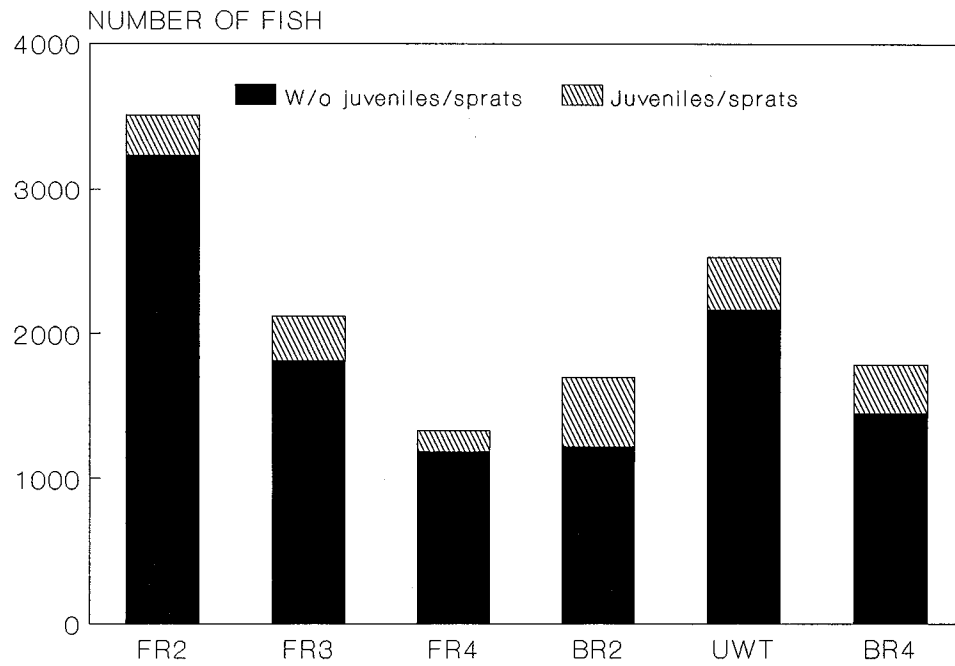


Figure 1. Average number of fishes per census ($n = 8$) per reef site.

abundance was recorded in July 1990 (14.0 above average) with the lowest in April 1991 (-7.0).

Spatial and temporal distribution of major fish families at BIRNM

The majority of fishes found at Buck Island reef are members of four major families; the parrotfishes (Scaridae), the damselfishes (Pomacentridae), the wrasses (Labridae) and the surgeonfishes (Acanthuridae). These families comprise 60-80% of individual fishes counted in each census (App. I and II; Gladfelter et al. 1991b). Figure 2 compares the average number of fishes recorded per period in each family in 1989 (n = 2 censuses) with 1990 and 1991 (n = 3 censuses for each). Note that the family pattern of abundance of fishes seen in 1989 was disrupted following the hurricane in 1990, but had been re-established by 1991. While the total number of scarids and acanthurids did not vary greatly and apparently abundance of these groups was unaffected by the hurricane, there was a decrease in the number of pomacentrids and labrids between 1989 and 1990; the labrids appear to be increasing again in 1991, while the pomacentrids remain at the 1990 levels.

In the following analyses, the percentage contribution of each family was computed as a proportion of the total contribution of the 4 families (= 100%). The percent contribution per reef site per year was averaged and the results presented in Table 3. For the total reef, the Scaridae contribute 23%, the Pomacentridae 26%, Labridae 31.4% and the Acanthuridae 19.4%. However, when forereef sites are compared to backreef sites, the Scaridae and Acanthuridae show similar distributions between sites (e.g. FR vs. BR; Scaridae 21.4% vs. 24.6%, while Acanthuridae 19.8% vs. 19.0%), while there is a clear difference in the distributions of the Pomacentridae and Labridae. The forereef has a much greater contribution by the Pomacentridae than the backreef, 31.9% vs. 20.0% (largely due to the high abundance of planktivorous pomacentrids on the forereef), while the reverse is true of the Labridae, which dominate in the backreef, 36.4% vs. the forereef, 26.4%.

There is also a clear distinction in the distribution of these families in different

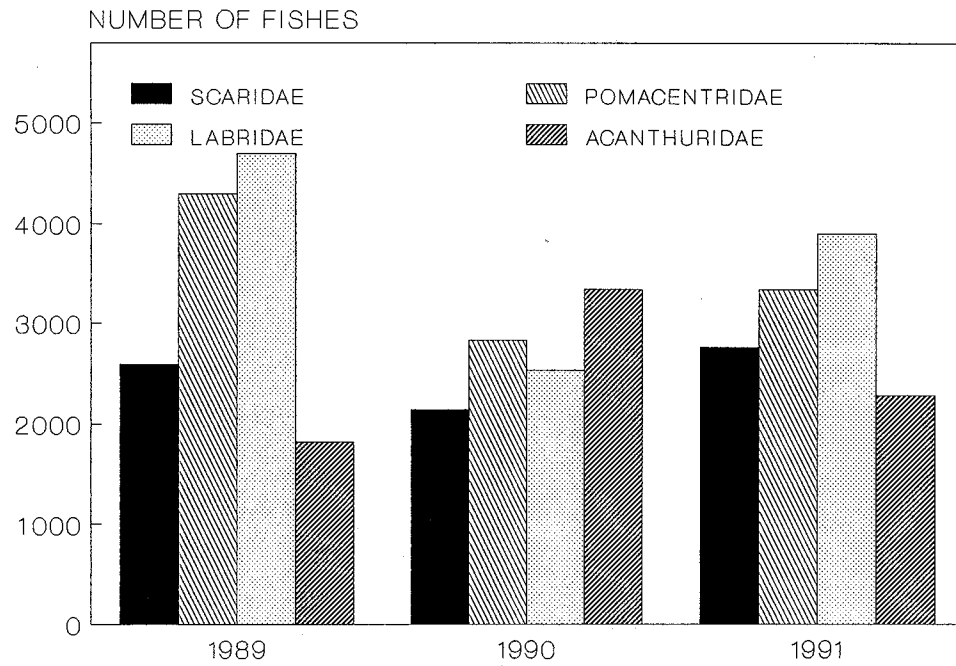


Figure 2. Contribution by major families at the combined six sites observed at Buck Island. Values given indicate the mean number of fish per census period.

Table 3. Major family distribution*: Total reef, forereef vs. backreef, by transect and by census site.

Distribution	Scaridae	Pomacentridae	Labridae	Acanthuridae
Total reef	23.0	26.0	31.4	19.4
Forereef	21.4	31.9	26.4	19.8
Backreef	24.6	20.0	36.4	19.0
Transect BI-2	17.2	40.8	31.0	11.1
Transect BI-3	23.5	25.6	29.3	21.5
Transect BI-4	28.4	11.6	33.9	25.6
FR2	13.4	54.0	27.8	4.8
FR3	25.0	28.6	23.8	22.3
FR4	25.9	13.2	27.6	32.2
BR2	20.9	27.5	34.2	17.4
UWT	22.0	22.5	34.8	20.6
BR4	30.9	9.9	40.2	19.0

*These 4 families represent 60-80% of total fish censused; values given are the percent contribution of this family to the total contribution by the 4 families (i.e. 100%) in the 8 censuses conducted from 1989-1991.

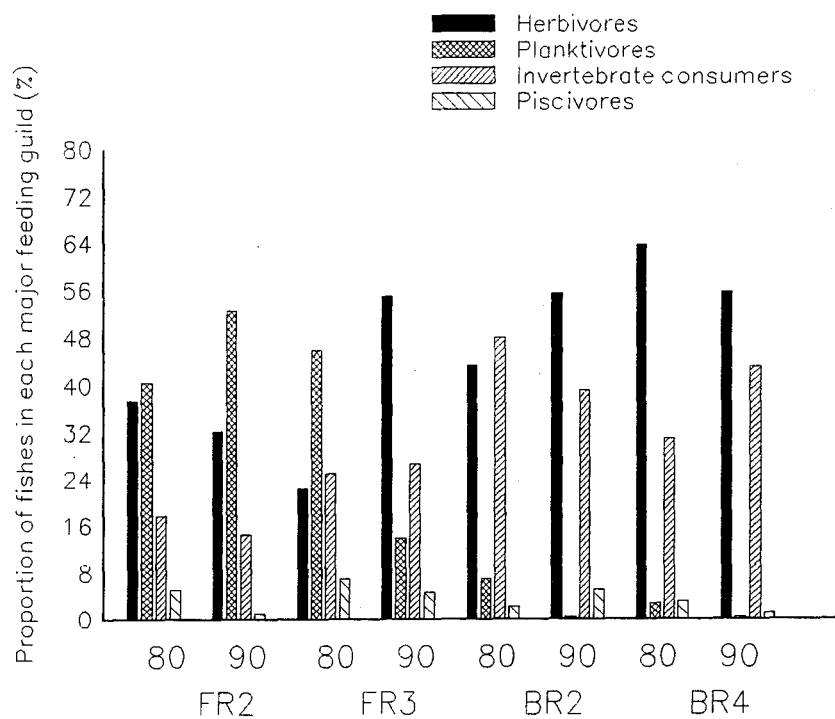
portions of the reef, i.e. the southern portion crossed by transect BI-2, the eastern portion where BI-3 is located and the northern area crossed by transect BI-4. The proportions of Scaridae and Acanthuridae increase from BI-2 to BI-4, i.e. from the southern reef to the northern reef, with the eastern portion of the reef showing intermediate values. In contrast, the Pomacentridae show a drastic decrease in their proportion of the total contribution declining from 40.8% of the total on BI-2 to 11.6% on BI-4, with 25.6% in the intermediate BI-3. Again, this distribution is heavily influenced by the abundance of planktivorous pomacentrids at FR2. The Labridae were a consistent proportion of the community in all 3 transects (23.8% to 27.8%).

Feeding guilds

Fishes can be divided among one of four major feeding guilds; herbivores, benthic invertebrate consumers (either hard or soft invertebrates), planktivores and piscivores. The diets of the fishes found at Buck Island are described in Randall (1978) and listed in Gladfelter and Gladfelter (1980) where a detailed trophic analysis of the Buck Island fish community is found. All fishes observed (with the exclusion of atherinids) were used to determine the proportional trophic contribution per year (1989-1991) and these proportions were averaged to determine the proportional trophic contribution listed for 1990. The 1980 values were the average proportional trophic contributions from censuses conducted monthly January through September 1979 (i.e. same period of the year as the 1990 data) with the atherinids excluded from the calculations (cf. Gladfelter and Gladfelter 1980). Fish censuses were conducted in exactly the same sites at FR2 and BR4 in 1980 and 1990, and in nearby similar (but not the exact sites) of BR2 and FR3. Visual methods were used in both studies, but actual technique varied (cf. Gladfelter et al. 1991 for further discussion).

The results of the current study are compared to the 1980 study in Figures 3a and 3b and Table 4. When all four sites are considered, there is no significant difference in the proportion of any trophic group between 1980 and 1990, although the distribution of the groups within the reef appears to have changed.

A



B

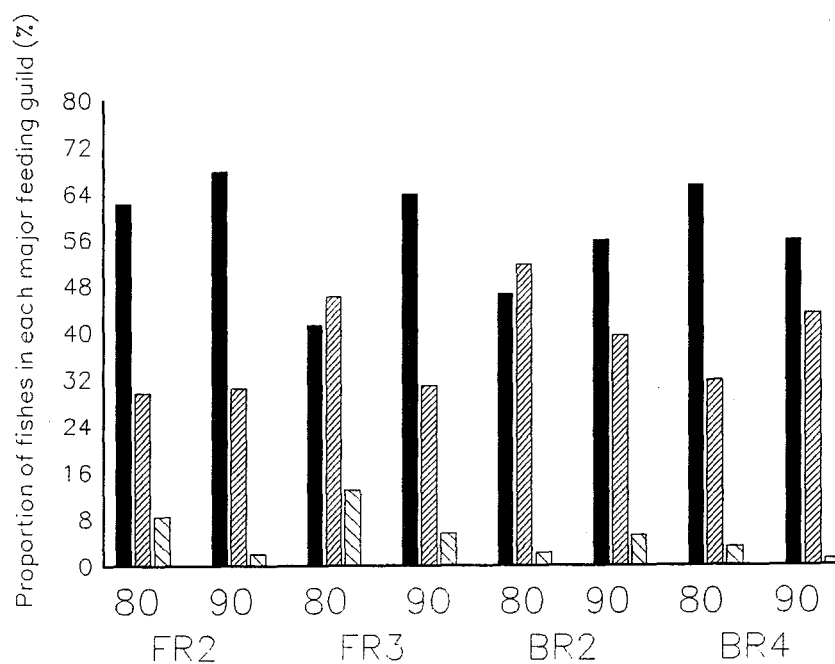


Figure 3a. A comparison of the proportion of fishes in each of four major feeding guilds at four reef sites between 1980 and 1990.

Figure 3b. A comparison of the proportion of fishes in each of the major feeding guilds at four reef sites between 1980 and 1990, excluding planktivores.

Table 4. Trophic comparisons by site between 1980 and 1990. Numbers indicate relative percentage of fishes in that trophic category (Herbivore, H; Invertebrate eater, I; Piscivore, Pi; Planktivore, Pl). *Censuses at FR2 and BR4 were conducted in exactly the same reef area in both 1980 and 1990; censuses at FR3 and BR2 were conducted in similar but not the identical reef zones in 1980 and 1990.

A. All fishes (except clupeids and atherinids)

	FR2		FR3*		BR2*		BR4	
H	37.3	32.2	22.3	55.0	43.2	55.5	63.7	55.6
Pl	40.4	52.4	45.8	13.8	6.9	0.3	2.6	0.3
I	17.7	14.4	24.9	26.5	47.9	39.1	30.8	43.0
Pi	5.0	0.9	7.0	4.7	2.0	5.1	3.0	1.0

B. All fishes (except clupeids, atherinids and planktivores in the Pomacentridae and Labridae).

	FR2		FR3*		BR2*		BR4	
H	62.2	67.8	41.1	63.8	46.4	55.7	65.3	55.8
I	29.5	30.3	45.9	30.7	51.5	39.2	31.6	43.1
Pi	8.3	1.9	12.9	5.5	2.1	5.1	3.1	1.0

Planktivores are a major component of the forereef communities, but virtually absent from the backreef (Fig. 3a). Interestingly, planktivores formed a greater proportion of the FR2 community in 1990 as opposed to 1980, 52.4 vs. 40% (Table 4, Fig. 3a). The invertebrate consumers (wrasses, grunts, etc.) form a larger component of the fish community in the backreef, as opposed to the forereef, even when planktivores are removed from the calculations (Fig 3a,b).

In three of the four sites (the exception being BR2), the contribution by piscivores decreased from 1980 to 1990. For example, in FR2 the decrease when all fishes are considered (Table 4a) is 5% to 0.9% and when planktivores excluded, 8.3 to 1.9%. When planktivores are excluded (Fig. 3b, Table 4), the contribution by herbivores increases between 1980 and 1990 in all sites except BR4.

Changes in individual taxa at BIRNM: 1989-1991

Several taxa (family, genus, species) which are important components of the Buck Island fish fauna were analyzed separately and their abundance plotted per census period (Figs. 4-9).

Scaridae. The parrotfishes were analyzed by considering juveniles separately from adults, and separating adults into respective genera, *Scarus* or *Sparisoma*. Adult parrotfishes increased in number after the hurricane between 1989 and 1990, and increased again between 1990 and 1991 (Fig. 4a). However, the only major increase occurred between July 1989 and July 1990. On the other hand, juvenile parrotfishes decreased after the hurricane (Fig. 4b), but showed an increase in 1991, particularly on the forereef.

Scarus had a major increase in the year following the hurricane, and these levels were sustained in 1991 with an additional increase in July 1991 over July 1990 (Fig 5a). The abundance of *Scarus* on Buck Island reef seems to increase in January, perhaps reflecting a migration to the reef at that period of the year. Prior to the hurricane, *Sparisoma* were three times as abundant as *Scarus* (Fig. 5a,b). The year after the

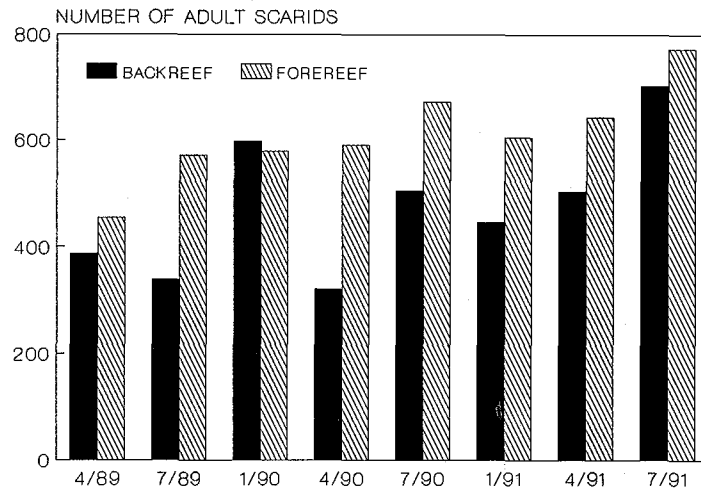


Figure 4a.

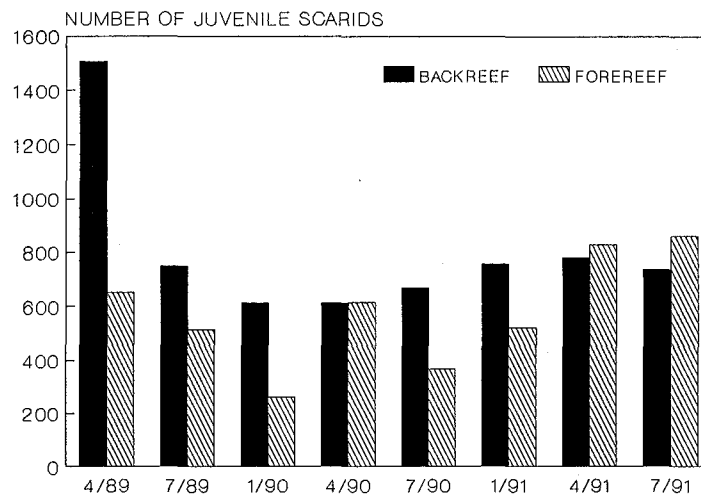
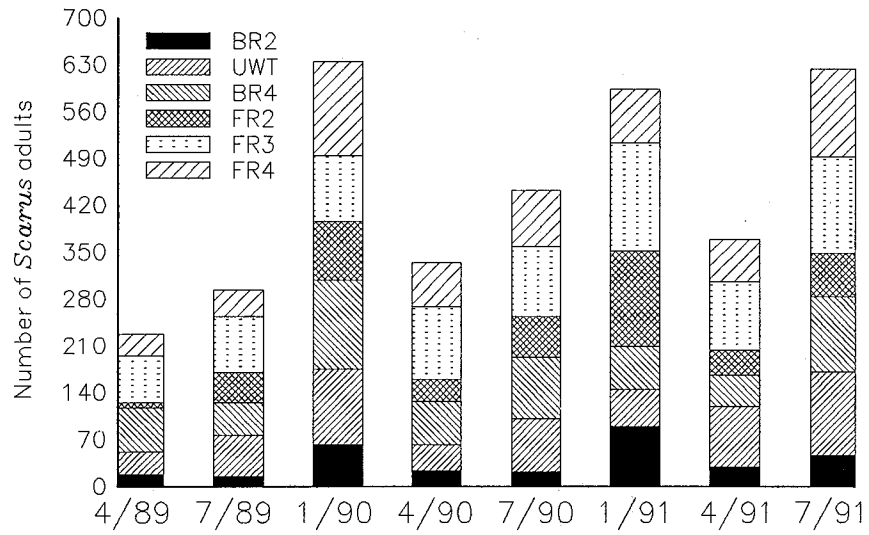


Figure 4b.

Figure 4. Total number of Scaridae (parrotfishes) in the combined forereef and combined backreef sites during each census period. a. Adults. b. Juveniles.

A



B

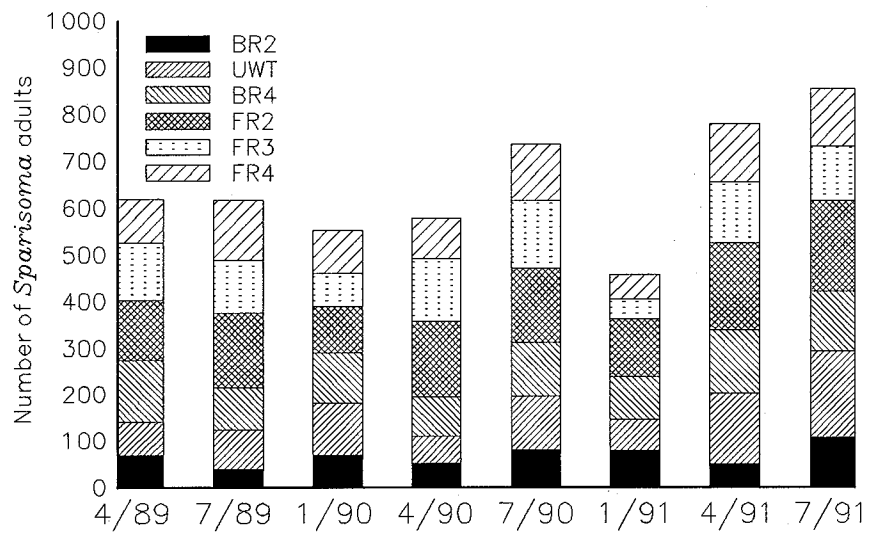
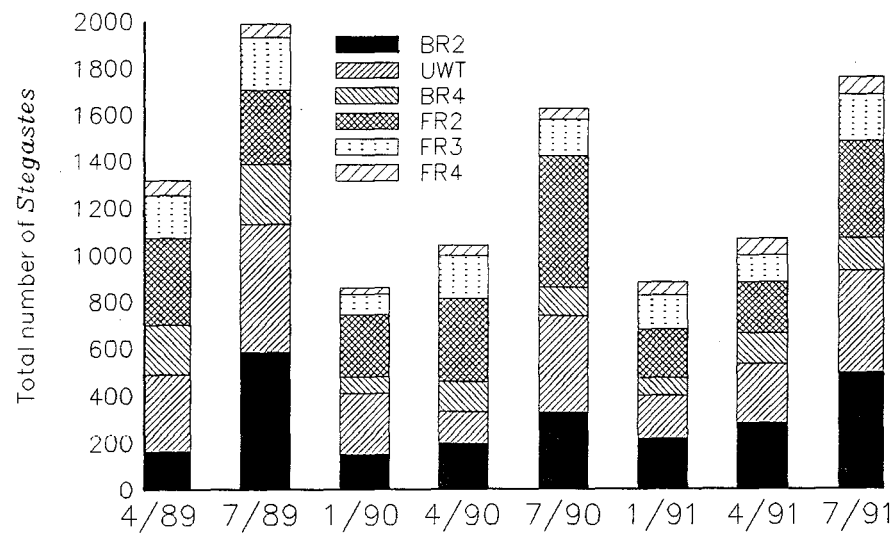


Figure 5. Total number of adults in each genus of Scaridae in each census site for each census period.
a. *Scarus* b. *Sparisoma*.

A



B

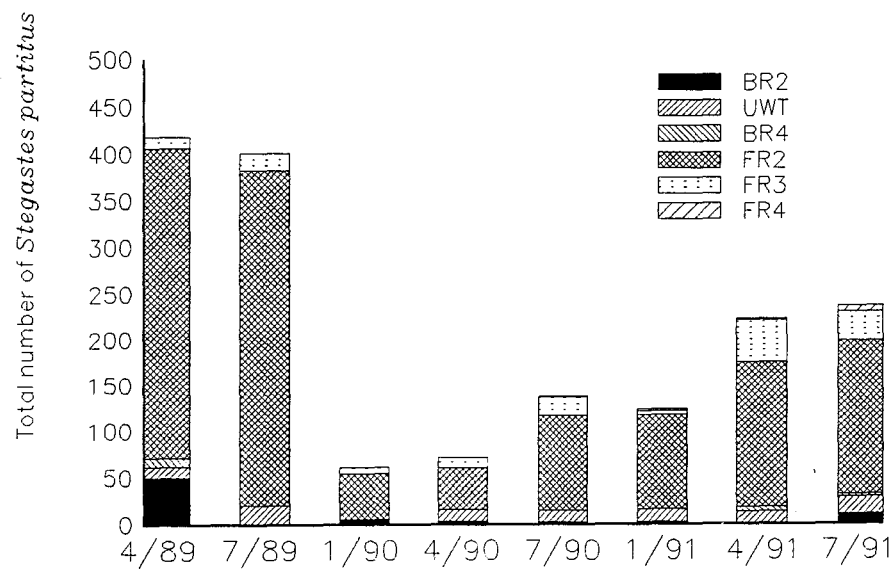
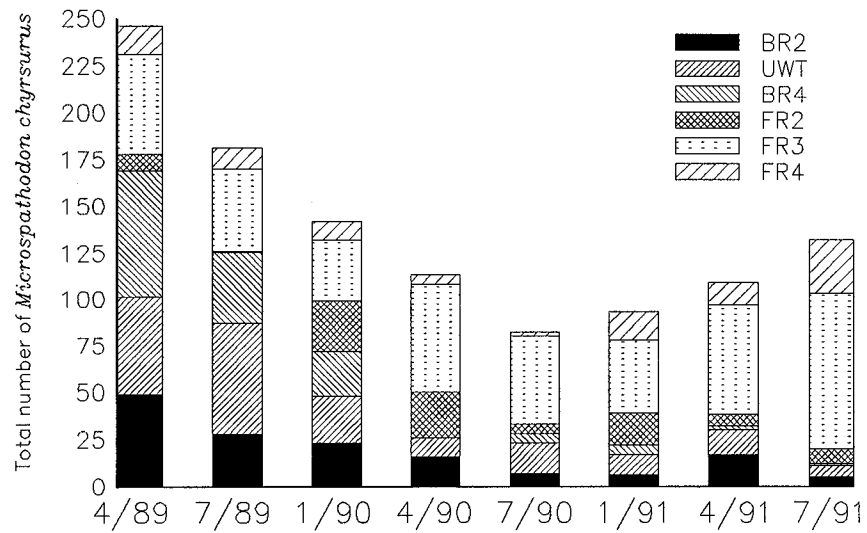


Figure 6. Total number of Pomacentridae (damselfishes) in each census site for each census period.
a. *Stegastes* spp. (with the exception of *S. partitus*). b. *Stegastes partitus*.

C



D

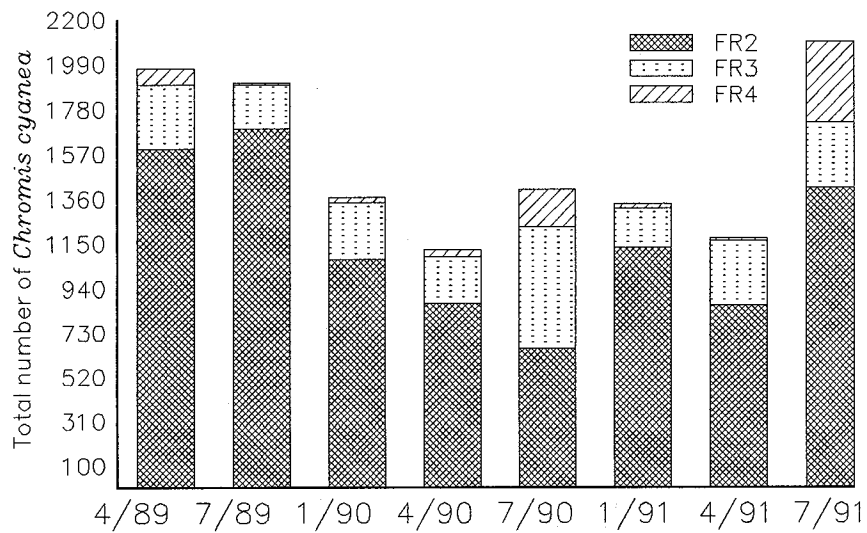


Figure 6. Total number of Pomacentridae (damselfishes) in each census site for each census period. c. *Microspathodon chrysurus*. d. *Chromis cyanea*.

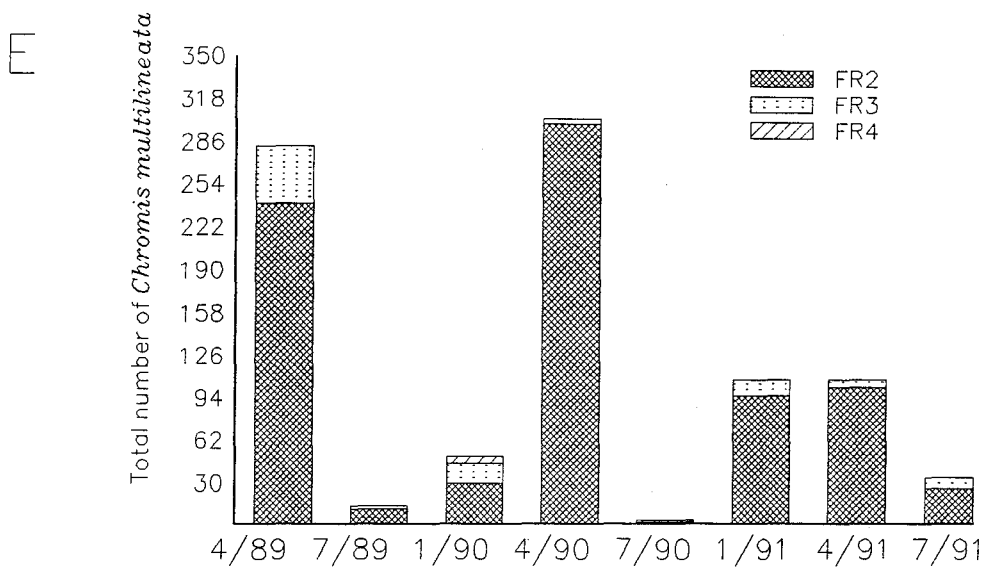


Figure 6e. Total number of *Chromis multilineata* in each census site for each census period.

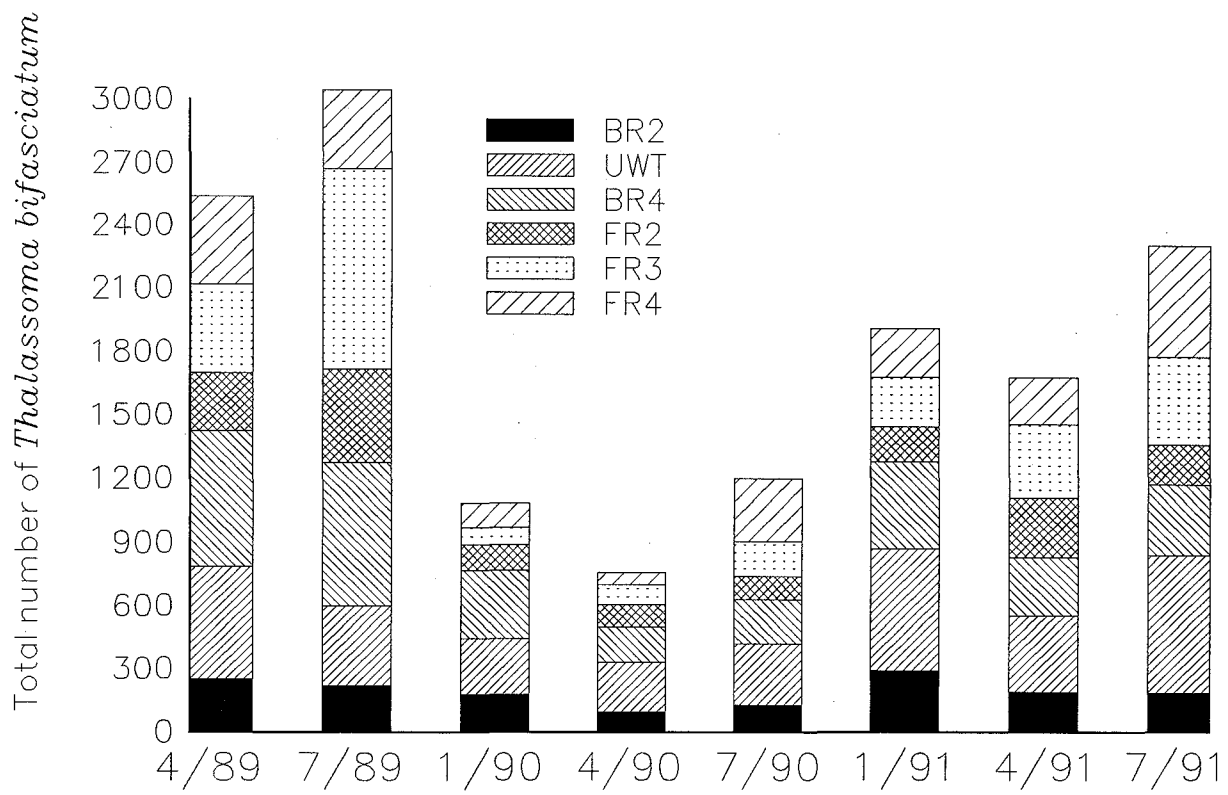
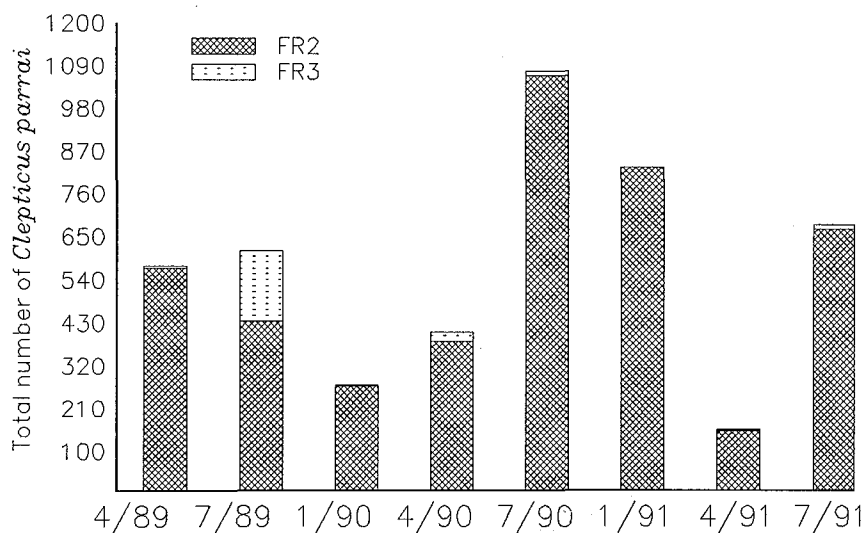


Figure 7c. Total number of *Thalassoma bifasciatum* in each census site for each period.

A



B

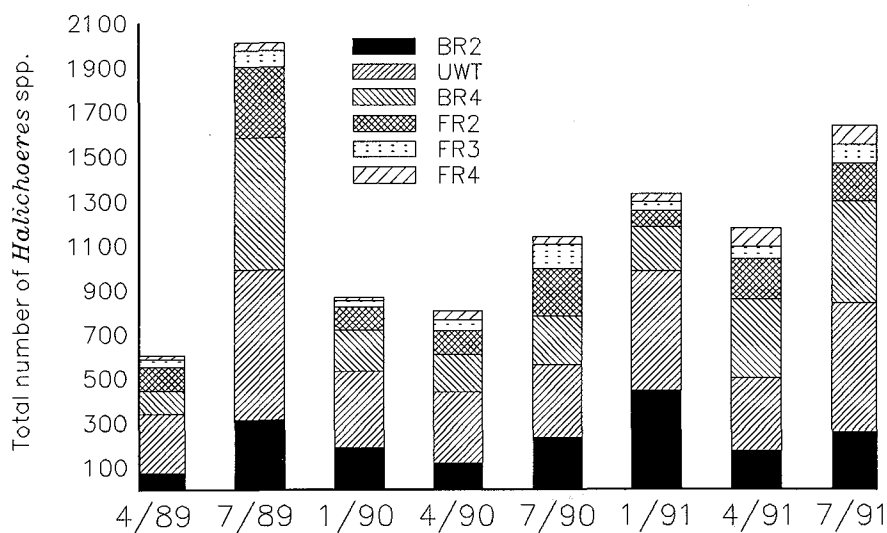


Figure 7. Total number of Labridae (wrasses) in each census site for each census period. a. *Clepticus parrai*. b. *Halichoeres* spp.

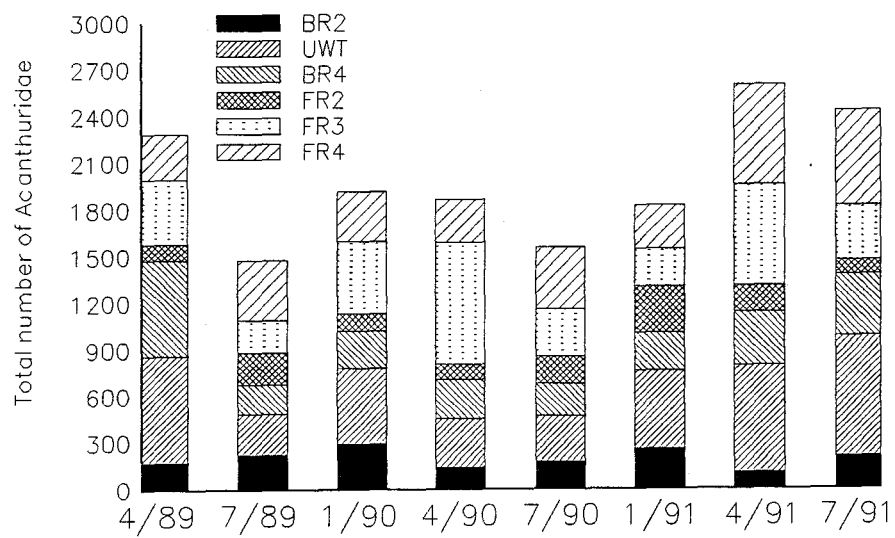


Figure 8. Total number of Acanthuridae (surgeonfishes) in each census site for each census period.

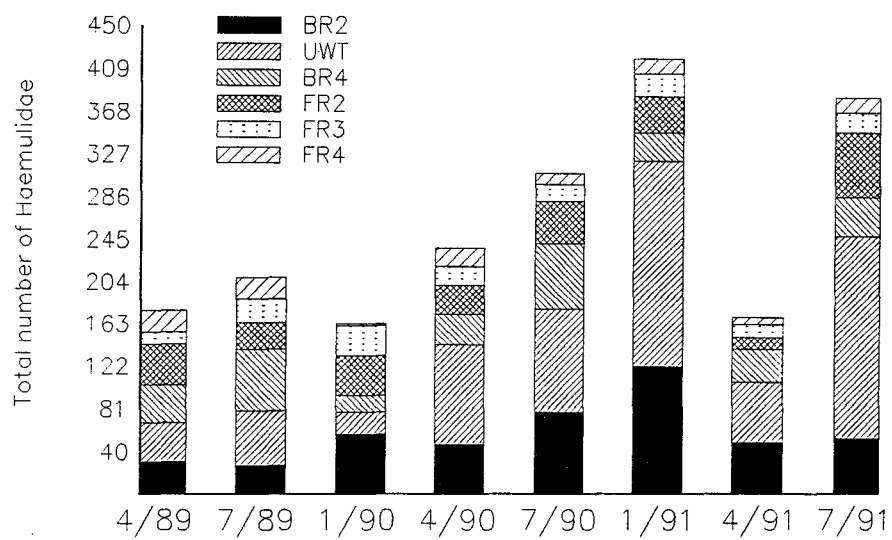


Figure 9. Total number of Haemulidae (grunts) in each census site for each census period.

hurricane, *Sparisoma* sustained the same population levels with a slight increase in 1991. The size of the *Sparisoma* population appears to be more stable than that of *Scarus*.

Pomacentridae. The damselfishes are divided into the turf dwelling territorial *Stegastes* and those with specialized habitats or diets: the yellowtail damselfish (*Microspathodon chrysurus*), the bicolor damselfish (*Stegastes partitus*), blue chromis (*Chromis cyanea*) and brown chromis (*Chromis multilineata*).

Stegastes spp. (with the exception of *S. partitus* to be discussed below) tended to decrease in numbers, due primarily to loss in the backreef sites, in the year following the hurricane (Fig 6a). In 1991, the backreef sites seem to recover slightly, but at the expense of the forereef, making the reef-wide total similar to 1990 and less than pre-hurricane levels. Note in all years censused, there is an increase in the July census.

The yellowtail damselfish, *Microspathodon chrysurus* lives primarily in shallow reefcrest and nearby zones where blades of *Millepora complanata* provide shelter. The populations examined prior to the hurricane showed a good number on all backreef censuses and on FR3 (Fig. 6b). The populations on the backreef sites seem to have been decimated by the hurricane, with no sign of recovery in 1991. In contrast, FR3 showed no change in a good size population of yellowtail damselfishes after the hurricane, and an actual increase in numbers by 1991.

The bicolor damselfish, *S. partitus*, also has specialized habitat requirements, needing rubble piles for nesting sites. Prior to the hurricane, this species was by far most abundant at FR2 (Fig. 6c). The hurricane apparently had a drastic effect, reducing the population at FR2 to about 15% of the pre-storm level. This species seems to be increasing steadily at FR2 and also increasing at FR3 in the 1991 censuses.

Chromis cyanea, the blue chromis, is by far the most abundant at FR2 and contributes over 30% of the individuals seen at this site each census. It is not normally seen at any backreef site (Fig. 6d). This species also decreased after the hurricane, in the 1990 censuses, and the decrease was primarily seen in site FR2. The trend seems to be toward a restoration of prior levels in 1991. This figure also illustrates that in some census periods,

the population was more evenly distributed on the forereef (e.g. July 1990, July 1991).

In contrast to *C. cyanea*, *C. multilineata*, the brown chromis is much less predictably found (Fig. 6e). and much less abundant with at most 10-30% of the *C. cyanea* population size and most often 1% or less. The censuses seem to show a high population in April, a low population in July and an intermediate level in January. As with the blue chromis, the brown chromis, when present, is most abundant at FR2.

Labridae. The wrasses are divided into three taxa: *Clepticus parrai* (creole wrasse; a planktivore that can be compared to the two species of *Chromis*; cf. above), *Halichoeres* spp. (several species of invertebrate consumers) and *Thalassoma bifasciatum* (bluehead wrasse, an ubiquitous species).

The creole wrasse is more abundant and more predictably seen than the brown chromis, but similar to both species of *Chromis*, is found most abundantly (and sometimes exclusively) on FR2 (Fig. 7a). The temporal pattern of abundance is not clear.

Halichoeres species are found much more commonly on the backreef than the forereef (and the most abundant species is *H. bivittatus*, the slippery dick). Their abundance in 1989 showed a drastic increase between April and July, a pattern not seen in subsequent years (Fig. 7b). There was a consistent increase in each month in 1991 as compared to 1990.

Prior to the hurricane, *T. bifasciatum* was fairly evenly distributed among the six reef zones (Fig. 7c). In 1990, after the hurricane, population levels decreased at all sites, but more drastically on the forereef than the backreef. All six sites showed a trend for recovery in 1991 and the mean number per site was much higher in January and April 1991 as compared to comparable months in 1990, although pre-storm levels still had not been achieved.

Acanthuridae. The surgeon fishes are also found in all six reef sites. This family seemed only slightly affected by Hurricane Hugo, with a tendency toward a slight increase in populations perhaps in 1991. Interestingly, the population at FR3 seems to increase in the

April censuses (Fig. 8), perhaps indicating a shift to that site from others in these relatively mobile populations at that time of year, or the site of recruitment to the population.

Haemulidae. The member of this family commonly seen is the french grunt (*H. flavolineatum*), but this family is not a large contributor to the fish community. Census size is often skewed by the presence of one large school; these are not predictably found. There appears to be a trend towards increase in population from 1989 to 1990, and a continuation in 1991, but this is primarily due to a few large schools observed in BR2 and UWT.

Discussion

The results of this study suggest that the fish community at Buck Island Reef National Monument is relatively predictable over time, yet there are apparent declines in certain taxa over the past ten years. There are two lines of evidence to support this statement. First, species number, distribution and abundance are very similar to the 1980 study (Gladfelter and Gladfelter 1980) despite changes in the benthic community during that period (Bythell et al. 1989; Gladfelter et al. 1991a). Second, the populations of some individual species which declined after the passage of Hurricane Hugo partway through the present study have tended to increase to close to pre-storm levels by 1991.

The effects of the hurricane on total abundance of fishes are hard to assess, because comparison of census data by different observers can yield conflicting results. Analyzing data from both observers, it appears that the effect of the storm was to decrease the overall abundance of fishes for at least a year after the storm, but within the second year following the storm, most sites had recovered to or above pre-storm levels. However, in an additional analysis of only those data collected by the same observer during the three years of the study it was found that there was no consistent trend in fish abundances per census date and in fact the highest abundance was July 1990 and the lowest in April 1991! These results cast doubts on the efficacy of this method (when different observers are used) to

detect changes in abundances of fishes over time. However, the total species present and the relative abundances of each can be assessed.

Interestingly, using all census data, the site showing the lowest proportional recovery in abundance by the 1991 censuses was FR2, the area most structurally damaged by Hurricane Hugo (Gladfelter et al. 1991a). It is also of interest to note that the mobile fishes (e.g. Acanthuridae and Scaridae) did not appear to have any or at least major population losses due to the storm, while the less mobile fishes (and those more tied to the benthos for feeding, nesting or shelter sites) showed a decline in abundance (e.g. territorial damselfishes, wrasses and juvenile parrotfishes). Most of the taxa affected by the hurricane did show signs of recovery in abundance by 1991, although the rate of recovery varied among taxa.

Doherty and Williams (1988) make the argument that stability is not a function of physical factors because although they agree that Ebersole and Ogden (1981) demonstrated stability on an artificial reef in St. John, Virgin Islands (Randall's Reef) in 4 censuses conducted over 19 years, the reef itself was degraded physically by storms in that time, thus (in their argument) changing the habitat. In the present case, at Buck Island, the habitat changes seen in the past 10 years are primarily due to the mortality of *Acropora palmata* (Gladfelter et al. 1991a) and less immediately obvious, but also significant, the mortality of *Diadema antillarum* (Lessios et al. 1983, Carpenter 1985). However, the intact, erect but dead skeletons of *A. palmata* have served to provide space for other benthic organisms (particularly algae, except in most oceanic settings). The physical structure of the reef in terms of topographic complexity has only slowly been changed, as storms have eventually compacted the *Acropora* zones (Rogers et al. 1982).

Three censuses per year is not sufficient to clearly detect seasonal patterns in abundance, yet it is important to note that the July censuses were always the highest in each year studied. This is consistent with the Gladfelter (1980) study, in which fish were censused monthly, and most probably reflects recruitment to the fish populations in the spring-summer period.

In this study, a total of 113 species were observed, as compared to 127 in the 1980 study. The difference in number of species could be because the censusing method in the

present study results in an underrepresentation of nocturnal and cryptic species, thus the decrease in total species number does not reflect a major change in the fish community. As in 1980, the most species and the greatest abundance of fishes is found at FR2 (even after that site received heavy physical damage from Hurricane Hugo, Gladfelter et al. 1991a). In both 1980 and 1990, planktivores were dominant members of the community although it should be noted that by 1990 the planktivores seemed more concentrated on the south reef than previously and the proportion of *Chromis cyanea* to the planktivore guild had increased substantially (Gladfelter et al. 1991b). There was no significant difference in the trophic comparisons between 1980 and 1990 (for the four sites with comparative data) yet actual distributions of individual trophic groups appear to have shifted in that period.

In the 1980 study, herbivores had the greatest contribution to the community in the north lagoon, a smaller proportion of the fauna in the south lagoon and lowest proportion on the forereef sites. By 1990, the herbivores had shown an increase in proportional contribution to fish fauna in FR3 (and FR2 when planktivores were removed from the total) and BR2, but a decrease in BR4 (north lagoon site of 1980). The two major groups of herbivores, the Scaridae and the Acanthuridae contributed the most to the fish fauna of the north reef (relative to the south reef) but the territorial turf dwelling damselfish seem to be declining overall on the reef (cf. Gladfelter et al. 1991b) and had almost identical abundances in the 1991 and 1990 censuses, both of which were lower than the pre-storm levels. Overall there appears to be a greater proportion of herbivores in 1990 than 1980, but that includes a decrease in herbivorous pomacentrids and an apparent increase in scarids and acanthurids, perhaps reflecting a shift in food quality and/or quantity due to changes in benthic algal community composition due to increased space (death of *A. palmata*, storms) and differential mortality by predators (e.g. demise of *Diadema*).

Declines in some groups relative to their abundances in 1980, notably snappers, grunts and groupers noted in 1985 (Tobias et al. 1987) have persisted, although this study suggest that grunts, at least may be increasing. These same groups have declined in fish catches throughout St. Croix (Tobias pers. comm.) and the region (Bohnsack pers. comm.) during the 1980's, and it is felt that decline is largely due to targeted fishing of spawning

aggregations. For the snappers and groupers, these aggregations are known to occur far from park boundaries. This reduces the adult population as well as curtailing reproductive success.

To conclude, the fish community at Buck Island has changed in the past ten years, but the magnitude of the change is relatively small and can be attributed to change in benthic habitat and disruptions of reproduction in some groups. The same fish species compose the community as in 1980; the fishes which were the dominant members of the 1980 community remain the dominant members in 1990. A severe perturbation, Hurricane Hugo, caused initial declines in some taxa, but these taxa are showing recovery. The fishes which have shown a decline over the past decade (e.g. snappers, grunts and groupers) have declined region wide. The herbivore feeding guild appears to be shifting to include a larger component of mobile herbivores (acanthurids and scarids) and a smaller component of herbivores tied to the benthos (e.g. pomacentrids). This may reflect the habitat changes due to mortality of *Diadema* and *Acropora*.

A final note on the relevance of the protection offered fishes at Buck Island is in order. The fish community at Buck Island has been important in scientific research (to help in our understanding of natural ecological processes), but it has also served as a major attraction for tourists to the reef, many of whom become advocates of reef preservation. Among fishes which can be seen regularly at Buck Island, but only rarely in sites frequently visited by spear fishermen are the easily approachable french and grey angel fishes and the relatively tame snappers and groupers. In a current study on coral reef fish recruitment patterns, at eight sites along the shores of St. Croix, not a single adult angelfish, snapper or grouper was observed in adult censuses (Caselle, pers. obs.). The need to preserve this community and to continue to understand its nature, through monitoring, is evident.

References

- Bythell JC, EH Gladfelter, WB Gladfelter, K French and Z Hillis (1989) Buck Island Reef National Monument - Changes in modern reef community structure since 1976. In: DK Hubbard (ed.) Terrestrial and Marine Geology of St. Croix, U.S. Virgin Islands.

West Indies Laboratory Spec Publ #8: 145-154

- Bohnsack JA (1983) Species turnover and the order versus chaos controversy concerning reef fish community structure. *Coral Reefs* 1: 223-228
- Bohnsack JA and SP Bannerot (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech Rept NMFS 41, 15 p
- Carpenter RC (1984) Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar Biol* 82: 101-108
- Chaplin CCG (1982) Fishwatcher's guide to the Western Atlantic. Harwood Books. Newton Square, Pennsylvania, 160 p
- Clarke RD (1988) Chance and order in determining fish-species composition on small coral patches. *J Exp Mar Biol Ecol* 115: 197-212
- Clavijo IE, JA Yntema and JC Ogden (1980) An annotated list of the fishes of St. Croix, U.S. Virgin Islands, West Indies Laboratory Publication
- Doherty PJ and D McB Williams (1988) Are local populations of fishes equilibrium assemblages? The empirical database. *Proc 6th Intl Coral Reef Symp*, pp 131-139
- Gladfelter EH, JC Bythell, S. Archer, SK Lewis and M Woodbury (1991a) Impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands: I. Effect on coral community structure and diversity relative to changes in the system since 1976. pp 6: 1-37. In Gladfelter EH, JC Bythell and WB Gladfelter (eds.) *Ecological studies of Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystem and establishment of long term monitoring sites. Part 1.*
- Gladfelter EH, Z Hillis and JC Bythell (1991b) Coral reef fish assemblages, Buck Island Reef National Monument: Seasonal and catastrophic changes. pp 6: 1-29. In Gladfelter EH, JC Bythell and WB Gladfelter (eds.) *Ecological studies of Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystem and establishment of long term monitoring sites. Part 1.*
- Gladfelter WB (1980) Fish Community structure and dynamics in five reef environments. pp VI 1 - VI 21. In: Gladfelter EH and WB Gladfelter (eds.) *Environmental studies of Buck Island National Monument, St. Croix, U.S.V.I. III. U.S. National Park Service Report*
- Gladfelter WB (1982) White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bull Mar Sci* 32: 639-643
- Gladfelter WB and EH Gladfelter (1978) Fish community structure as a function of habitat structure on West Indian patch reefs. *Rev Biol. Trop (suppl 1)*: 65-84.

- Gladfelter WB, JC Ogden and EH Gladfelter (1980) Similarity and diversity among coral reef fish communities: a comparison between the tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology* 61: 1156-1168
- Gladfelter WB, EH Gladfelter, RK Monahan, JC Ogden and RF Dill (1977) Fish. Environmental studies of Buck Island National Monument, St. Croix, USVI. U.S. National Park Service Report, 1-15
- Lessios HA, DR Robertson and JD Cubit (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226: 335-337
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr* 5: 665-847
- Rogers CS, TH Suchanek and FA Pecora (1982) Effects of hurricanes David and Frederick (1979) on shallow *Acropora palmata* reef communities: St. Croix, USVI. *Bull Mar Sci* 32: 532-548.
- Sale PF (1980) Assemblages of fishes on patch reefs - predictable or unpredictable? *Envir Biol Fishes* 5: 243-249
- Simpson G (1979) Fish community dynamics. pp VIII 1-VIII 40. In: Gladfelter EH, WB Gladfelter, DK Hubbard, RC Carpenter and GS Simpson. Environmental studies of Buck Island Reef National Monument, St. Croix, USVI. II U.S. National Park Service Report
- Stokes FJ (1980) Coral reef fishes of the Caribbean. Collins, London, 160pp
- Tobias W, E Telemaque and M Davis (1987) Buck Island fish and shellfish populations. VIRMC II Research Series #7 U.S. National Park Service and VIRMC, 27p
- Wolf, NG (1985) Odd fish abandon mixed-species groups when threatened. *Behav Ecol Sociobiol* 17: 47-52

Appendix I. Total fish list per census period

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	24	38	15	15	39	48	141	98
ABTA	0	0	8	0	0	0	0	1
ACBA	535	131	172	213	142	240	474	575
ACCH	22	78	116	314	204	53	91	59
ACCO	1610	1268	1633	1341	1204	1533	2029	1794
AENA	2	1	3	2	2	2	1	1
ALHA	60	1000	130	0	1000	50	0	310
ALSC	6	1	2	1	1	3	5	1
ANVI	0	0	0	0	0	0	1	1
APBI	0	0	2	0	1	0	0	0
AUMA	25	20	32	17	15	11	9	21
BAVE	1	0	1	2	0	0	3	0
BOLU	3	4	0	0	2	2	1	0
BORU	6	3	4	7	9	4	4	8
CABA	0	3	0	2	1	1	0	1
CALA	0	1	0	0	0	0	0	0
CAPU	19	7	4	5	5	2	4	0
CARO	12	14	6	1	8	16	7	13
CARU	85	400	95	55	80	169	62	115
CHCA	19	27	19	24	22	11	13	19
CHCY	1950	1902	1366	1121	1406	1338	1175	2095
CHMU	283	13	50	303	2	106	108	34
CHST	1	0	6	0	4	1	1	3
CLPA	574	613	270	405	1074	827	156	679
COGL	2	9	7	51	39	14	13	2
DAAM	0	3	0	1	6	1	1	1
ECNA	0	1	0	0	0	0	0	0
EMAT	0	0	0	0	0	0	0	10
EPAD	0	0	2	2	1	1	2	0
EPCR	11	9	1	5	0	2	1	1
EPFU	4	17	2	0	1	1	9	5
EPGU	2	3	6	10	23	21	19	15
EPST	6	1	2	1	5	0	3	0
EULE	0	0	0	7	0	0	0	0
FITA	1	0	0	0	0	0	0	0
GECI	37	24	48	55	54	37	30	31
GOEV	0	0	0	0	0	0	0	4
GOOC	0	0	0	0	0	4	0	0
GRLO	4	7	12	3	11	2	11	13
GYMO	0	0	1	0	0	0	0	0
HAAL	0	2	0	0	0	0	1	0
HAAU	0	0	0	0	0	0	0	4
HABI	394	1512	503	423	573	1106	864	1105
HACA	0	0	0	0	0	1	2	0
HACH	2	2	4	0	1	304	4	0
HAFL	111	125	111	174	235	755	117	296
HAGA	149	306	160	265	258	116	404	427
HAJU	0	28	0	0	60	0	0	746
HAMA	32	0	88	26	28	0	0	1
HAPI	27	149	35	51	184	4	9	7
HAPL	30	40	37	39	50	27	33	43
HAPO	0	2	0	0	1	1	2	0
HARA	21	41	71	47	95	54	46	199
HASC	34	39	15	24	24	27	11	34
HEBR	0	0	0	0	112	10	0	0

HOAS	3	2	0	0	0	0	3	22
HORU	34	25	30	44	53	47	59	34
HOTR	0	0	2	1	0	0	1	4
HYCH	0	1	1	0	0	2	1	0
HYGU	0	0	0	2	0	0	2	0
HYNI	6	4	6	10	6	2	6	9
HYPV	11	3	14	12	6	7	5	3
HYUN	0	4	2	0	1	0	0	2
INVI	0	1	0	0	0	0	0	0
KYSE	7	3	31	6	12	10	3	2
LAPO	0	0	0	0	0	0	0	1
LAQU	0	0	1	0	0	1	0	0
LATR	19	13	17	21	22	16	17	10
LUAN	11	3	0	0	5	4	3	3
LUAP	54	55	17	34	62	60	53	37
LUGR	1	0	1	2	12	4	2	0
LUJO	1	3	0	0	0	0	0	0
LUMA	21	16	30	70	11	100	14	41
MAPL	11	5	5	6	15	8	12	6
MATR	0	2	13	0	5	0	1	0
MENI	1	0	0	1	1	0	2	0
MICH	246	181	142	113	82	93	109	132
MUMA	66	92	118	122	107	101	51	74
MYBO	0	0	0	1	0	1	0	0
MYJA	0	1	0	1	1	0	0	0
MYTI	4	5	1	3	3	4	3	4
MYVE	0	1	0	0	0	1	0	0
OCCH	187	36	55	57	20	28	12	7
OPAT	0	0	0	1	0	0	0	0
POAR	1	7	2	1	6	16	0	0
POPA	11	13	18	16	24	35	17	6
PSMA	12	14	16	27	24	15	9	12
RYSB	1	0	0	0	1	0	0	0
SCCO	0	0	0	0	1	0	0	1
SCCR	26	138	389	102	158	222	119	220
SCGU	1	0	0	0	0	0	0	0
SCMA	0	0	0	0	0	1	0	0
SCRE	1	0	0	0	1	0	0	1
SCTA	15	32	74	16	42	178	12	51
SCVE	186	123	171	215	242	194	251	365
SETA	0	0	3	0	0	0	0	0
SETI	27	35	15	23	21	27	20	9
SPAU	125	119	81	83	93	152	79	106
SPBA	9	8	25	20	3	20	10	16
SPCH	48	59	97	109	122	59	180	144
SPJU	2156	1263	873	1227	1044	1279	1640	1599
SPPI	12	19	50	59	19	0	0	7
SPRU	118	184	130	112	177	98	146	161
SPSP	1	0	7	4	0	2	0	1
SPVI	337	254	252	274	343	226	373	431
STDO(DI,ME	564	742	281	228	469	253	231	640
STLE	203	696	200	225	484	258	431	783
STPA	418	401	61	128	155	123	220	235
STPL	44	233	23	95	72	94	263	277
STTI	264	28	0	0	0	0	0	0
STVA	506	152	355	464	597	309	139	279
SYIN	1	3	1	3	2	1	0	2
THBI	2533	3039	1077	759	1199	1697	1674	2299
TYCR	0	0	0	0	14	0	0	0

Appendix IIa. Forereef 2 total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	3	1	0	1	1	13	4	1
ABTA	0	0	1	0	0	0	0	1
ACBA	11	8	41	28	32	50	51	8
ACCH	16	1	3	11	20	35	23	21
ACCO	80	201	67	61	126	216	97	62
AENA	1	1	1	1	1	1	1	1
ALSC	2	0	0	1	0	0	0	1
AUMA	5	2	11	2	2	3	1	2
BAVE	1	0	1	2	0	0	3	0
BOLU	0	2	0	0	0	0	0	0
BORU	1	1	2	4	3	2	1	0
CAPU	7	3	2	2	4	1	4	0
CARO	7	12	2	1	1	4	5	4
CARU	8	20	2	8	3	12	6	11
CHCA	7	6	7	8	7	4	6	4
CHCY	1596	1690	1076	872	655	1130	861	1414
CHMU	240	11	30	299	1	96	102	26
CHST	0	0	0	0	0	1	0	0
CLPA	570	433	267	383	1064	827	153	668
COGL	0	7	0	0	0	3	0	0
DAAM	0	2	0	0	2	0	0	0
ECNA	0	1	0	0	0	0	0	0
EPAD	0	0	1	0	0	1	1	0
EPCR	6	5	0	1	0	2	1	0
EPFU	1	4	0	0	0	0	0	1
EPGU	0	1	1	3	5	4	6	8
EPST	0	1	0	0	0	0	1	0
FITA	1	0	0	0	0	0	0	0
GECI	0	0	1	0	0	4	1	1
GRLO	0	1	8	1	4	0	2	5
GYMO	0	0	1	0	0	0	0	0
HAAU	0	0	0	0	0	0	0	4
HABI	0	75	14	3	20	17	31	12
HACH	0	0	0	0	0	3	0	0
HAFL	24	20	26	26	37	28	11	57
HAGA	76	104	62	57	98	50	142	142
HAMA	30	0	18	7	9	0	0	0
HAPI	0	140	7	36	83	0	0	0
HAPL	9	2	7	0	3	1	0	2
HARA	1	1	2	4	5	8	7	15
HASC	6	4	5	3	1	2	0	0
HOAS	0	0	0	0	0	0	0	18
HORU	9	9	1	21	27	22	41	21
HOTR	0	0	2	1	0	0	1	4
HYCH	0	1	1	0	0	2	1	0
HYGU	0	0	0	2	0	0	2	0
HYNI	5	4	5	9	6	2	6	9
HYPU	10	3	13	9	6	6	5	2
HYUN	0	3	2	0	1	0	0	2
INVI	0	1	0	0	0	0	0	0
KYSE	6	1	0	0	0	0	0	0

LAQU	0	0	1	0	0	0	0	0
LATR	2	2	2	3	1	3	4	0
LUAN	1	0	0	0	0	0	0	0
LUAP	0	6	1	0	0	0	2	5
LUMA	0	1	2	2	1	1	1	4
MAPL	9	5	5	4	12	7	12	6
MATR	0	1	0	0	0	0	0	0
MENI	1	0	0	0	0	0	0	0
MICH	9	1	27	24	5	17	6	8
MUMA	4	13	15	4	5	4	5	13
MYTI	0	2	0	0	0	0	2	0
MYVE	0	0	0	0	0	1	0	0
OCCH	7	7	4	23	8	9	1	1
POAR	0	0	0	0	0	2	0	0
POPA	4	4	3	2	6	2	5	1
PSMA	0	11	9	3	10	4	3	4
SCCR	2	33	81	25	35	47	25	29
SCMA	0	0	0	0	0	1	0	0
SCRE	1	0	0	0	1	0	0	1
SCTA	0	0	0	0	6	67	5	2
SCVE	5	13	6	7	20	27	7	34
SETA	0	0	3	0	0	0	0	0
SETI	13	5	5	15	6	9	6	6
SPAU	39	43	18	19	30	24	42	48
SPBA	9	5	6	5	0	18	0	5
SPCH	15	9	15	31	26	12	53	24
SPPI	12	0	0	0	0	0	0	0
SPRU	26	60	19	45	51	27	27	61
SPSP	1	0	2	1	0	0	0	0
SPVI	48	49	47	68	52	61	65	62
STDO(DI,ME	60	68	23	8	9	24	16	50
STLE	11	66	4	41	5	1	1	0
STPA	335	362	49	45	102	102	157	167
STPL	16	108	6	29	19	23	108	166
STVA	286	77	229	271	529	156	93	186
SYIN	0	2	0	1	0	0	0	1
THBI	277	444	121	108	107	166	279	187

SUBTOTAL	3932	4179	2393	2651	3273	3365	2502	3598
----------	------	------	------	------	------	------	------	------

HAJU	0	0	0	0	60	0	0	351
PLAR	240	20	0	0	0	0	0	0
SPJU	246	187	122	201	61	172	296	251

TOTAL FR2	4418	4386	2515	2852	3394	3537	2798	4200
-----------	------	------	------	------	------	------	------	------

Appendix IIb. Forereef 3 total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	10	4	2	0	7	1	113	3
ACBA	81	22	28	31	21	28	39	56
ACCH	1	1	0	38	23	1	2	4
ACCO	336	181	435	714	254	209	612	293
AENA	1	0	0	0	0	0	0	0
ALSC	0	0	0	0	0	2	0	0
AUMA	4	2	3	4	3	5	4	7
BOLU	0	0	0	0	0	2	0	0
BORU	2	0	0	1	3	1	4	3
CALA	0	1	0	0	0	0	0	0
CAPU	5	0	0	0	0	1	0	0
CARO	2	0	4	0	6	8	0	5
CARU	3	65	14	2	2	64	8	5
CHCA	2	2	3	1	1	0	0	1
CHCY	298	203	266	217	572	188	305	306
CHMU	43	2	15	4	0	12	6	8
CLPA	4	180	3	22	10	0	3	11
DAAM	0	0	0	0	1	1	0	0
EPCR	2	0	1	2	0	0	0	0
EPFU	1	2	1	0	1	0	0	0
EPGU	0	2	0	1	1	1	4	0
GECI	0	1	0	1	0	1	2	0
GOOC	0	0	0	0	0	2	0	0
GRLO	0	3	4	2	7	2	7	8
HABI	0	29	10	0	5	19	10	17
HAFL	9	0	22	11	12	11	7	11
HAGA	28	44	15	38	29	17	43	54
HAMA	1	0	0	4	3	0	0	0
HAPI	2	0	0	0	62	0	0	0
HAPL	2	18	6	7	4	4	3	6
HARA	4	1	7	6	12	5	3	13
HASC	1	5	1	0	1	7	3	2
HOAS	1	0	0	0	0	0	2	0
HORU	2	1	1	0	0	0	1	2
HYNI	1	0	1	1	0	0	0	0
HYPU	1	0	1	3	0	0	0	0
HYUN	0	1	0	0	0	0	0	0
INVI	0	0	0	0	0	6	0	0
KYSE	0	0	0	5	3	2	1	0
LATR	2	0	1	2	1	4	1	2
LUAN	0	1	0	0	0	0	1	0
LUAP	28	32	8	13	30	39	24	5
LUMA	12	5	17	63	6	91	8	27
MAPL	0	0	0	1	0	0	0	0
MENI	0	0	0	1	1	0	2	0
MICH	53	44	33	58	47	39	59	83
MUMA	15	8	7	23	2	26	6	5
MYBO	0	0	0	1	0	0	0	0
MYJA	0	0	0	1	0	0	0	0
MYTI	2	1	0	1	1	1	1	3
MYVE	0	1	0	0	0	0	0	0
OCCH	132	24	12	19	1	9	4	0
POAR	0	2	0	1	6	1	0	0

POPA	3	2	3	4	9	11	3	1
PSMA	0	0	1	8	4	0	1	1
SCCR	2	37	59	23	6	59	1	26
SCTA	9	8	8	0	16	33	0	0
SCVE	59	38	32	86	82	71	102	118
SETI	5	5	1	1	4	2	4	0
SPAU	38	16	13	35	28	4	6	7
SPBA	0	0	7	0	2	0	1	0
SPCH	2	8	16	23	21	2	16	21
SPPI	0	19	50	59	0	0	0	0
SPRU	22	27	11	19	41	10	43	26
SPSP	0	0	3	3	0	1	0	0
SPVI	61	62	40	57	54	27	67	62
STDO(DI,ME)	80	139	45	35	103	82	50	112
STLE	3	13	2	8	8	10	6	3
STPA	12	19	7	11	20	4	46	31
STPL	2	49	0	28	17	5	37	33
STVA	97	25	40	116	29	50	23	54
SYIN	0	0	0	0	1	0	0	0
THBI	417	958	80	96	166	234	347	418
SUBTOTAL	1903	2313	1339	1911	1749	1415	2041	1853
ALHA	0	230	0	0	0	0	0	50
HAJU	0	0	0	0	0	0	0	15
SPJU	247	242	105	325	247	221	253	403
PLAR	123	0	0	0	0	0	0	0
TOTAL FR3	2273	2785	1444	2236	1996	1636	2294	2321

Appendix IIc. Forereef 4 total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	1	0	0	2	13	7	3	6
ABTA	0	0	1	0	0	0	0	0
ACBA	86	4	40	54	27	30	104	97
ACCH	5	29	0	23	41	4	13	8
ACCO	197	356	287	202	330	251	519	503
AENA	0	0	2	0	0	0	0	0
ALSC	0	0	0	0	1	0	0	0
ANVI	0	0	0	0	0	0	0	1
AUMA	8	8	3	3	3	3	3	9
BORU	0	0	0	1	2	0	1	3
CARO	1	2	0	0	1	3	0	2
CARU	18	23	33	18	33	61	7	18
CHCA	2	2	0	1	3	0	1	1
CHCY	76	9	24	32	179	20	9	375
CHMU	0	0	5	0	1	0	0	0
CHST	0	0	6	0	0	0	0	0
COGL	0	1	0	0	0	0	1	1
DAAM	0	0	0	0	0	0	0	1
EMAT	0	0	0	0	0	0	0	10
EPAD	0	0	0	0	1	0	1	0
EPCR	0	0	0	0	0	0	0	1
EPFU	0	0	1	0	0	0	3	0
EPGU	0	0	1	0	0	1	0	0
EPST	0	0	0	1	0	0	0	0
EULE	0	0	0	7	0	0	0	0
GECI	9	16	6	15	4	1	2	5
GRLO	2	1	0	0	0	0	0	0
HABI	0	10	1	6	11	22	24	37
HACA	1	0	0	0	0	0	0	0
HAFL	14	14	2	11	7	9	4	9
HAGA	22	17	13	23	10	12	55	32
HAMA	0	0	0	0	0	0	0	1
HAPI	0	0	0	0	0	0	0	3
HAPL	3	2	0	5	2	3	3	3
HAPO	0	1	0	0	0	0	0	0
HARA	6	6	0	5	10	1	6	12
HASC	3	3	0	2	1	2	0	2
HORU	1	4	0	1	1	2	2	0
HYPU	0	0	0	0	0	1	0	1
KYSE	0	2	29	1	3	3	1	0
LAPO	0	0	0	0	0	0	0	1
LATR	1	5	7	5	6	1	3	3
LUAN	1	1	0	0	1	2	0	0
LUAP	3	1	1	2	7	5	3	5
LUMA	3	2	3	1	1	3	2	2
MICH	15	11	10	5	2	15	12	29
MUMA	10	22	21	13	34	7	9	16
MYJA	0	1	0	0	0	0	0	0
MYTI	1	1	1	1	1	0	0	0
OCCH	16	3	14	6	5	4	3	1
POAR	1	3	1	0	0	4	0	0
POPA	2	3	9	8	9	6	8	0
PSMA	8	1	0	1	2	0	1	0

SCCO	0	0	0	0	1	0	0	0
SCCR	0	23	62	13	42	25	19	36
SCTA	3	7	31	8	6	20	3	4
SCVE	30	10	47	44	36	36	41	92
SETI	1	0	1	0	0	1	1	0
SPAU	20	40	10	12	16	15	12	23
SPBA	0	0	5	3	0	1	5	2
SPCH	14	8	11	15	25	2	38	22
SPPI	0	0	0	0	17	0	0	0
SPRU	16	53	26	19	31	6	17	16
SPSP	0	0	2	0	0	0	0	0
SPVI	43	27	45	41	49	30	55	60
STDO(DI,ME)	34	20	9	21	22	19	18	31
STLE	8	6	0	3	13	2	4	4
STPA	0	0	0	0	1	2	2	6
STPL	4	18	1	22	6	21	33	24
STVA	17	15	17	9	5	15	15	16
SYIN	0	0	0	1	0	0	0	0
THBI	422	368	112	57	294	231	222	525
SUBTOTAL	1128	1159	900	723	1316	909	1288	2059
ALHA	0	0	0	0	0	0	0	30
HAJU	0	8	0	0	0	0	0	55
SPJU	157	85	34	89	60	129	279	208
TYCR	0	0	0	0	14	0	0	0
TOTAL FR4	1285	1252	934	812	1390	1038	1567	2352

Appendix II.d. Backreef 2 total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	0	0	5	9	5	0	0	0
ACBA	42	29	5	21	13	34	12	26
ACCH	0	1	91	43	32	4	1	0
ACCO	131	191	196	76	128	217	88	180
AENA	0	0	0	1	0	0	0	0
ALSC	0	0	0	0	0	1	2	0
APBI	0	0	2	0	1	0	0	0
AUMA	3	2	6	3	2	0	0	0
BOLU	1	0	0	0	1	0	0	0
BORU	1	0	0	0	0	0	0	0
CAPU	0	1	0	1	0	0	0	0
CARO	0	0	0	0	0	0	1	0
CARU	13	222	26	6	11	21	7	24
CHCA	4	2	8	11	6	7	6	4
CHST	0	0	0	0	0	0	0	2
COGL	2	0	7	48	33	11	12	1
DAAM	0	1	0	0	2	0	1	0
EPCR	0	1	0	2	0	0	0	0
EPFU	1	2	0	0	0	0	0	0
EPGU	0	0	1	1	6	4	3	0
EPST	0	0	0	0	0	0	1	0
GOEV	0	0	0	0	0	0	0	4
HAAL	0	2	0	0	0	0	0	0
HABI	60	282	115	79	190	406	148	210
HACH	0	0	4	0	1	0	4	0
HAFL	21	18	42	28	54	106	38	33
HAGA	4	9	12	18	6	18	10	9
HAMA	0	0	13	7	1	0	0	0
HAPI	13	9	27	0	16	3	2	0
HAPL	4	5	8	9	15	9	6	12
HAPO	0	0	0	0	0	0	1	0
HARA	5	4	21	12	19	16	9	36
HASC	6	4	7	10	9	6	0	8
HOAS	2	0	0	0	0	0	0	3
HORU	5	7	21	17	22	7	8	6
KYSE	0	0	0	0	0	1	0	0
LAQU	0	0	0	0	0	1	0	0
LATR	10	4	2	4	7	4	3	3
LUAN	2	0	0	0	2	0	2	3
LUAP	13	3	8	1	11	11	6	15
LUJO	0	1	0	0	0	0	0	0
LUMA	3	5	5	1	1	0	3	2
MATR	0	0	12	0	4	0	1	0
MICH	49	28	23	16	7	6	17	5
MUMA	24	27	13	41	39	32	13	21
MYJA	0	0	0	0	1	0	0	0
MYTI	1	0	0	0	0	0	0	1
OCCH	10	0	11	6	2	1	1	0
POPA	0	0	0	0	0	0	0	1
PSMA	0	0	0	0	0	4	1	1
SCCR	12	11	35	9	5	39	18	23
SCGU	1	0	0	0	0	0	0	0
SCTA	0	3	22	0	3	31	0	7

SCVE	5	0	5	14	13	19	11	16
SETI	0	7	2	4	0	2	0	0
SPAU	3	0	0	1	0	1	1	0
SPBA	0	1	1	10	1	1	2	8
SPCH	4	1	6	7	10	13	5	1
SPRU	16	8	21	3	8	28	17	28
SPSP	0	0	0	0	0	1	0	0
SPVI	54	29	41	40	61	35	25	76
STDO(DI,ME)	112	179	78	83	180	77	74	110
STLE	6	228	55	66	127	97	174	369
STPA	50	0	5	3	2	2	0	10
STPL	12	10	2	4	14	25	32	14
STVA	35	0	14	44	5	41	0	0
SYIN	1	0	0	0	0	0	0	1
THBI	246	217	174	89	125	287	186	179
SUBTOTAL	987	1554	1152	848	1201	1629	952	1452
ALHA	60	1000	130	0	1000	50	0	230
HAJU	0	10	0	0	0	0	0	35
HEBR	0	0	0	0	112	0	0	0
SPJU	85	94	113	204	90	216	199	175
TOTAL BR2	1132	2658	1395	1052	2403	1895	1151	1892

Appendix IIe. Underwater Trail total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	0	30	8	3	0	27	21	88
ABTA	0	0	6	0	0	0	0	0
ACBA	147	44	16	27	41	62	172	335
ACCH	0	42	0	142	62	8	28	24
ACCO	544	178	469	142	191	436	491	418
AENA	0	0	0	0	1	0	0	0
ALSC	4	0	2	0	0	0	2	0
ANVI	0	0	0	0	0	0	1	0
AUMA	0	0	4	3	3	0	0	1
BOLU	2	2	0	0	0	0	0	0
BORU	0	1	0	1	1	1	0	2
CABA	0	0	0	0	1	0	0	0
CAPU	2	1	2	2	1	0	0	0
CARU	24	65	7	5	16	12	16	23
CHCA	3	10	0	1	0	0	0	3
CHST	0	0	0	0	2	0	1	1
COGL	0	1	0	3	0	0	0	0
EPAD	0	0	0	1	0	0	0	0
EPCR	3	2	0	0	0	0	0	0
EPFU	0	7	0	0	0	1	5	4
EPGU	0	0	0	0	3	9	2	0
EPST	5	0	2	0	5	0	1	0
GOOC	0	0	0	0	2	0	0	0
GRLO	2	0	0	0	0	0	0	0
HAAL	0	0	0	0	0	0	1	0
HABI	246	628	245	226	216	489	228	489
HACA	1	0	0	0	0	0	0	0
HACH	0	1	0	0	0	300	0	0
HAFL	16	28	10	79	78	579	43	169
HAGA	8	43	21	75	61	28	88	52
HAMA	1	0	41	7	8	3	0	1
HAPI	9	0	0	0	13	1	0	2
HAPL	8	6	10	12	15	9	10	12
HARA	3	7	36	13	30	17	13	39
HASC	13	16	1	4	6	6	3	14
HOAS	0	1	0	0	0	0	1	1
HORU	12	2	6	1	3	15	5	4
HOTR	0	0	0	0	0	0	1	0
KYSE	0	0	0	0	0	0	0	1
LATR	3	1	0	4	5	2	4	0
LUAN	6	0	0	0	1	2	0	0
LUAP	2	9	1	2	3	0	12	2
LUGR	0	0	1	1	11	0	0	0
LUJO	0	1	0	0	0	0	0	0
LUMA	1	2	0	1	1	2	2	3
MAPL	2	0	0	1	0	1	0	0
MATR	0	1	0	0	1	0	0	0
MICH	52	59	25	10	16	11	13	6
MUMA	10	11	41	11	16	25	13	15
MYBO	0	0	0	0	0	1	0	0
MYTI	0	1	0	0	0	0	0	0
OCCH	5	2	10	2	3	2	0	1
OPAT	0	0	1	0	0	0	0	0

POAR	0	2	0	0	0	0	0	0
POPA	2	3	0	1	0	10	1	4
PSMA	1	1	4	6	3	3	2	2
SCCO	0	0	0	0	0	0	0	1
SCCR	3	12	58	19	29	26	24	55
SCTA	3	8	3	0	3	10	3	8
SCVE	28	42	52	20	48	19	63	62
SETI	6	13	4	2	10	10	5	1
SPAU	7	7	11	5	7	11	4	15
SPBA	0	0	2	1	0	0	0	1
SPCH	11	7	26	18	24	8	16	38
SPRU	19	14	25	7	11	3	30	23
SPSP	0	0	0	0	0	0	0	1
SPVI	36	56	50	27	74	44	103	111
STDO(DI,ME)	108	229	113	46	127	30	54	88
STLE	163	253	115	85	262	107	167	322
STPA	12	20	0	12	12	13	12	18
STPL	5	39	1	1	6	6	25	23
STVA	48	26	29	2	15	40	3	1
SYIN	0	0	0	1	1	0	0	0
THBI	537	379	265	238	287	579	363	658
SUBTOTAL	2123	2313	1723	1270	1735	2968	2052	3142
HAJU	0	0	0	0	0	0	0	160
SPJU	558	434	268	319	337	252	284	295
TOTAL UWT	2681	2747	1991	1589	2072	3220	2336	3597

Appendix II. Backreef 4 total species list per census

SPECIES	APR-89	JUL-89	JAN-90	APR-90	JUL-90	JAN-91	APR-91	JUL-91
ABSA	10	3	0	0	13	0	0	0
ACBA	168	24	42	52	8	36	96	2
ACCH	0	4	22	57	26	1	24	53
ACCO	442	161	179	146	175	204	222	338
AENA	0	0	0	0	0	1	0	0
ALSC	0	1	0	0	0	0	1	0
AUMA	5	6	5	2	2	0	1	2
BOLU	0	0	0	0	1	0	1	0
CABA	0	3	0	0	0	0	0	1
CAPU	5	2	0	0	0	0	0	0
CARO	2	0	0	0	0	1	0	2
CARU	19	5	13	16	15	9	18	4
CHCA	1	5	1	2	5	0	0	6
CHST	1	0	0	0	2	0	0	0
COGL	0	0	0	0	6	0	0	0
DAAM	0	0	0	1	1	0	0	0
EPAD	0	0	1	1	0	0	0	0
EPCR	0	1	0	0	0	0	0	0
EPFU	1	2	0	0	0	0	1	0
EPGU	2	0	2	5	8	2	4	0
EPST	1	0	0	0	0	0	0	0
GRLO	0	2	0	0	0	0	2	0
HABI	88	488	118	109	131	153	274	283
HACA	0	0	0	0	0	0	1	0
HACH	1	1	0	0	0	0	0	0
HAFL	27	45	9	19	47	22	14	21
HAGA	11	79	47	39	54	41	66	138
HAMA	0	0	15	1	6	0	0	0
HAPI	3	0	1	15	9	0	7	2
HAPL	4	7	6	6	11	1	11	8
HAPO	0	1	0	0	1	1	2	0
HARA	2	22	5	7	19	7	8	38
HASC	5	7	1	5	6	4	5	8
HOAS	0	1	0	0	0	0	0	0
HORU	5	2	1	4	0	1	2	1
KYSE	1	0	2	0	6	4	1	1
LATR	1	1	5	3	2	2	2	2
LUAN	1	1	0	0	2	0	0	0
LUAP	8	4	8	10	11	5	6	5
LUGR	1	0	0	1	0	4	2	0
LUJO	1	1	0	0	0	0	0	0
LUMA	2	1	3	2	1	3	4	3
MAPL	0	0	0	0	3	0	0	0
MATR	0	0	1	0	0	0	0	0
MICH	68	38	24	0	5	5	2	1
MUMA	4	11	21	30	11	7	6	4
MYTI	0	0	0	1	1	3	0	0
OCCH	17	0	6	1	1	3	3	4
POAR	0	0	1	0	0	9	0	0
POPA	0	1	3	1	0	1	0	0
PSMA	3	1	2	9	5	4	1	4
RYSA	1	0	0	0	1	0	0	0
SCCR	7	22	94	13	41	31	20	51

SCTA	0	6	10	8	8	12	1	18
SCVE	59	20	29	44	43	22	27	43
SETI	2	5	2	1	1	3	4	2
SPAU	18	13	29	12	12	18	14	13
SPBA	0	2	4	1	0	0	2	0
SPCH	2	26	23	15	16	22	52	38
SPPI	0	0	0	0	2	0	0	7
SPRU	19	22	28	19	35	24	12	17
SPVI	95	31	29	41	53	29	58	60
STDO(DI,ME)	170	107	3	35	28	21	19	18
STLE	12	130	124	59	69	41	79	85
STPA	9	0	0	0	0	0	5	3
STPL	5	9	2	11	10	4	28	17
STVA	23	9	42	22	14	7	5	22
SYIN	0	1	1	0	0	1	0	0
THBI	634	673	325	166	213	408	277	332
 SUBTOTAL	 1966	 2007	 1289	 992	 1140	 1177	 1390	 1657
 HAJU	 0	 10	 0	 0	 0	 0	 0	 145
SPJU	863	221	231	89	249	289	329	267
 TOTAL BR4	 2829	 2238	 1520	 1081	 1389	 1466	 1719	 2069

Coral reef community structure assessment based on planar and three-dimensional area cover: A comparison of techniques

Chapter 3

John C. Bythell¹, Mary Bythell¹ and Elizabeth H. Gladfelter²

Present addresses: ¹Centre for Tropical Coastal Management, Department of Marine Sciences, University of Newcastle upon Tyne NE1 7RU, UK. ²PO Box 26472, Gallows Bay Station, St. Croix, U.S. Virgin Islands 00824.

Introduction

Both local and regional disturbances on coral reefs are becoming more widely reported (Rogers 1985, Brown et al. 1990). Although we are presently unable to state for certain that there have been any biological or ecological effects of global climate change (D'Elia et al. 1991), the need for comprehensive long-term monitoring of what may be particularly sensitive ecosystems (Jokiel and Coles 1990) is now clearly recognized (D'Elia et al. 1991).

Coral reef communities present some special problems for assessing species abundances and community structure. Not least, the environment is underwater and access time for field work is strictly limited. Much emphasis has therefore been placed on the relative efficiency of different assessment techniques: information gained versus time or effort expended (Weinberg 1981). A major conceptual problem is that corals and many other organisms on the reef are clonally replicated and exist as variable sized colonies rather than discrete individuals. Surface area cover is therefore a more ideal measure of species abundance, and hence relative resource use, than is the number of colonies (Magurran 1988).

Researchers on coral reefs have relied largely on methods used for the analysis of plant communities, for example point intersect (Rutzler 1978, Kinzie and Snider 1978), line intersect (Loya and Slobodkin 1971, Loya 1972), area coverage (Pearson 1974, Weinberg 1978, Bouchon 1981) or "plotless" methods (Loya 1978). Weinberg (1981) compared these methods on a reef plot that had previously been completely mapped and analyzed for species abundance distributions. He concluded that visual estimation of percent cover within 1 m² quadrats was the most accurate technique. All of these methods estimate the relative planar (i.e. two-dimensional) surface of reef occupied by different species. Reefs are extremely complex three-dimensional structures. Perhaps most importantly, the community structure itself influences the spatial arrangement of the reef. That is, reef building corals secrete their own substrate, the topography of which is highly variable between species (Pichon 1978). Thus, not only will cryptic species tend to be overlooked when employing a two-dimensional approach, but relative estimates of resource use will be biased depending upon the distribution of the respective species' morphologies within a community.

Here we compare two techniques which may be used to assess three-dimensional cover: visual assessment of all surfaces within 1 m² quadrats, and chain transects (Porter 1972, Rogers et al. 1983). Coral community structure measures determined by these techniques were compared with a standard method of coral community assessment: vertical photo-quadrats, with planar surface areas determined by computer digitization. Our comparison does not allow a determination of the accuracy of the different techniques, since the true surface areas of corals and other organisms in the study areas were not determined. It does, however, allow a comparison of the results and conclusions which may be drawn about community organization when employing the different methods.

Methods

Each of the techniques employed were repeated at three separate sites at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands (Gladfelter et al., 1991 and Chapter 1, this volume). Within each of the three sites, replicate determinations were made along four fixed 20 m transects which were permanently marked at each end and at the center with steel marker stakes. A measuring tape was stretched taut across the stakes to serve as a guide for each of the surveys.

The three sites were of distinctly different community composition and topographic structure, which was expected to influence the results of the different techniques. They can be broadly described as follows:

- Site 1.* Relatively diverse coral community, with moderately high structural relief produced mainly by live colonies of *Montastrea annularis* and *Porites porites*. Moderate coral cover (13-29% determined by chain transects).
- Site 2.* Less diverse with very low structural relief; a fairly flat coralline pavement with abundant medium to large sized colonies of encrusting *Diploria clivosa* and hemispherical *D. strigosa*. Highest overall coral cover of the three sites (32-40% determined by chain transects).

Site 3. Lowest coral diversity and very low coral cover (0.3-3.3% determined by chain transects), but with high structural relief provided by largely dead stands of *Acropora palmata*.

Visually assessed 1m² quadrats. Quadrats constructed from 3/4" PVC pipe with painted 10 cm divisions along each side were placed sequentially along each meter at the center of the transect line. The observer first estimated a spatial index for the quadrat. The estimates ranged from 1 (flat) to approximately 4 for a high-complexity substrate (the index theoretically has an open upper limit). The value represented the estimated three-dimensional to two-dimensional surface area ratio at a resolution of approximately 1 cm, that is, surface area contours less than 1 cm wide and/or deep were ignored when estimating the ratio.

Surface areas for all species and substrate types within the quadrat were then estimated by the observer and scaled to the estimated spatial index ratio. For example, a 10 cm² coral colony would be estimated at 1% cover on a flat substrate, or 0.25% in a high complexity area (with a surface area ratio of 4). A resolution of approximately 1 cm was also applied to the estimates of benthic cover. Bushy gorgonians were largely omitted from the estimates with only the thicker basal attachment being included.

Chain transects. A 50 cm length of light chain with 1.26 cm links was placed over the surface contour immediately below the taut measuring tape. Surfaces overhanging the transect line were also assessed, including both upper and lower surfaces. Specific substrates under each chain link were recorded and the chain moved repeatedly to allow data to be summed for each horizontal meter along the transect. The spatial resolution of the technique is similar to that employed for visual quadrat assessment, being limited by the width of the chain. In addition to calculating the percent composition of each species/substrate type along the transect, a spatial complexity index was also determined as the ratio between horizontal distance (20 m) and the total length of chain used to cover the surface contour of the transect (Rogers et al., 1983).

Photo quadrats. Photographs (Ektachrome 100) were taken using a Nikonos V camera with 28 mm lens and SB103 strobe on a PVC framer which was temporarily attached to the transect line measuring tape. Frames encompassed 1 x 0.65 m of the substrate, including 0.5 m on either side of the transect line. Sequential frames were overlapped by 5 cm to photograph the entire transect. Developed slides were projected and adjusted to fit on a 12 x 12 cm grid. Coral colonies were traced by hand onto paper and sequential photographs used to compose the equivalent of 1 x 1 m traced drawings. The drawings were then digitized using a Summagraphics 12 x 12 cm digitizing pad and an IBM PC-compatible computer running Easydij 7.0 software. This system allowed planar surface area assessments to be made for each coral species or type of substrate.

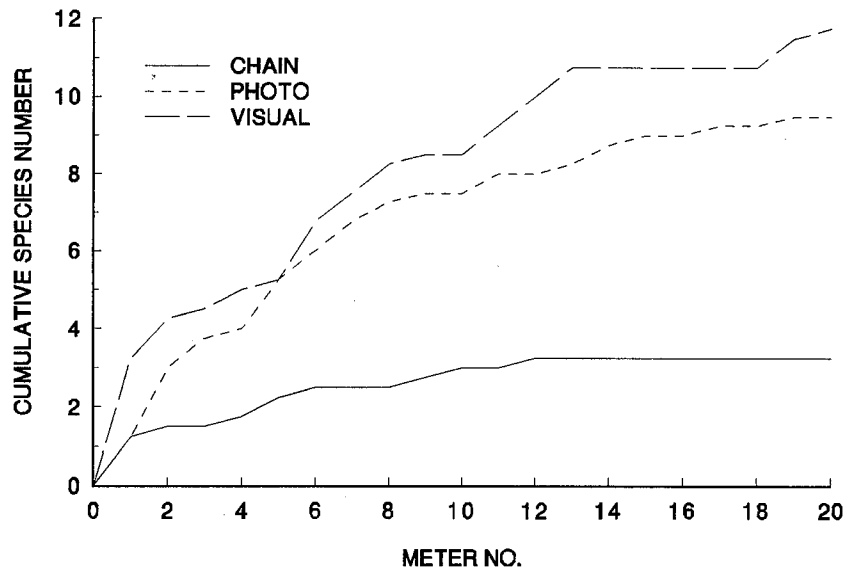
Statistical analyses. Univariate statistical measures were calculated using percent surface area cover (quadrat techniques) or number of chain links (chain transects) as "individuals", since size of coral colonies is extremely variable. Results of the different techniques were used to calculate standard measures of abundance (percent cover) and diversity (Shannon H', Pielou's J and Simpson's inverse 1/D) of coral communities including hydrocorals for each 20 m transect. A graphical technique (k-dominance curves; Lambshead et al., 1983) was used to describe species abundance distributions independent from any bias towards species richness or evenness.

Results

Efficiency

Different numbers of species were detected by the three techniques, with the most species consistently recorded by visual quadrats and the least by chain transects at all sites (Figs. 1-3). The curves suggest that differences between the methods would not be resolved by increased sampling, since average species numbers generally appear to reach their asymptotic maxima within 10-15 m along the transect. Where the curves do not appear to

A



B

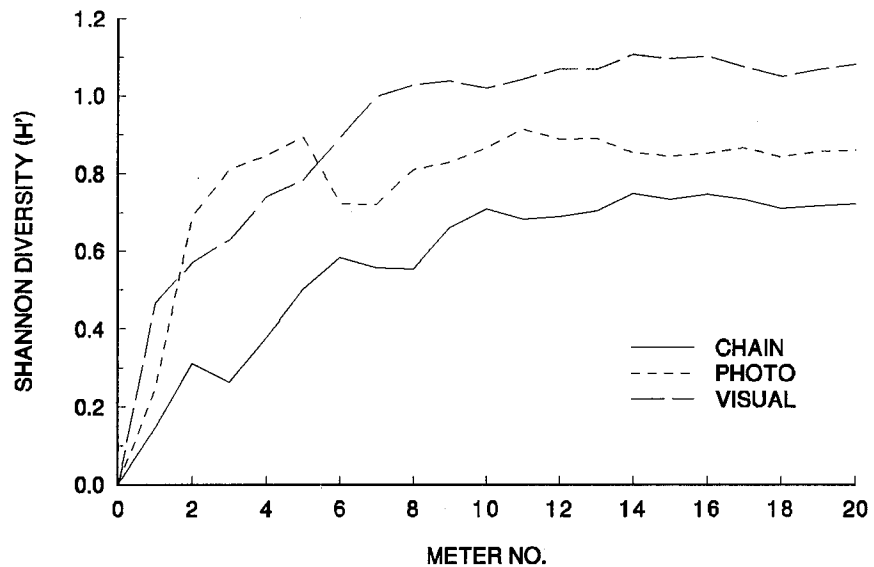
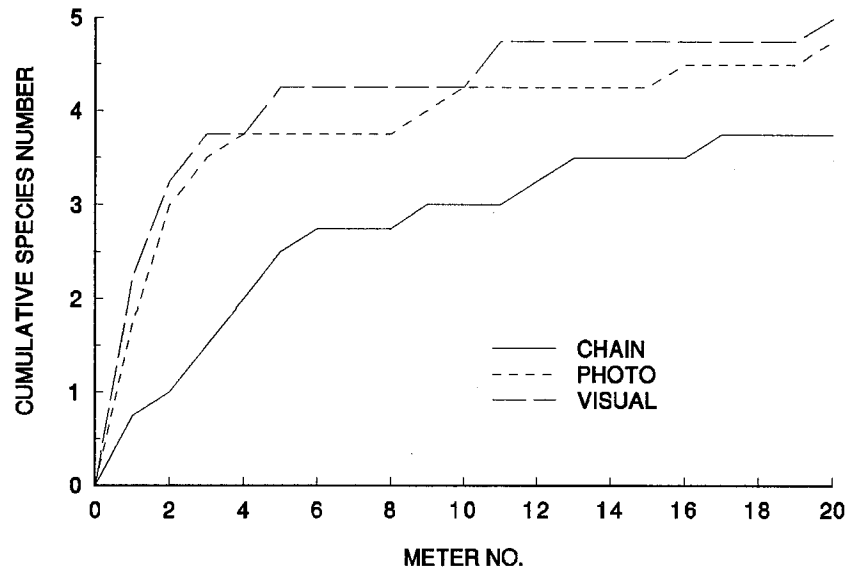


Figure 1. Cumulative random-order species number (A) and Shannon H' diversity (B) against length along the transect for each of the three techniques employed at site 1. Values shown are means of the four replicate transects. CHAIN = chain transect, PHOTO = photo-quadrats and VISUAL = visual quadrat estimates (three-dimensional surfaces).

A



B

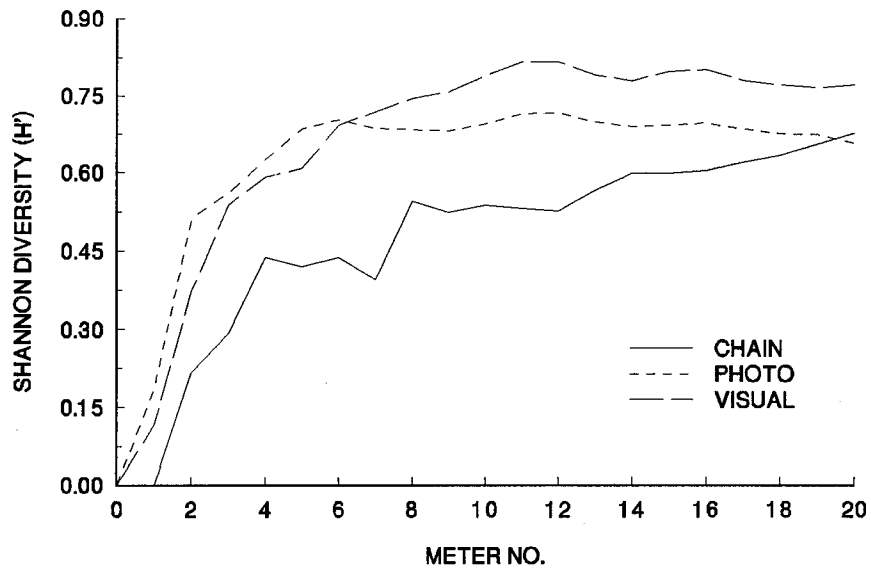
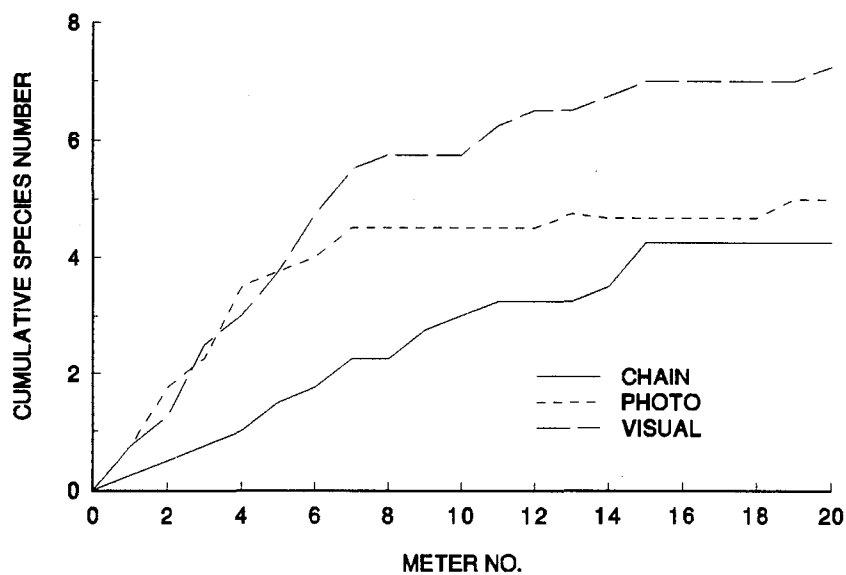


Figure 2. Cumulative random-order species number (A) and Shannon H' diversity (B) against length along the transect for each of the three techniques employed at site 2. Values shown are means of the four replicate transects. CHAIN = chain transect, PHOTO = photo-quadrats and VISUAL = visual quadrat estimates (three-dimensional surfaces).

A



B

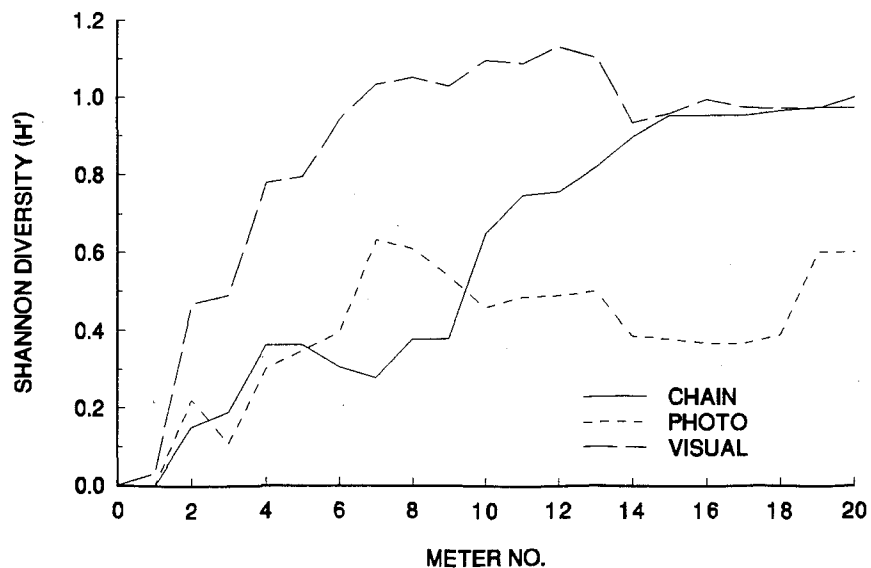


Figure 3. Cumulative random-order species number (A) and Shannon H' diversity (B) against length along the transect for each of the three techniques employed at site 3. Values shown are means of the four replicate transects. CHAIN = chain transect, PHOTO = photo-quadrats and VISUAL = visual quadrat estimates (three-dimensional surfaces).

level out (e.g. Fig. 1a, photo-quadrat and visual quadrat data) the effect of additional sampling would tend to exaggerate the differences between the techniques. Results for coral species diversity (Shannon H') were not as consistent as species richness (Figs. 1b - 3b). At the topographically most complex site (site 3), the "3-D" techniques (visual quadrats and chain transects) produced similar results for Shannon diversity, while photo-quadrats showed a lower value. At site 2, the least spatially complex, Shannon diversity indices from all techniques were comparable, whereas at site 1 (moderate complexity, coral diversity and coral cover) results were different for all three techniques.

Photo-quadrats required the least field-time underwater (15-30 min. per 20 m transect), followed by visual quadrats (30-40 min.) and chain transects (40-70 min.), once the tape measure guide had been placed. Although the photo-transect technique required less actual bottom-time, the diver had to return to the boat after each transect to change film. Chain transect and visual quadrat data could be quickly transcribed and entered on a computer database (approximately 1 h per transect), whereas each 20 m photo-transect required several hours tracing and digitizing.

Community structure measures

Figures 4-6 show k-dominance curves obtained by the three techniques at each site. The curves appear similar for the different techniques (Figs. 4 and 5), and/or overlap at various stages (Fig. 6).

The different survey methods all rank the three sites in the same order of percent total coral cover (site 2 > site 1 > site 3; Table 1). Within sites, there was a significant difference between the methods only at site 2 (lowest topographic complexity), where a significantly higher mean percent cover was detected by chain transects than the other techniques. Interestingly, there were no significant differences in mean percent coral cover determined by three-dimensional visual quadrats and two-dimensional photo-quadrats at any site.

As suggested by the overlapped k-dominance curves, univariate measures of coral species diversity were not consistent between survey techniques at the three sites (Tables 2-4). For example, chain transects produced a ranking of site 3 > site 1 = site 2 for Shannon

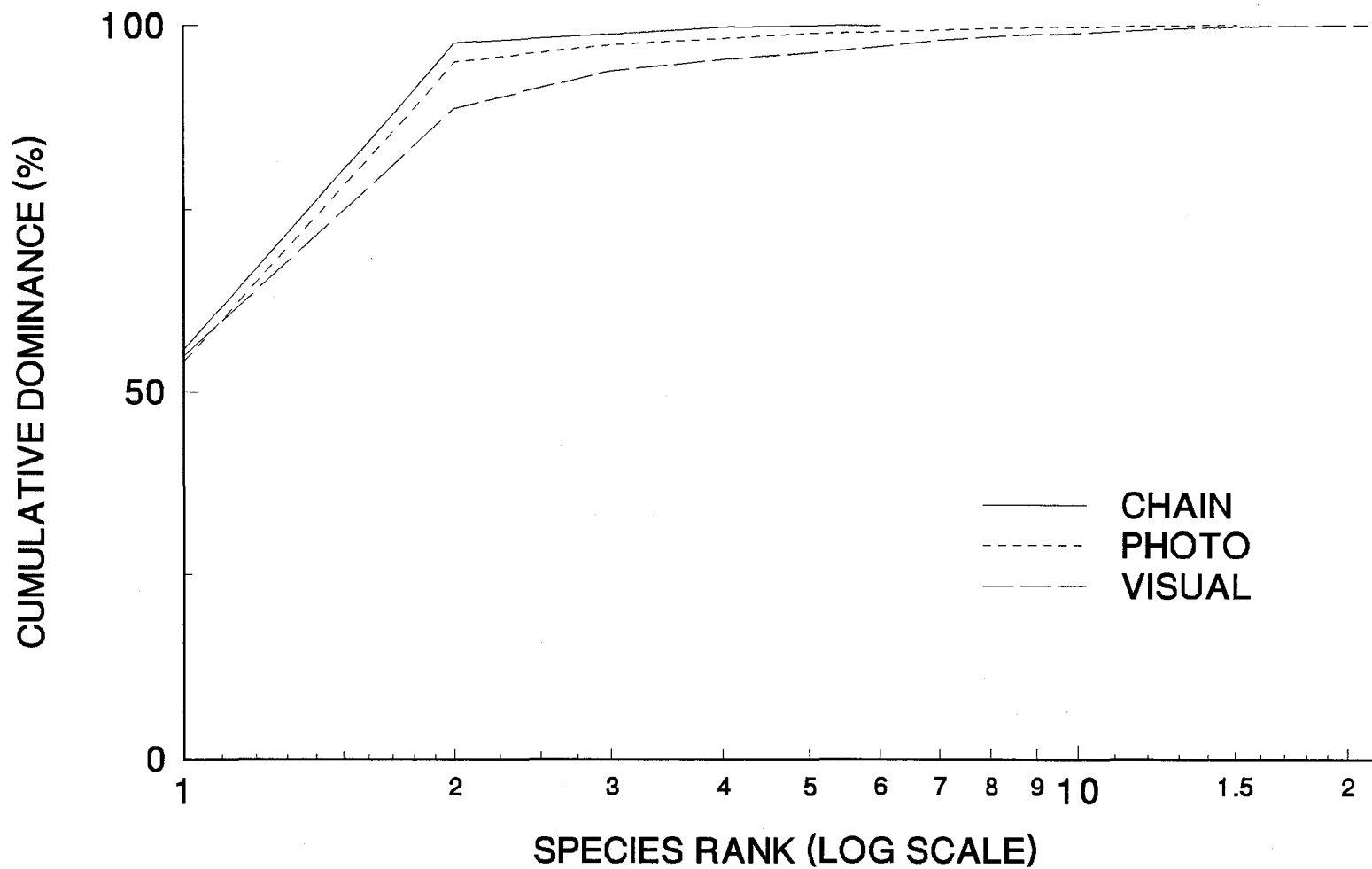


Figure 4. K-dominance curves produced from different survey techniques at site 1: CHAIN = chain transects, PHOTO = photo-quadrats and VISUAL = visually assessed quadrats (three-dimensional surfaces). Data were combined from all four transects.

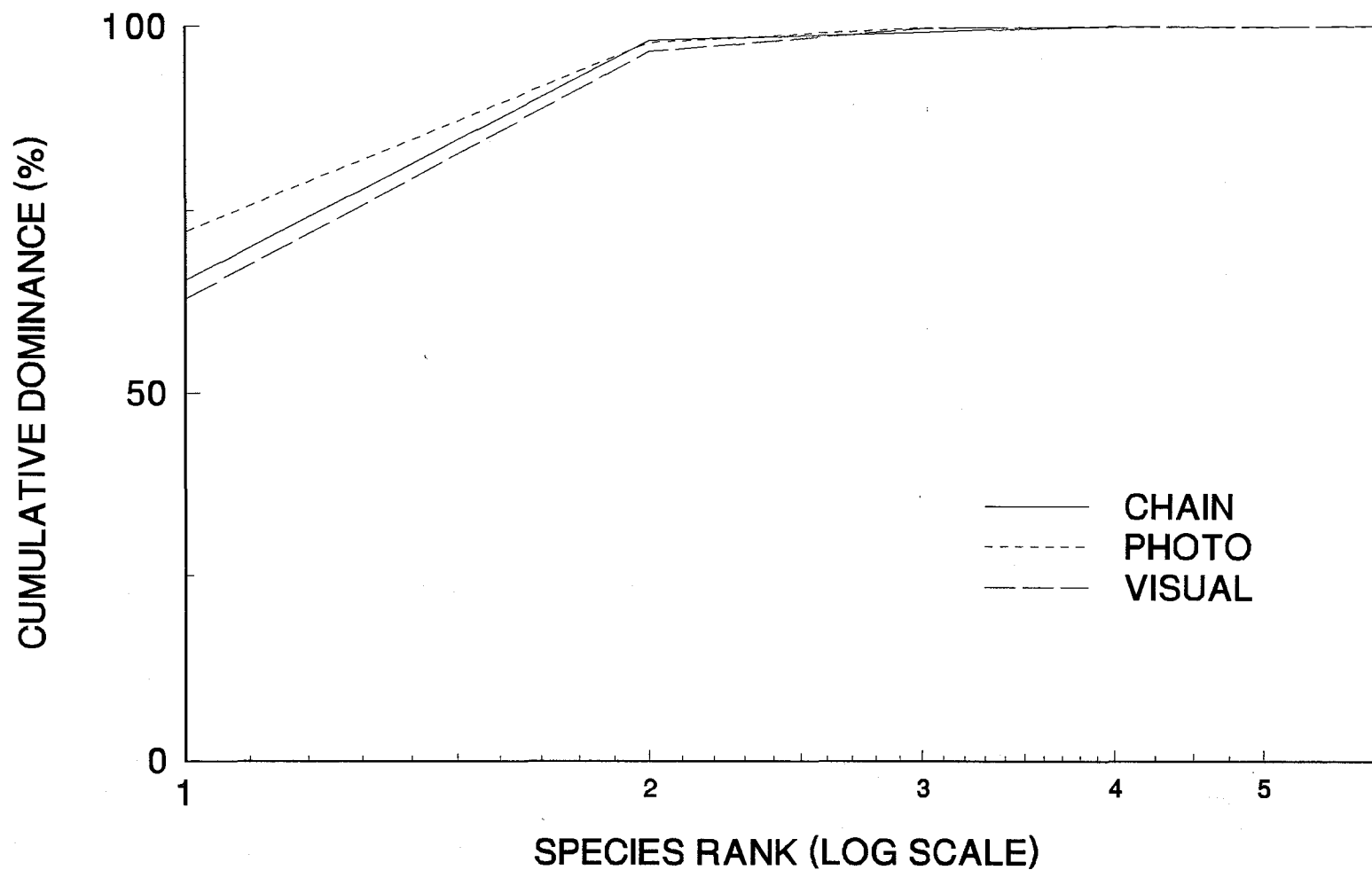


Figure 5. K-dominance curves produced from different survey techniques at site 2: CHAIN = chain transects, PHOTO = photo-quadrats and VISUAL = visually assessed quadrats (three-dimensional surfaces). Data were combined from all four transects.

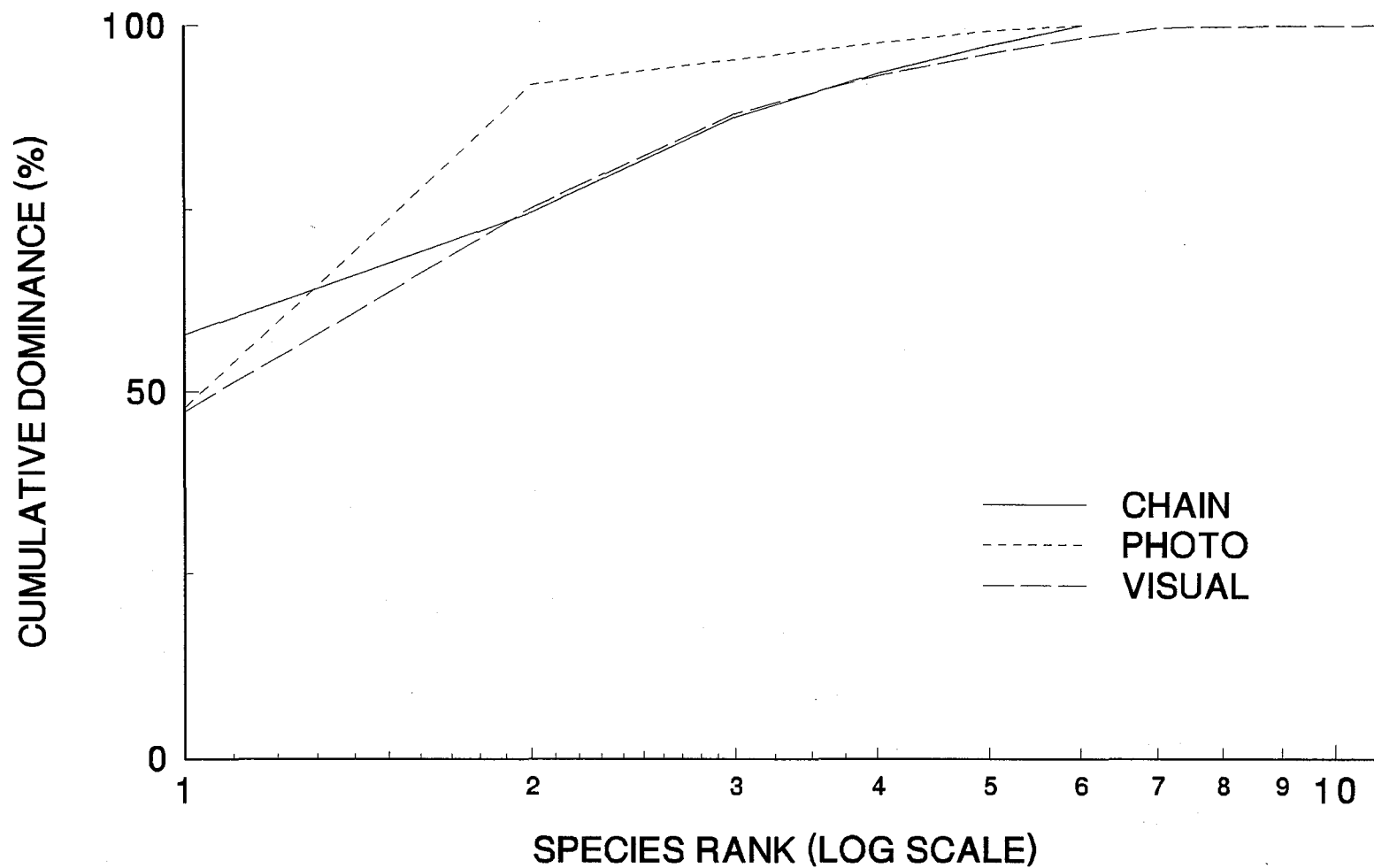


Figure 6. K-dominance curves produced from different survey techniques at site 3: CHAIN = chain transects, PHOTO = photo-quadrats and VISUAL = visually assessed quadrats (three-dimensional surfaces). Data were combined from all four transects.

Table 1. Percent total coral cover determined by the three techniques at each of the three sites. Data are presented as means of the four transects $\pm$ two standard errors. Significance levels for 1-way ANOVA are indicated by probabilities. Significant differences at $p = 0.05$ for pairs of means were determined by Student-Newman-Keuls (SNK) post-hoc comparisons, where C = chain transects, V = visual quadrats and P = photo-quadrats.

	CHAIN TRANSECTS (C)	VISUAL QUADRATS (V)	PHOTO- QUADRATS (P)	1-WAY ANOVA	Significant Pairs (SNK) ($p < 0.05$)
SITE 1	21 ± 7.9	11 ± 2.8	12 ± 3.7	$0.1 > p > 0.05$	-
SITE 2	37 ± 3.4	26 ± 4.8	25 ± 2.8	$0.01 > p > 0.001$	C:V, C:P
SITE 3	1.5 ± 1.2	2.1 ± 0.1	1.6 ± 0.2	$p > 0.5$	-

Table 2. Coral species diversity (Shannon H') determined by the three techniques at each of the three sites. Data are presented as means of the four transects $\pm$ two standard errors. Significance levels for 1-way ANOVA are indicated by probabilities. Significant differences at $p = 0.05$ for pairs of means were determined by Student-Newman-Keuls (SNK) post-hoc comparisons, where C = chain transects, V = visual quadrats and P = photo-quadrats.

	CHAIN TRANSECTS (C)	VISUAL QUADRATS (V)	PHOTO- QUADRATS (P)	1-WAY ANOVA	Significant Pairs (SNK) ($p < 0.05$)
SITE 1	0.7 ± 0.11	1.1 ± 0.13	0.9 ± 0.06	$0.01 > p > 0.001$	C:V, P:V
SITE 2	0.7 ± 0.12	0.8 ± 0.04	0.7 ± 0.11	$p > 0.2$	-
SITE 3	1.0 ± 0.15	1.0 ± 0.25	0.5 ± 0.20	$0.05 > p > 0.01$	P:C

Table 3. Coral species evenness (Pielou's J) determined by the three techniques at each of the three sites. Data are presented as means of the four transects $\pm$ two standard errors. Significance levels for 1-way ANOVA are indicated by probabilities. Significant differences at $p = 0.05$ for pairs of means were determined by Student-Newman-Keuls (SNK) post-hoc comparisons, where C = chain transects, V = visual quadrats and P = photo-quadrats.

	CHAIN TRANSECTS (C)	VISUAL QUADRATS (V)	PHOTO- QUADRATS (P)	1-WAY ANOVA	Significant Pairs (SNK) ($p < 0.05$)
SITE 1	0.7 ± 0.19	0.4 ± 0.06	0.4 ± 0.02	$0.05 > p > 0.01$	C:V, C:P
SITE 2	0.5 ± 0.11	0.5 ± 0.02	0.4 ± 0.10	$p > 0.3$	-
SITE 3	0.7 ± 0.18	0.5 ± 0.14	0.3 ± 0.11	$0.05 > p > 0.01$	P:C

Table 4. Coral species diversity (inverse Simpson's dominance index $1/D$) determined by the three techniques at each of the three sites. Data are presented as means of the four transects $\pm$ two standard errors. Significance levels for 1-way ANOVA are indicated by probabilities. Significant differences at $p = 0.05$ for pairs of means were determined by Student-Newman-Keuls (SNK) post-hoc comparisons, where C = chain transects, V = visual quadrats and P = photo-quadrats.

	CHAIN TRANSECTS (C)	VISUAL QUADRATS (V)	PHOTO- QUADRATS (P)	1-WAY ANOVA	Significant Pairs (SNK) ($p < 0.05$)
SITE 1	1.8 ± 0.19	2.2 ± 0.12	2.0 ± 0.08	$0.05 > p > 0.01$	C:V, P:V
SITE 2	1.8 ± 0.29	1.9 ± 0.15	1.7 ± 0.27	$p > 0.4$	-
SITE 3	2.2 ± 0.43	2.1 ± 0.60	1.4 ± 0.20	$0.05 > p > 0.01$	P:C

H' and Simpson's 1/D, whereas photo-quadrats produced a ranking of site 1 > site 2 > site 3. There were significant within-site differences between techniques only at the more topographically complex sites, opposite to the results for percent cover. At site 1, Shannon H' and Simpson's 1/D were estimated to be significantly higher by visual quadrats than the other techniques, whereas at site 3 chain transects produced significantly higher values than photo-quadrats.

Spatial indices, a measure of the topographic complexity, were not significantly different for visual quadrat estimates and chain transect measurements at the more complex sites (site 1 and 3; Table 5). At site 2, visual estimates were significantly higher than those determined by chain transect. This may account for the significantly different (lower) percent coral cover estimates for visual quadrats over chain transects at this site.

Photo-quadrat versus visual quadrat coral cover

The lack of any significant differences between coral cover determinations from planar photo-quadrats and three-dimensional visual quadrat estimates (Table 3) was surprising. Differences between chain transects and photo-quadrats were to be expected since the area covered by the two techniques differs greatly, but the two quadrat methods encompassed the same area of substrate using a fundamentally different measure. The percent coral cover estimates (visual) and measurements (photo-quadrats) are plotted against one another for individual 1 m² quadrats from each of the three sites in Figures 7-9. The variance between the techniques increased with percent coral cover. At lower cover, the results of the two techniques approached parity, even though the underlying relationship may not be directly proportional. Slopes of the principal axis of the bivariate plots (Sokal and Rohlf, 1981) were significantly different from 1 at the higher complexity sites (site 1: $b = 1.46$, 95% confidence limits = 1.17 - 1.86, site 3: $b = 0.3$, 95% CL = 0.18 - 0.43), but not at the low complexity site (site 2: $b = 1.01$, 95% CL = 0.89 - 1.15). Thus, photo-quadrats generally gave a higher percent cover estimate than visual quadrats at site 1, a lower estimate at site 3 and a similar estimate at site 2 when all quadrats are considered.

Table 5. Spatial indices estimated by the observer for visual quadrats and determined by the ratio of surface contour (chain) length versus horizontal distance for chain transects. Data are presented as means of the four transects $\pm$ two standard errors at each of the three sites. Significance levels for Student's t-test are indicated by probabilities.

	CHAIN TRANSECTS	VISUAL QUADRATS	Student's t-test
SITE 1	1.5 $\pm$ 0.14	1.7 $\pm$ 0.22	p>0.2
SITE 2	1.1 $\pm$ 0.04	1.5 $\pm$ 0.12	0.01>p>0.001
SITE 3	1.9 $\pm$ 0.45	2.5 $\pm$ 0.68	p>0.2

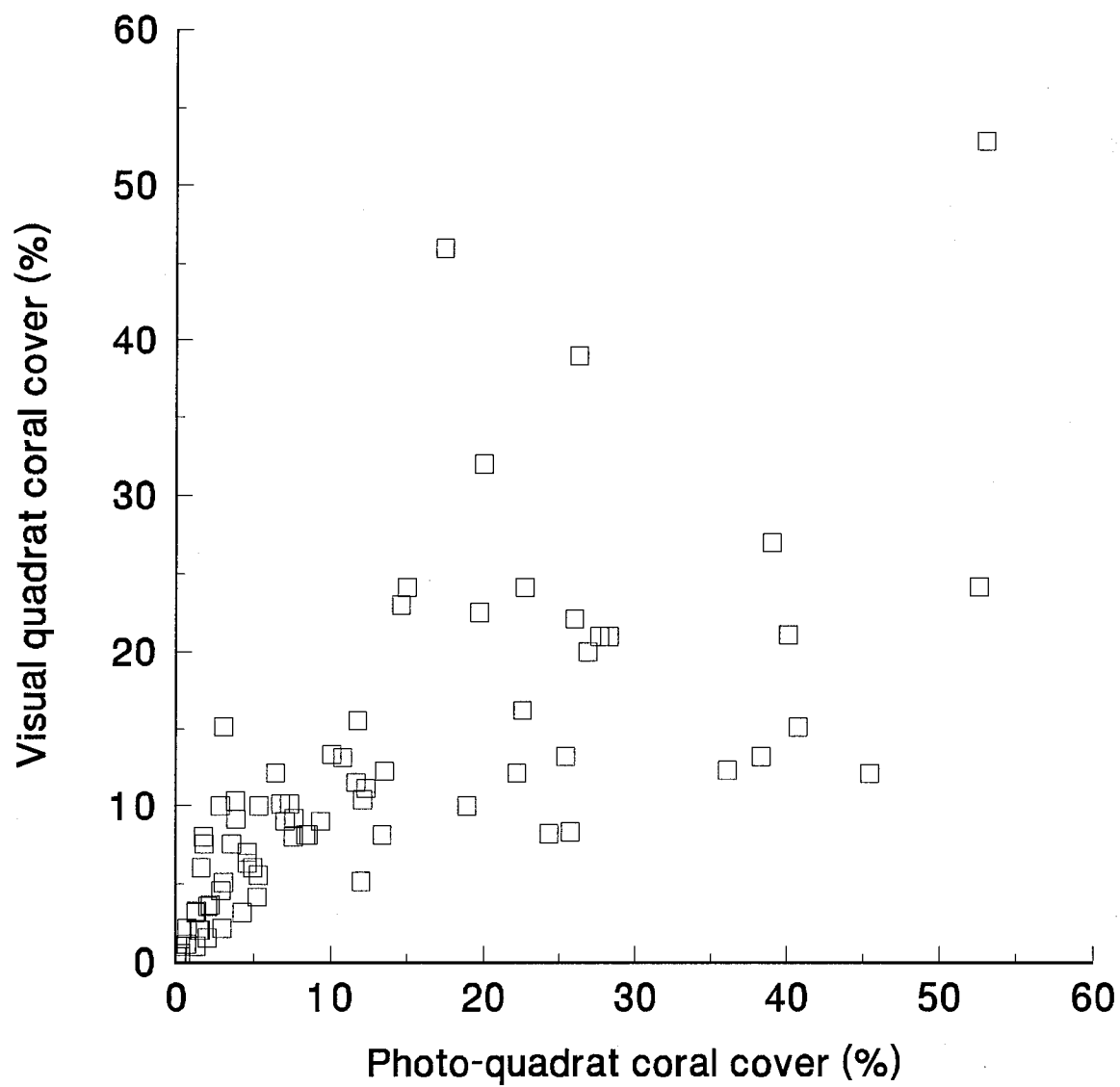


Figure 7. Bivariate scatterplot for visual quadrat coral cover estimates versus photo-quadrat determinations at site 1. Slope of the principal axis ($Y_1 = -3.70 + 1.46.Y_2$) was significantly different from 1 (95% confidence limits = 1.17 - 1.86).

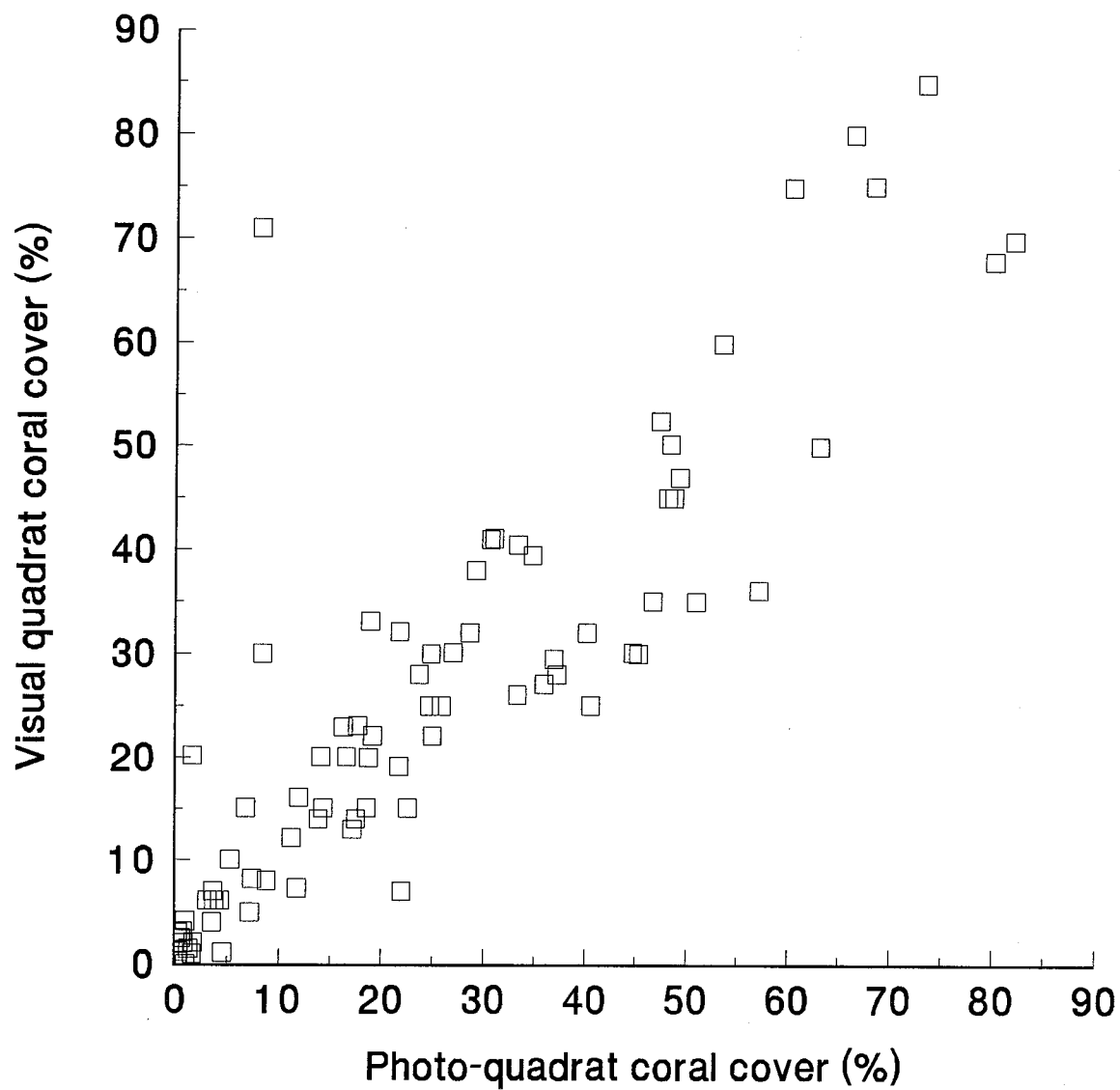


Figure 8. Bivariate scatterplot for visual quadrate coral cover estimates versus photo-quadrate determinations at site 2. Slope of the principal axis ($Y_1 = -1.30 + 1.01 \cdot Y_2$) was not significantly different from 1 (95% confidence limits = 0.89 - 1.15).

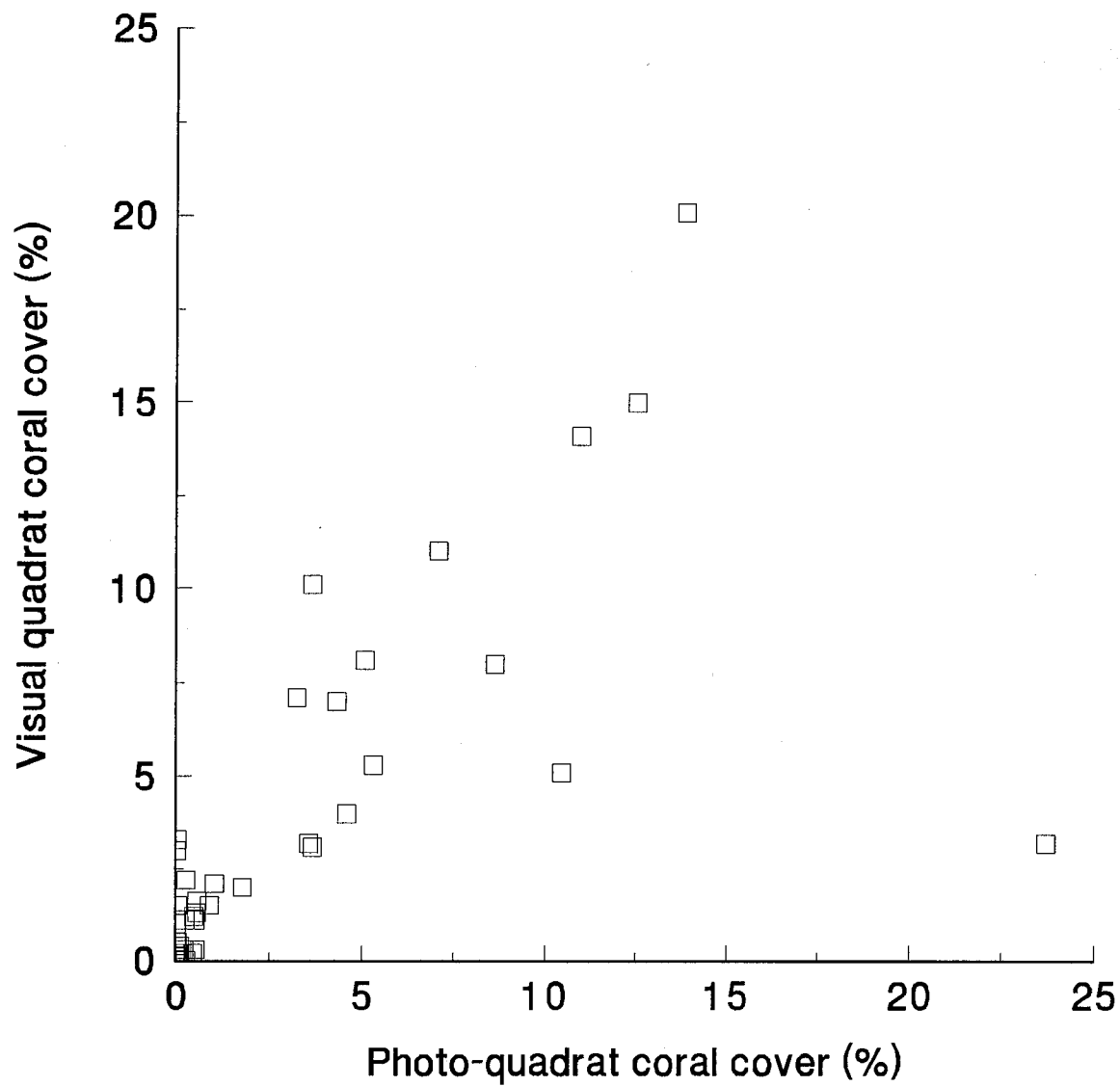


Figure 9. Bivariate scatterplot for visual quadrat coral cover estimates versus photo-quadrat determinations at site 3. Slope of the principal axis ($Y1 = 1.17 + 0.30 \cdot Y2$) was significantly different from 1 (95% confidence limits = 0.18 - 0.43).

Discussion

While all three techniques produced consistent results for population abundances (percent cover), community structure descriptions varied depending on the technique employed. The techniques ranked sites differently for univariate measures of diversity. Although we were not able directly to test the accuracy of the different methods, the sites were ranked site 1 > site 3 > site 2 for coral species richness. The results may therefore support Weinberg's (1981) finding that visually-assessed quadrats were the most accurate for determining community structure. However, examinations of the k-dominance curves (Lambshead et al., 1983, Warwick et al., 1990), suggested that the species-abundance distributions described by the different techniques were essentially similar. The different rankings of univariate measures may therefore have been artifacts of the emphasis placed on more dominant or rarer species in the community by each index (Magurran, 1988), although Simpson's dominance index and Shannon diversity gave similar results. The evidence strongly suggests that univariate descriptors (Shannon H' , Simpson's D , etc.) should not be solely relied upon to differentiate structure of coral communities.

Although chain transect and visually estimated total surface area cover both take into account the three-dimensional nature of the coral reef, they cannot be considered strictly equivalent. A random line-transect (chain transects) will be more likely to strike horizontal than vertical surfaces, i.e. it will be influenced by the planar (two-dimensional) distribution of surfaces as well as three-dimensional distribution. In addition, in this study the chain transects only sampled 0.5% of the planar surface area sampled by quadrats, assuming a chain width of 0.5 cm. Thus the differences in number of species detected by the two techniques are not surprising. Cumulative species curves show that it would be infeasible to sample sufficiently with the chain transect technique to increase significantly the number of species detected in 20 m. Given these apparent deficiencies in the chain transect technique, it is perhaps more surprising that the results were so similar to those of the other techniques. Magurran (1988) pointed out that Shannon H' and many other diversity indices are strongly influenced by the percentage of the true community species richness included in the sample, with reliability of

the index decreasing sharply as the percentage decreases. This would also help explain the inconsistent results for these univariate diversity measures, and the apparently more accurate determination by visual quadrats, which sampled a larger percentage of the true species number present.

An unusual result of this study was the lack of a significant difference in most instances between results of the "3-D" visual quadrats and "2-D" photo-quadrats. Visual estimates of the spatial complexity of the different sites appeared close to the measurements made by chain transects in all but the least complex site. It is therefore unlikely that there were serious errors in the visual interpretation of the three-dimensional surface cover. Similarity between the estimates can then either be explained by high variability masking any true differences, or by the total surface cover of specific corals being proportional to the planar coverage. The latter seems unlikely given the dependence of the coral-alga association on sunlight (but see Sheppard, 1981). A direct comparison of the coral cover estimates by the two techniques actually suggested that both may occur at different sites. At the low spatial complexity site (site 2), two-dimensional measurements were directly proportional to three-dimensional estimates, because corals were generally arranged on a flat, planar surface. At the higher complexity sites (sites 1 and 3), the results were not directly proportional, but approached closer to parity (the lower variance) at lower percent cover values. Thus, at our sites, mean percent cover determined by the two techniques was not significantly different, due to the low cover overall. These results suggest that at higher cover the two techniques may produce different mean values, but with higher variance at more complex sites.

In conclusion, there are benefits and disadvantages to both the three-dimensional assessment techniques. Chain transects provide a precise measure of benthic cover and its spatial complexity, independent from subjective bias by the observer. However, they are time consuming to perform, incompletely sample the species within the community and, like two-dimensional line-intersect transects (Weinberg, 1981), may suffer from inaccuracy. Visually assessed quadrats are quicker to perform and more effectively sample a much greater area, leading to more reliable measures of species diversity. Quadrat assessments depend on the somewhat subjective estimates of the observer, however, and Gladfelter et al. (1991) have shown that significant changes in coral cover detected by fixed chain transects could not be

distinguished using haphazardly placed quadrats. Further study is needed to assess the accuracy of the two techniques, but at present it would seem beneficial to combine both techniques for coral community analysis and long-term monitoring.

References

- Bouchon C (1981) Quantitative study of the scleractinian coral communities of a fringing reef of Reunion Island (Indian Ocean). *Mar Ecol Prog Ser* 4:273-288
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163-170
- D'Elia CF, Buddemeier RW, Smith SV (1991) Workshop on coral bleaching, coral reef ecosystems and global change: Report on proceedings. Maryland Sea Grant College Publication, 49 pp
- Gladfelter EH, Bythell JC, Gladfelter WB, Lewis SK, Woodbury, M (1991) Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites. Part 1. US Dept Interior, National Park Service, Spec Rpt 260 pp
- Gladfelter WB, Gladfelter EH, Monahan RK, Ogden JC, Dill RF (1977) Environmental studies of Buck Island National Monument. US National Park Service Rpt, 144 pp
- Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:225-232
- Kinzie RA, Snider RH (1978) A simulation study of coral reef survey methods. In: Stoddart DR, Johannes RE (eds) *Coral reefs: research methods*. UNESCO, Paris, 231-250
- Lambshead PJD, Platt HM, Shaw KM (1983) The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *J Nat Hist* 17:859-874
- Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar Biol* 13:100-123
- Loya Y (1978) Plotless and transect methods. In: Stoddart DR, Johannes RE (eds) *Coral reefs: research methods*. UNESCO, Paris: 197-217
- Loya Y, Slobodkin LB (1971) The coral reefs of Eilat (Gulf of Eilat, Red Sea). In: Stoddart DR, Yonge CM (eds) *Regional variation in Indian Ocean coral reefs*. Symp Zool Soc Lond, Acad Press: 127-139

- Magurran AE (1988) Ecological diversity and its measurement. Princeton Univ Press, 179 pp
- Pearson, RG (1974) Recolonization by hermatypic corals of reefs damaged by *Acanthaster*. Proc 2nd Int Coral Reef Symp 2:207-215
- Pichon M (1978) Problems of measuring and mapping coral reef colonies. In: Stoddart DR, Johnannes RE (eds) Coral reefs: research methods. UNESCO, Paris: 219-230
- Porter JW (1972) Patterns of species diversity in Caribbean reef corals. Ecology 53:745-748
- Rogers CS (1985) Degradation of Caribbean and Western Atlantic coral reefs and decline of associated fisheries. Proc 5th Int Coral Reef Congr 6:491-496
- Rogers CS, Gilnack M, Fitz III CH (1983) Monitoring of coral reefs with linear transects: A study of storm damage. J Exp Mar Biol Ecol 66:285-300
- Rutzler K (1978) Sponges in coral reefs. In: Stoddart DR, Johnannes RE (eds) Coral reefs: research methods. UNESCO, Paris: 299-313
- Sheppard CRC (1981) Illumination and the coral community beneath tabular *Acropora* species. Mar Biol 64:53-58
- Sokal RR, Rohlf FJ (1981) Biometry: The principals and practice of statistics in biological research, 2nd edn, Freeman and Co, New York, 859 pp
- Warwick RM, Clarke KR, Suharsono (1990) A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. Coral Reefs 8:171-179
- Weinberg S (1978) The minimal area problem in invertebrate communities of Mediterranean rocky substrata. Mar Biol 49:33-40
- Weinberg S (1981) A comparison of coral reef survey methods. Bijdr Dierk 51:199-218

Chronic and catastrophic natural impacts on three common Caribbean reef corals: Causes and scale of partial and whole-colony mortality

Chapter 4

John C. Bythell¹, Elizabeth H. Gladfelter² and Mary Bythell¹

Present addresses: ¹Centre for Tropical Coastal Management, Department of Marine Sciences and Coastal Management, University of Newcastle upon Tyne NE1 7RU, UK. ²PO Box 26472, Gallows Bay, St. Croix, U.S. Virgin Islands 00820.

Introduction

Evidence that coral reef community structure is influenced by disturbance has been mounting over the past three decades (Connell 1978, Bak and Luckhurst 1980, Porter et al 1982, Hughes and Jackson 1985, Hughes 1989). However, quantifying levels of disturbance at different localities is impeded not only by the diversity of types of disturbance (broadly, biological versus physical), but also by the range of time-scales over which they occur. Perhaps more importantly, we have little information on how individual species are affected by the different types and scale of disturbance. Thus, for example, it has been impossible to rigorously test theories of coral community organization (Slobodkin and Sanders 1969, Connell and Slatyer 1977), or to objectively determine the significance of anthropogenic impacts on reefs (Brown 1988, Rogers 1988).

Hurricanes and other severe disturbances such as bleaching events and disease epidemics have an immediate and obvious effect on the dynamics of coral reef communities (Highsmith et al. 1980, Woodley et al. 1981, Gladfelter 1982, Porter et al. 1982, Rogers et al. 1982, Harriott 1985, Hughes 1989, Brown and Suharsono 1990, Edmunds and Witman 1991, Rogers et al. 1991). Such events, although seemingly deleterious over short time-scales, may be necessary to prevent competitive exclusion of species, and therefore to help maintain the diverse community structure typical of many coral reefs (Connell 1978). Even without (or in between) these sporadic impacts, coral populations may be highly dynamic. Chronic events cause death or partial mortality of coral colonies, while larval recruitment and growth may be sufficient to offset the losses, resulting in an apparently stable population structure (Hughes 1985, Hughes and Jackson 1985). A wide range of chronic biological disturbances have been identified on coral reefs, including various types of predation (Bak and van Es 1980, Sammarco 1982, Knowlton et al 1990) and disease (Antonius 1981a, b). However, their importance relative to physical damage from storms and sedimentation, and to other biological interactions such as space competition (overtopping and shading or direct aggression; Lang 1973, Porter 1974), has not been determined.

We have made repeated monthly observations of permanently tagged colonies of the massive corals *Montastrea annularis* and *Diploria strigosa* and the plating-mounding form of *Porites astreoides* over a two-year period (1989 - 1991). The study area, surrounding an uninhabited island which lies upstream of any local pollution sources, consists of a mainly shallow water (< 12 m depth) bank-barrier reef (Bythell et al. 1989, Gladfelter et al. 1990). It has been managed by the U.S. National Park Service since 1962 and bans on fishing, collecting and anchoring are strictly enforced. The aim of the study was to define the rates and primary causes of partial and whole colony mortality in an area relatively free of anthropogenic impacts. In the early stages of the study (September 17-18, 1989) Hurricane Hugo, a major Category V hurricane (Case and Mayfield 1990), passed directly over the area, the worst storm to affect the area since 1928 (Hubbard et al. 1990, Gladfelter et al. in prep.). We were therefore able to contrast chronic disturbances with a catastrophic event and examine the type and magnitude of their effects on mortality in the three species.

Materials and methods

Description of the study area. The study was carried out at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands (17°47'N, 64°37'W) as part of a long-term monitoring program of Caribbean region U.S. National Park Service reef sites (Rogers 1988). The three coral species studied, *Montastrea annularis* (Ellis and Solander), *Diploria strigosa* (Dana) and *Porites astreoides* Lesueuer are dominant in many areas at Buck Island (Bythell et al. 1989), and represent 22%, 10% and 12% of live coral cover respectively, averaged between zones. Several distinct morphological variants of *M. annularis* exist, and Knowlton et al. (1992) have identified three as possible separate species. The majority of colonies at Buck Island correspond to their morph I, with heads forming separate lobes 5-20 cm in diameter. A smaller number of their morph II, which form large colonies of continuous tissues with distinctive raised ridges, were also present in the study area but were excluded from this analysis.

Site selection. Fifteen study sites were established in December 1988 containing approximately 25 permanently marked heads of one of the three species. Sites were selected in areas of locally high population densities, adjacent to permanently marked cross-reef transects (Gladfelter et al. 1990), and included backreef and forereef locations on both the north and south sides of the island (Fig. 1). Within sites, 25-30 coral heads were selected by swimming a haphazard, roughly circular transect and marking all heads encountered with numbered plastic tags. Tags were attached to the nearby substrate using masonry nails and plastic cable ties. At only one location were all three species found to co-occur in sufficient densities to establish overlapping sites (sites M4, D4 and P4).

Definition of the coral colony. For the purposes of this study, the coral colony was defined as the physiologically separate tissues which may have arisen either from sexual recruitment or by fission of a parent colony. In addition, genetically similar heads composed of such separate units could be distinguished in the field by the close proximity of separate tissues and similarities in skeletal morphology and tissue color. Due to the massive morphology of the species studied and the lack of similar colonies nearby, these heads were often believed to include all such material derived from a single settlement (the genet, Harper 1977), although viable coral fragments may be widely scattered by storms (Highsmith et al, 1980, Tunnicliffe 1981).

Monthly observations. Each colony was inspected monthly for tissue damage and necrosis. Extent of the damage was estimated according to total surface area of the colony affected: I. < 10 %, II. 10 - 50 %, or III. > 50 %. Details of larger areas of mortality (> 10% of the colony surface area) were recorded, including approximate area and location within the colony. Laminated photographs of each colony taken from various angles were taken into the field where necessary for reference. The reference photographs were repeated after any major mortality event to provide a baseline for subsequent observations. A short-term (58 d) photographic and visual study (Gladfelter et al. 1991) showed that repair rates were similar for the three species. This study also showed that larger areas of tissue loss would not be fully repaired or disguised by fouling algae between monthly observations, although small lesions

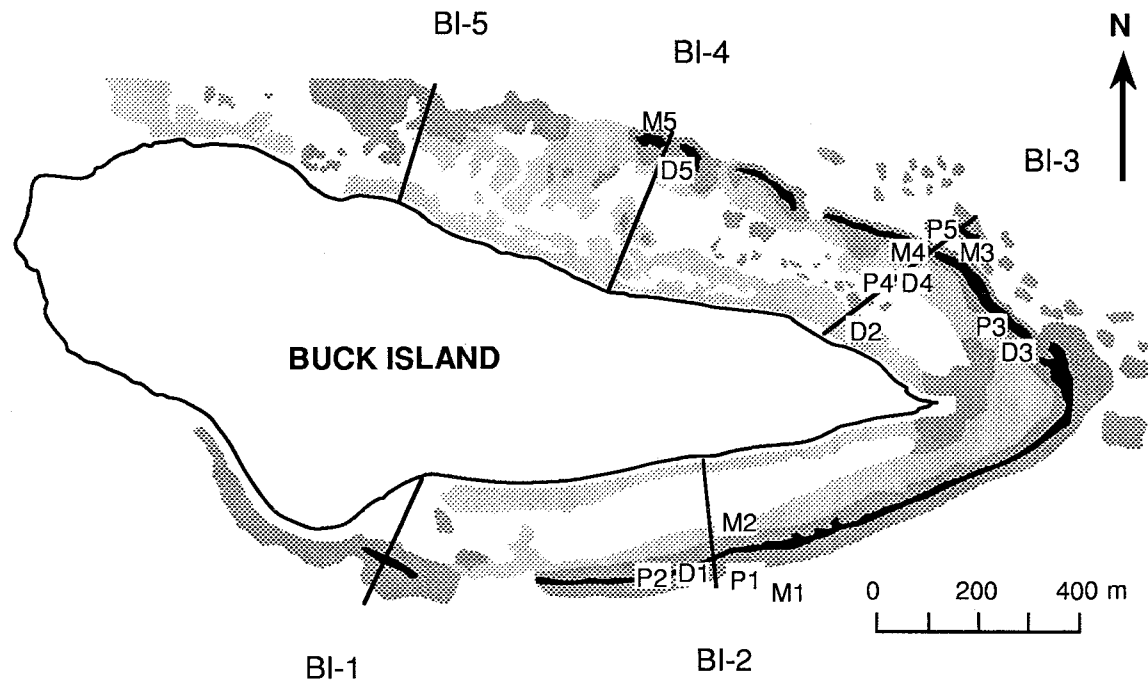


Figure 1. Map of the study area showing the locations of the fifteen tagged coral study sites. Sites were located around one of five cross-reef transects (BI-1 to BI-5), which were first surveyed in the mid 1970's and were recently re-established (Gladfelter et al. 1991). Each site originally contained approximately 25 tagged colonies of one of three species: *Diploria strigosa* (sites D1 to D5), *Montastrea annularis* (sites M1 to M5) or *Porites astreoides* (sites P1 to P5). Several colonies have died since they were tagged in 1988/9, and sites D1 and P2 were destroyed by burial under a rubble rampart created during Hurricane Hugo. The reef crest zone is shown in black, backreef and forereef zones are shown by darker shading and low-relief lagoonal pavement in light shading.

such as single parrotfish bites could be repaired within as little as five days. Consistency between observers was tested by comparing assessments made by three observers who monitored the same 30 colonies on the same day and differences were found to be insignificant (Cochran's Q-test, $0.5 > p > 0.1$).

Planar surface area changes and frequency of mortality. Vertical photographs of all tagged corals were taken between April and July 1989 and repeated 26 months later in 1991. Camera distance was fixed by means of a temporary positioning line attached to the tag marker and positioned vertically by eye, with the aid of a small bubble-type spirit level. Actual camera distances were varied colony-to-colony but were kept constant between repeat photographs. Transparencies were projected onto a 30 cm x 30 cm computer digitizing pad and planar surface areas determined with reference to a linear scale which was placed next to the tag in each photograph (Summagraphics II digitizer with Easydj 7.0 planimetering software). Changes between the 1989 and 1991 photographs were recorded, including the surface area of any tissue loss (partial mortality), total colony mortality, and cases of colony fission and fusion. These data were related to the monthly monitoring record to determine the cause and time of change. Occasionally, two or more events of tissue damage of approximately similar magnitude were recorded in the monthly monitoring. In these cases, surface area losses determined by computer digitization were divided equally among the causes. Standard error in surface area determinations was established from repeated photographs of the same colonies. Confidence limits (2 SE) were linearly correlated with mean surface area ($r=0.99$, 8 df), resulting in errors of less than 5% for colonies larger than 2 cm² and less than 3% for colonies larger than 18 cm² surface area.

In calculating frequency of mortality events due to various causes, certain assumptions were made. Frequency of partial mortality events may exceed the number of colonies showing partial mortality, since each colony may be affected by more than one event. However, whole-colony mortalities were treated as single events, possibly with multiple causes. It was assumed that if a colony was seriously damaged ($> 10\%$ surface area loss) by several factors, each contributed equally to the final demise of the colony. Thus, for example, a colony affected by two separate grazing events and later killed by a disease event was scored 2/3 and 1/3 for

grazing- and disease-related whole colony mortality. If the colony had survived, it would have been scored as 2 (grazing) plus 1 (disease) partial mortality events.

Results

Effects of Hurricane Hugo

The planar surface area of tissue mortality due to Hurricane Hugo was 1.8%, 8.3% and 30% of the initial sample planar surface area in *Montastrea annularis*, *Porites astreoides* and *Diploria strigosa*, respectively. These losses represent 11%, 31% and 97% of the mortality due to all factors combined during the course of the 26 mo. study. The relative losses are shown in Fig. 2, scaled to the median surface area of whole heads of each of the three species (*M. annularis* = 1894 cm², *P. astreoides* = 153 cm², *D. strigosa* = 1319 cm²), in order to show absolute levels of surface area of mortality.

Hurricane damage was strongly influenced by location (Table 1). Two sites on the south reef crest (P2 and D1) were completely destroyed by burial under a 1 m deep rubble rampart created by the virtual destruction of the shallow forereef on the south side of the island. Site P1 was located off the south forereef and approximately 77% tissue loss was recorded in the tagged *P. astreoides* colonies. Elsewhere, hurricane damage was remarkably light; 0-3.9% of the initial sample surface area. At the single location with contiguous sites (M4, P4 and D4), *M. annularis* actually showed slightly greater losses to hurricane damage than the other species, although this was only just significant in comparison with *P. astreoides* (Kolmogorov-Smirnov D = 0.23, 0.05 > p > 0.01, all other combinations p > 0.05). The Kolmogorov-Smirnov two-sample test was used due to the highly non-normal distribution of mortality data; colonies tended to be either undamaged or completely killed by the hurricane (Fig. 3). Although the hurricane resulted in reductions in planar surface area of less than 4% at sites on the north side of the island, this accounted for about 28% of the whole-colony mortalities recorded over 26 months due to all factors.

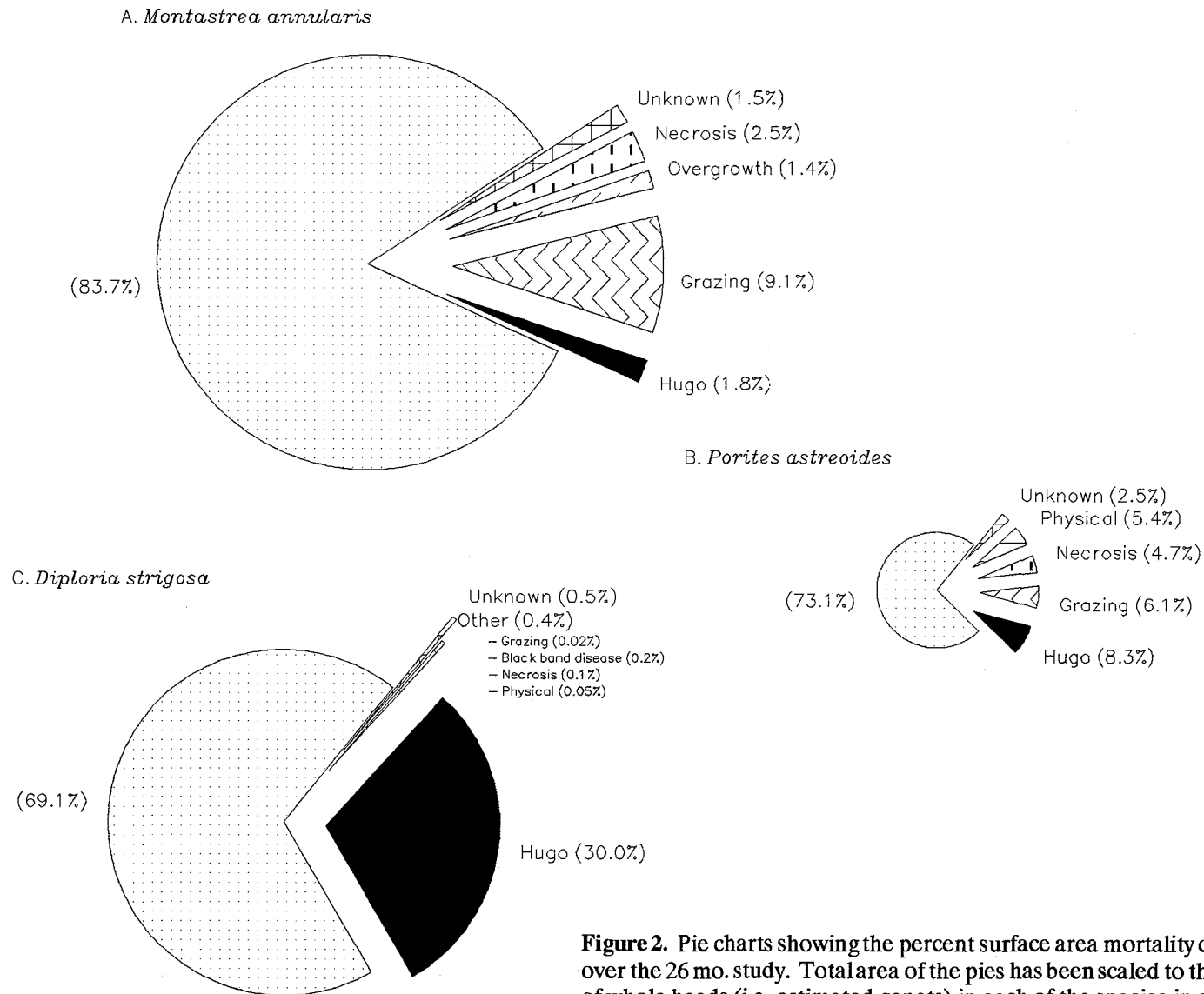


Figure 2. Pie charts showing the percent surface area mortality due to different factors over the 26 mo. study. Total area of the pies has been scaled to the median surface area of whole heads (i.e. estimated genet) in each of the species in order to show absolute levels of surface area loss. Percent mortality data were derived from computer-digitized vertical photographs, with causes of particular areas (events) of mortality determined from monthly visual monitoring. Data were combined from all sites. See text for explanation of the different causes of mortality such as necrosis (tissue necrosis), overgrowth (algal and invertebrate overgrowth), grazing (parrotfish grazing) and physical (physical breakage or toppling).

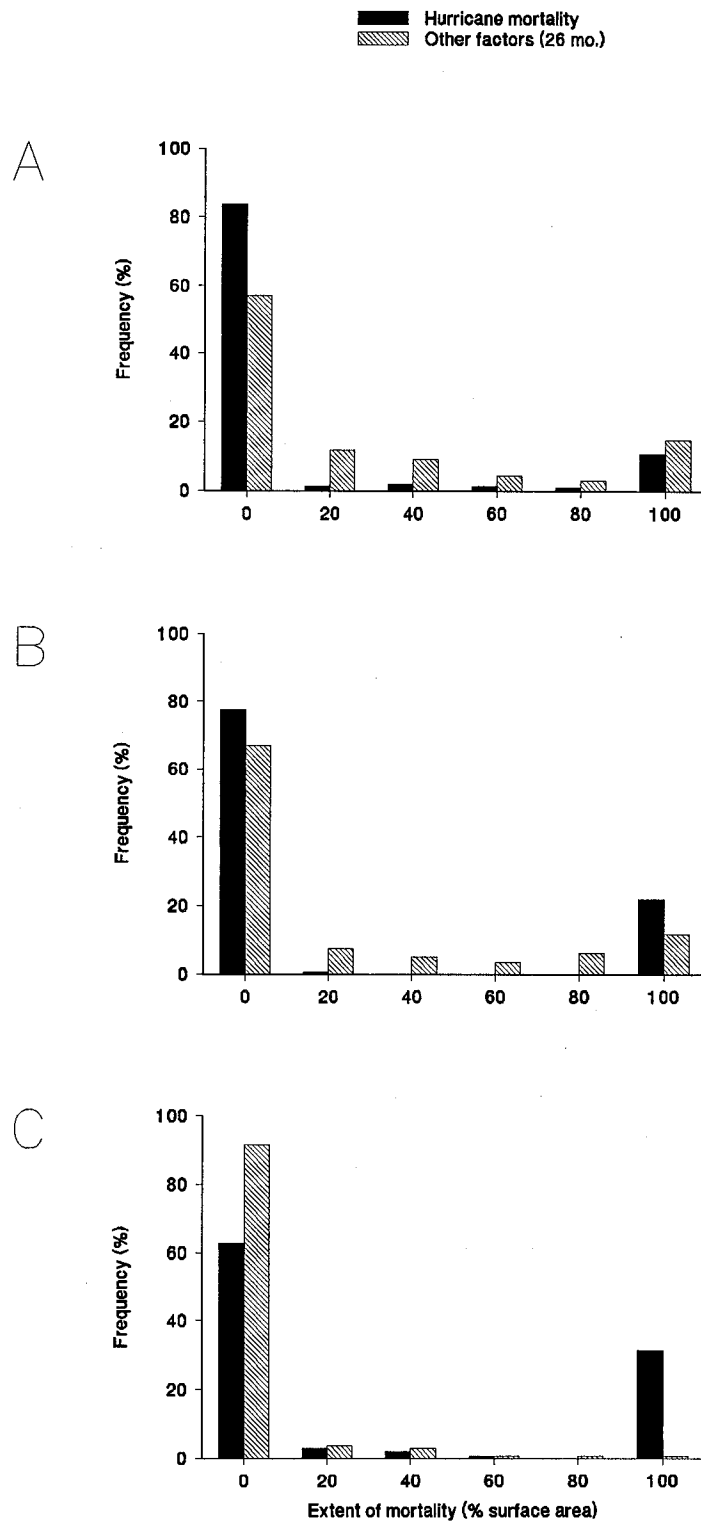


Figure 3. Frequency distribution of planar surface area mortality by severity (percent of surface area affected) due to Hurricane Hugo and all other factors combined over the 26 mo. study. Data were combined from all sites. A. *Montastrea annularis*, B. *Porites astreoides*, C. *Diploria strigosa*.

Table 1. Planar surface area losses and frequency of mortality caused by the direct effects of Hurricane Hugo. Surface area losses include both total and partial mortality. "Total" losses are expressed as a percent of the initial sample size at each site, whereas "relative" losses are expressed as a percent of the losses caused by all factors over the 26 mo. study. TSA = the total initial sample surface area and, in parentheses, the sum of surface area mortality due to all factors. n = number of colonies, with number of cases of partial mortality, followed by number of fatalities due to all causes in parentheses. Total n of physiologically isolated tagged colonies analyzed = 978.

SITE	SURFACE AREA LOSSES		FREQUENCY OF PARTIAL COLONY MORTALITY		FREQUENCY OF TOTAL COLONY MORTALITY			n
	TOTAL (%)	RELATIVE (%)	TOTAL (%)	RELATIVE (%)	TOTAL (%)	RELATIVE (%)	TSA (cm ²)	
A. <i>Montastrea annularis</i> (n = 512)								
M1	0.3	2.0	0.7	1.6	1.5	18.2	9569 (1648)	135 (61, 11)
M2	0	0	0	0	0	0	802 (196)	26 (11, 2)
M3	3.1	27.4	7.0	35.3	7.0	37.5	1472 (168)	86 (17, 16)
M4	3.9	18.2	9.0	20.4	9.1	34.2	10861 (2337)	234 (103, 62)
M5	0	0	0	0	0	0	4287 (48)	31 (2, 0)
B. <i>Porites astreoides</i> (n = 323)								
P1	77.1	93.1	2.3	33.3	74.4	94.1	2956 (2447)	43 (3, 34)
P2	100	100	0	0	100	100	2248 (2248)	38 (0, 38)
P3	0.2	2.4	0	0	1.0	5.9	16957 (1554)	96 (19, 17)
P4	1.7	5.6	0	0	2.4	20.0	6869 (2107)	42 (20, 5)
P5	0.1	0.3	1.0	2.9	0	0	27533 (6913)	104 (35, 16)
C. <i>Diploria strigosa</i> (n = 143)								
D1	100	100	0	0	100	100	40786 (40786)	37 (0, 37)
D2	0	0	0	0	0	0	4764 (33)	16 (1, 0)
D3	0	0	0	0	0	0	27296 (596)	20 (3, 0)
D4	0.4	52.5	17.5	100	15.0	85.7	21350 (156)	40 (7, 7)
D5	0.1	5.2	3.3	12.5	6.7	100	42738 (485)	30 (8, 2)

Chronic tissue damage

Outside the three sites P1, P2 and D2, chronic mortality over the 26 mo. study generally accounted for a greater loss of tissue than Hurricane Hugo (Table 2). Frequency of chronic mortality was significantly different between sites for all species (likelihood ratio, $p < 0.05$). Chronic mortality resulted in a greater frequency of partial versus whole colony mortality, the opposite of the case with hurricane-related mortality (likelihood ratio, $p < 0.001$ for all species).

Predation by grazing parrotfishes was the most serious cause of chronic coral tissue loss (Table 3), although *Diploria strigosa* was notable for being largely unaffected by chronic factors. Larger queen and stoplight parrotfish (*Scarus vetula*, *Sparisoma viride*) were the main grazers, producing an obvious scar or groove recognizable for several weeks after the event. Damselfish grazing caused tissue loss without obvious skeletal damage, but was usually identifiable by the nearby tended algal mat. Tissue necrosis was also a frequent occurrence, but this condition may have arisen from various causes. Tissues were occasionally seen sloughing off the skeleton, possibly due to disease or "stress-related necrosis" (Antonius 1981b). Necrosis was also seen to occur in close association with clumps or mats of filamentous cyanobacteria. Invertebrate grazing, for example by the gastropod *Coralliophila* sp., may cause tissue loss of similar appearance, but was not observed at any site during the study. As with hurricane damage, *M. annularis* and *P. astreoides* colonies tended to either escape from damage by chronic factors or be completely killed, whereas *D. strigosa* showed little whole colony mortality due to factors other than the hurricane (Fig. 3). Only *M. annularis* showed a significant difference in the distribution of hurricane-related mortality versus other factors over the 26 mo. study, however (Kolmogorov-Smirnov; $p < 0.01$. $p > 0.4$ and $p > 0.6$ for *Porites astreoides* and *D. strigosa* respectively).

Table 2. Planar surface area losses and frequency of mortality due to chronic factors (other than by the direct effects of Hurricane Hugo) over the 26 mo. study. Losses are presented as a percent of the initial (1989) sample at each site. Refer to Table 1 for sample sizes. "-" = no sample; all colonies were destroyed in the hurricane. "*" = small sample size (74% of colonies destroyed in the hurricane).

SITE	SURFACE AREA LOSSES (%)	FREQUENCY OF PARTIAL COLONY MORTALITY (%)	FREQUENCY OF TOTAL COLONY MORTALITY (%)
<i>A. Montastrea annularis</i> Morph I			
M1	16.9	44.4	6.7
M2	24.4	42.3	7.7
M3	8.3	12.8	11.6
M4	17.6	35.0	17.4
M5	1.1	6.4	0
<i>B. Porites astreoides</i>			
P1	5.7*	4.6*	4.6*
P2	-	-	-
P3	8.9	19.8	16.7
P4	29.0	47.6	9.5
P5	18.7	33.7	15.4
<i>C. Diploria strigosa</i>			
D1	-	-	-
D2	0.7	6.2	0
D3	2.2	15.0	0
D4	0.3	0	2.5
D5	1.1	23.3	0

Table 3. Total planar surface area losses > 10% surface area over the 26 mo. study due to chronic factors by specific cause. See table 1 for sample sizes. Data were combined for all sites and are presented as a percent of the initial (1989) surface area of tissue for each species. *Tissue necrosis may have been caused by several factors (see text). "Unknown" factors, ie. mortality not detected during monthly observations were probably caused by a cumulative loss of small amounts of tissue over time.

CAUSE	<i>Montastrea annularis morph I</i> (%)	<i>Porites astreoides</i> (%)	<i>Diploria strigosa</i> (%)
BIOLOGICAL			
Predation - parrotfishes	9.06	6.09	0.02
Predation - damselfishes	0.07	0	0
Overgrowth - algae	1.35	0	0
Overgrowth - other invertebrates	0.03	0	0
Tissue necrosis*	2.45	4.72	0.10
Black band disease	0	0	0.18
Subtotal	12.96	10.81	0.30
PHYSICAL			
Toppling followed by scouring and/or burial	0	5.36	0.05
UNKNOWN	1.47	2.50	0.49
TOTAL	14.43	18.67	0.84

Effect of colony size

M. annularis and *P. astreoides* show classic distributions dominated by the smallest size-classes, while *D. strigosa* appears to have a more even distribution throughout its size range (Fig. 4). When data for estimated genet sizes are examined, however, it appears that *M. annularis* has a very similar distribution to *D. strigosa*. Mortality rates decreased with colony size in *M. annularis* and *P. astreoides* (Figs. 5 and 6). It appears that the probability of a colony being damaged by chronic factors increases with colony size (Figs. 5b, 6b), but the likelihood of the damage resulting in whole colony mortality decreases with size (Figs. 5a and c, 6a and c). *P. astreoides* showed higher colony mortality rates due to the hurricane than *M. annularis*, and the decrease in mortality with size was not as pronounced. Mortality rates were not apparently dependent on size-class in *D. strigosa* (Fig. 7; log-likelihood ratio $p > 0.5$ except partial mortality due to the hurricane, $p=0.001$). Colony losses to chronic factors were so low in *D. strigosa* that no relation with colony size would be evident (a single colony was killed out of a sample of 143).

Although *M. annularis* had high colony mortality rates, the colonies were all lobes believed to be part of a larger genet, and no whole heads were killed during the study (i.e. 0 out of 68 heads believed to represent whole genets), whereas both the other species sustained considerable loss of estimated genets (*P. astreoides*: 71/193, *D. strigosa*: 37/107).

Temporal variation in chronic tissue damage

Incidence rates of parrotfish predation and appearance of tissue necrosis over time determined from monthly observations are presented in Figures 8 and 9. In general, these conditions appeared to increase following the hurricane, but without longer-term pre-hurricane data this cannot be confirmed. Frequencies of both conditions varied significantly between time periods ($p < 0.01$), except for grazing in *D. strigosa* and tissue necrosis in *P. astreoides*. The different levels of parrotfish grazing in the three species is striking (Fig. 7), with consistently highest incidence rates in *M. annularis* and lowest in *D. strigosa*.

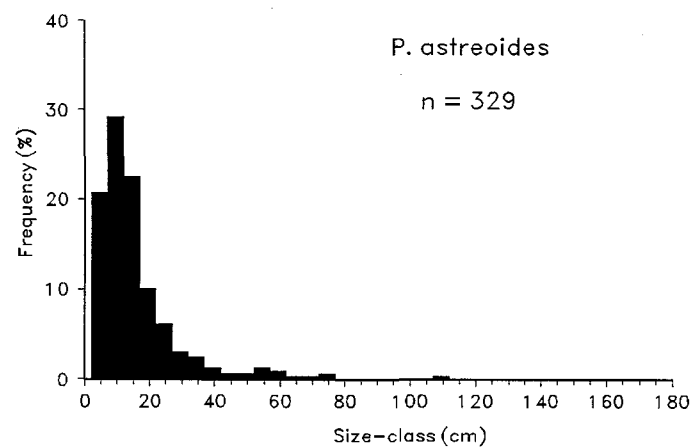
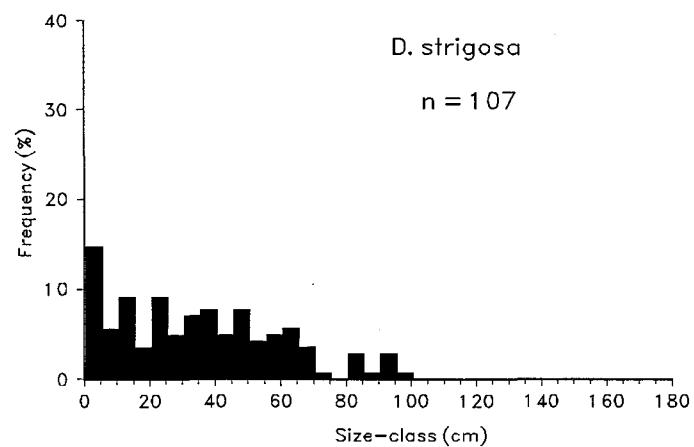
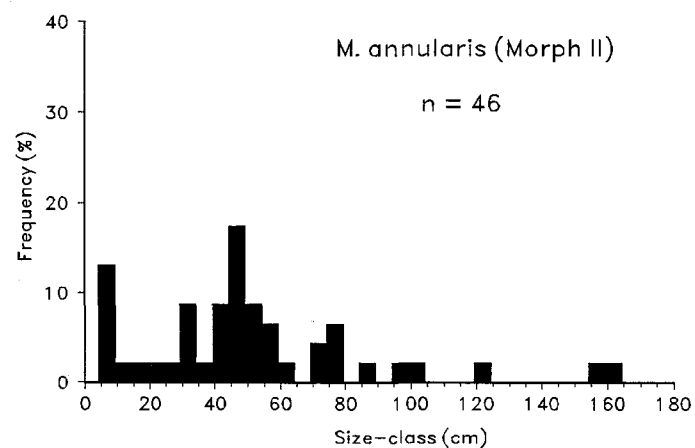
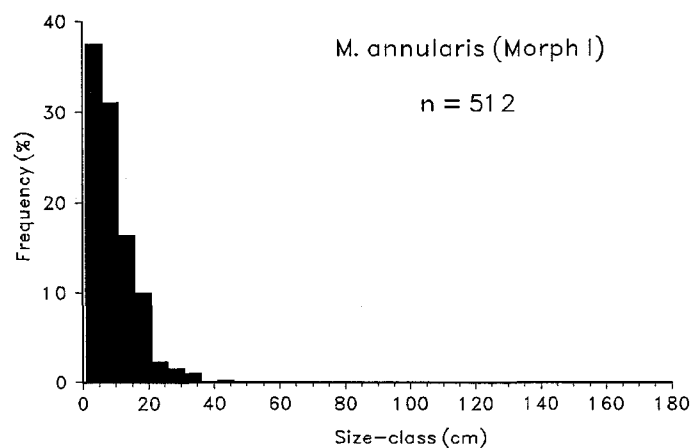


Figure 4a. Size-frequency distributions based on planar surface area for physiologically isolated colonies of the three species studied. Both Morph I and Morph II (Knowlton et al. 1992) of *Montastrea annularis* were included.

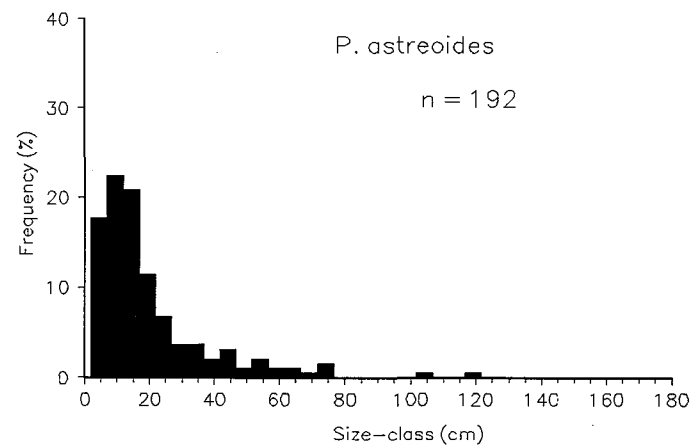
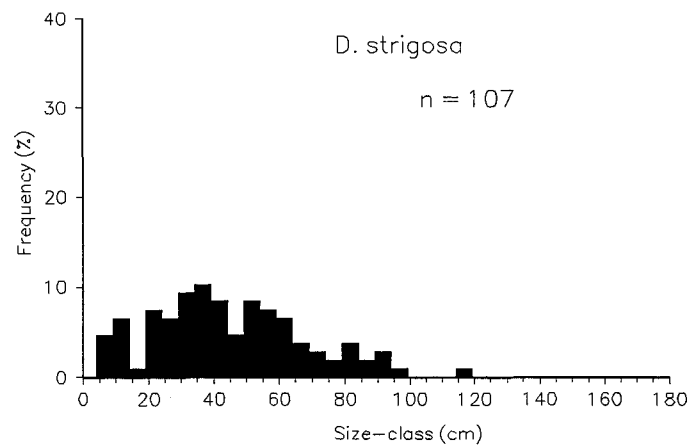
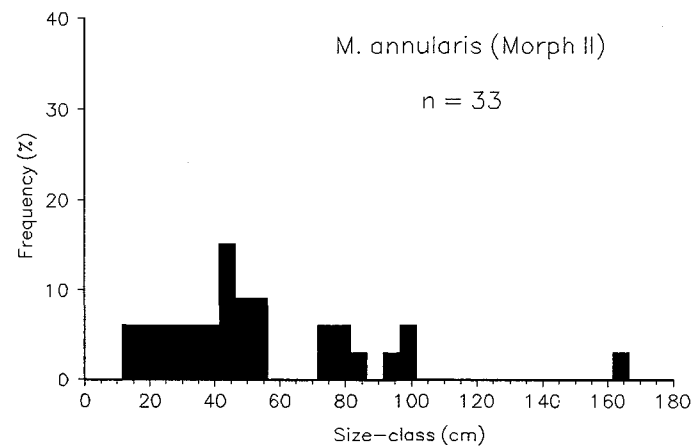
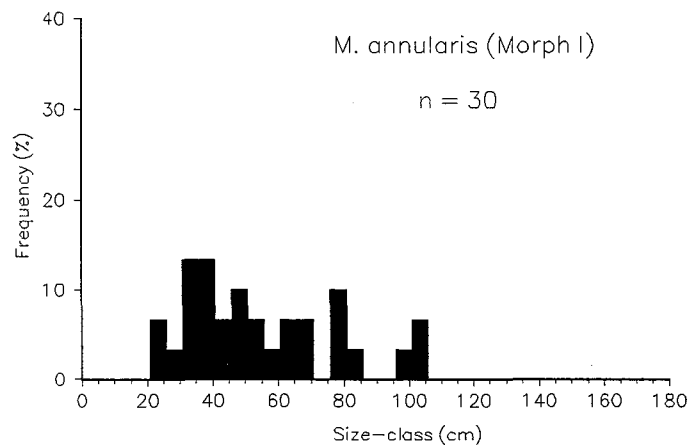
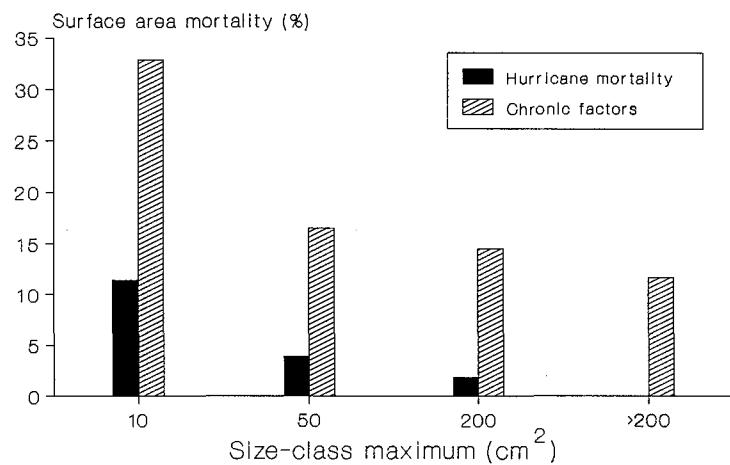
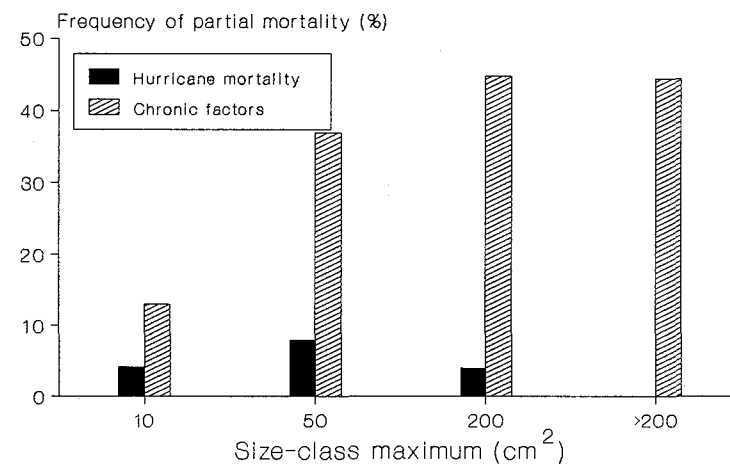


Figure 4b. Size-frequency distributions based on planar surface area for whole heads (estimated whole genets) of the three species studied. Both Morph I and Morph II (Knowlton et al. 1992) of *Montastrea annularis* were included.

A.



B.



C.

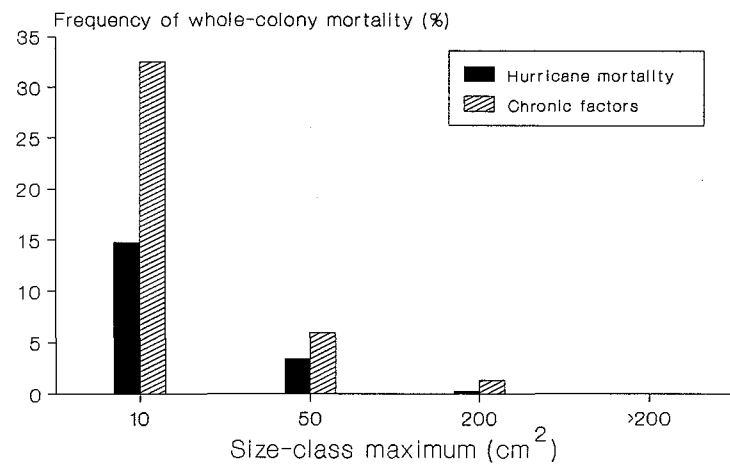
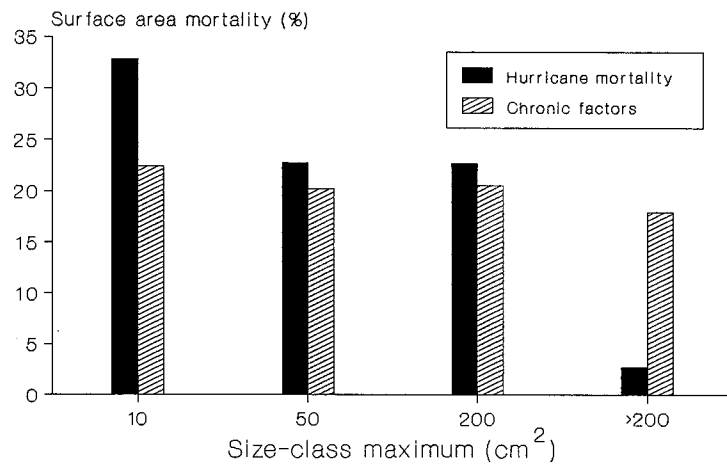
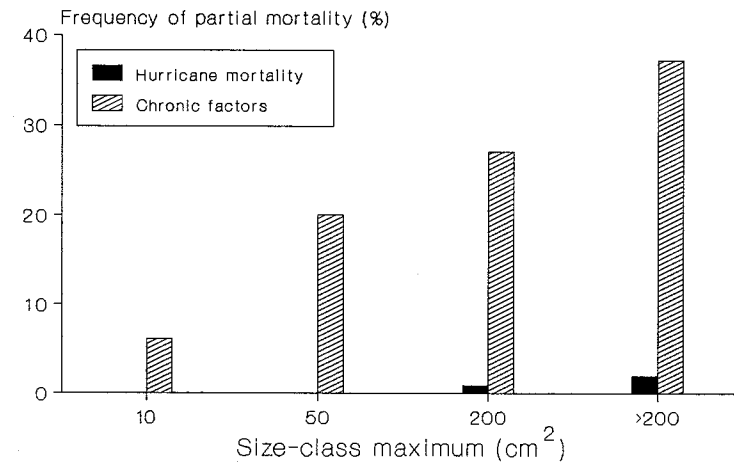


Figure 5. Mortality in *Montastrea annularis* in relation to size-class due to the hurricane and to all factor combined over the 26 mo. study. A. Distribution of planar surface area losses, B. distribution of partial colony mortality, C. distribution of whole colony mortality (physiological isolates).

A.



B.



C.

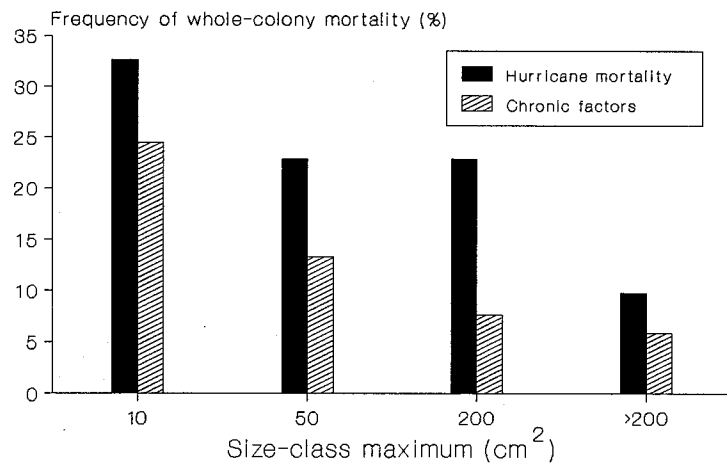
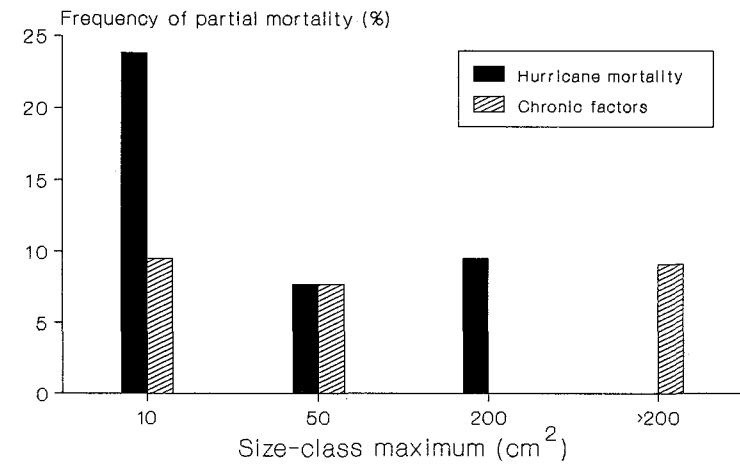


Figure 6. Mortality in *Porites astreoides* in relation to size-class due to the hurricane and to all factor combined over the 26 mo. study. A. Distribution of planar surface area losses, B. distribution of partial colony mortality, C. distribution of whole colony mortality (physiological isolates).

A.



B.



C.

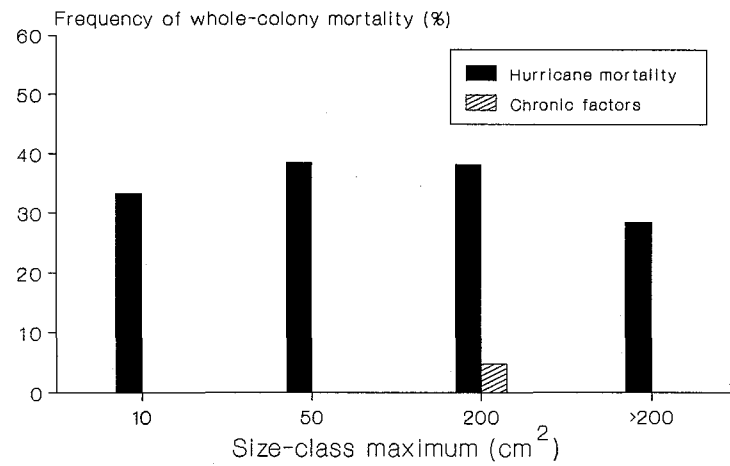


Figure 7. Mortality in *Diploria strigosa* in relation to size-class due to the hurricane and to all factor combined over the 26 mo. study. A. Distribution of planar surface area losses, B. distribution of partial colony mortality, C. distribution of whole colony mortality (physiological isolates).

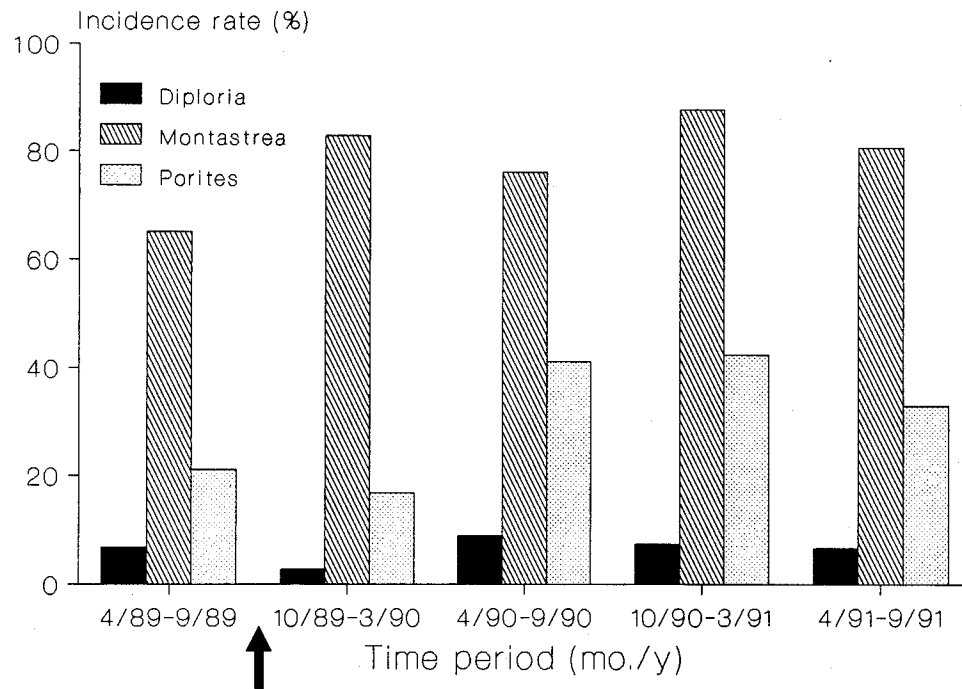


Figure 8. Percent incidence rates of parrotfish grazing over time in the three study species. Incidence rate was calculated as the occurrence of fresh cases (colonies with grazing scars which did not show them during the previous monitoring) per month, averaged over each 6-month period. The arrow indicates the time of impact of Hurricane Hugo.

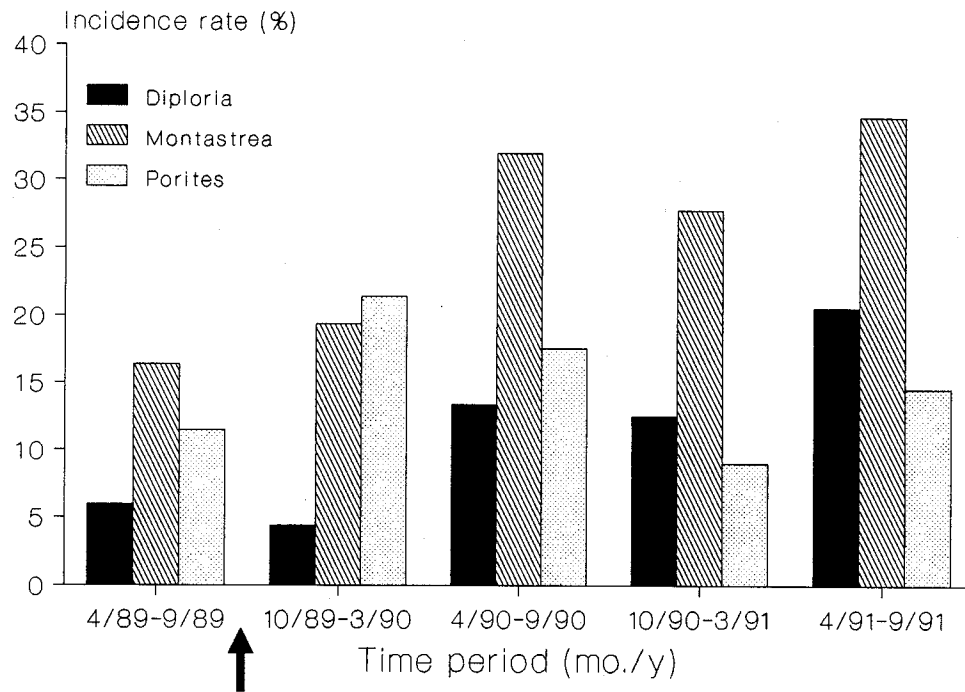


Figure 9. Percent incidence rates of tissue necrosis over time in the three study species. Incidence rate was calculated as the occurrence of fresh cases (colonies with fresh tissue loss which did not show them during the previous monitoring) per month, averaged over each 6-month period. The arrow indicates the time of impact of Hurricane Hugo.

Variation between reef-zones

The study sites we have chosen occupy three broadly defined reef-zones of the Buck Island reef system, backreef, shallow forereef (< 6 m) and deeper forereef (6 - 12 m). Some of the physical and biological characteristics of these zones are summarized in Table 4, together with results of this study.

Mortality, fission and fusion

When all factors were combined over the 26 mo. study, colony fission was seen to be a significant source of new colonies in *P. astreoides* and *M. annularis*, but high mortality rates resulted in a reduced population size in the former, whilst *M. annularis* population size remained stable (Table 5). Fission did not produce a significant number of new *D. strigosa* colonies and the population was substantially reduced by mortality. Colony fusion did not play an important role in changing population sizes.

Discussion

This study supports the idea that hurricanes may act as a structuring force on coral community organization (Woodley et al. 1981, Porter et al. 1982, Hughes 1989). Although strong hurricanes may impact the study site only at 60+ y intervals (Hubbard et al. 1990), both of the massive species studied have size distributions and population dynamics which suggest that the age of much of the population spans this time period, and possibly much longer. Populations of *Diploria strigosa*, while being virtually immune to chronic-scale impacts over a 26 mo. period, suffered extensively during Hurricane Hugo. Conversely, *Montastrea annularis* showed substantial chronic losses, mainly to predation and tissue necrosis over the study period. Hurricane mortality was also significant, but decreased sharply with colony size. Differential responses to natural impacts such as this will undoubtedly influence community structure over longer biological and evolutionary time-scales (Connell and Slatyer 1977,

Table 4. Summary statistics for three of the major zone-types at Buck Island. Data for coral species composition and cover are taken from 1989 pre-Hurricane Hugo surveys (Gladfelter et al 1991). The three species studied are ranked for their average percent composition of total coral cover in each zone (+ < 10%, ++ 10% > 20%, +++ > 20%). Tissue turnover rates (y) were calculated as the time required to lose the initial sample surface area due to chronic factors at the total (partial plus whole-colony) mortality rate encountered in the study. MA = *Montastrea annularis*, PA = *Porites astreoides*, DS = *Diploria strigosa*. Error limits are 2 SE. * = Values calculated without including hurricane-damaged sites.

PARAMETER		BACKREEF	SHALLOW FOREREEF (0 - 6 m)	DEEPER FOREREEF (6 - 12 m)
Sites (this study)		M2, M4, P3, P4 D2, D3, D4, D5	P1, P2 P5, D1	M1, M3 M5
Wave exposure		LOW	HIGH	MODERATE
Coral species richness		8 ± 1	9 ± 1	14 ± 3
Percent coral cover		5 ± 3	13 ± 6	18 ± 13
Species composition:	MA	+	+	+++
	PA	+++	+++	+
	DS	+++	+	+
Tissue turnover rates:	MA	12 y	--	28 y
	PA	15 y	9 y*	--
	DS	179 y	--	--
Frequency of chronic partial mortality events:	MA	36%	--	29%
	PA	28%	33%*	--
	DS	10%	--	--
Frequency of whole colony mortality due to chronic factors:	MA	16%	--	7%
	PA	14%	15%*	--
	DS	0.9%	--	--
Frequency of whole colony mortality due to Hurricane Hugo:	MA	8%	--	3%
	PA	1%	38%	--
	DS	8%	100%	--

Table 5. Changes in population sizes (colony number) due to all causes over the 26 mo. study.

	<i>M. annularis</i>	<i>P. astreoides</i>	<i>D. strigosa</i>
Average number of colonies per estimated genet in 1989	13.0	1.7	1.3
Colony mortality	17.8%	34.1%	32.2%
Fission	18.4%	16.7%	0.7%
Fusion	0.6%	1.8%	1.4%
Net change per 100 colonies 1989 - 1991	+0.01	-19.2	-32.9

Hughes and Jackson 1980, Hughes 1989).

This study gives some indication of the relative ecological significance of the hurricane impact on different species. It is important to note that only slight changes in coral cover may involve highly significant whole colony losses in terms of the population dynamics of normally resistant species such as *Diploria strigosa*. This species showed hurricane-related reductions in planar surface area of 0.4% and 0.1% at two sites on the north side of Buck Island: changes undetectable by standard methods of reef community assessment (Hubbard et al. 1991, Gladfelter et al. 1991). This apparently tiny loss represented 86% and 100% of the whole colony mortality rates due to chronic factors over 26 months, however. At the one site on the south reef, destruction was total. Size-frequency distributions for both the massive species studied suggest that they have not recruited successfully in large numbers in recent years. It therefore seems unlikely that *D. strigosa* populations will recover rapidly. To regain the pre-hurricane population structure in all areas will take decades at least. *M. annularis* colonies, while apparently not recruiting in abundance, routinely undergo a high degree of chronic mortality which is apparently replaced by colony fission and growth. Since no whole genet loss was recorded in our study, the pre-hurricane population structure could be regained in just a few years.

Porites astreoides shows the life-history characteristics and population dynamics of a more opportunistic or "mobile" species (Loya 1976, Jackson and Hughes 1985, Hughes and Jackson 1985). Its size-frequency distributions suggest an actively-recruiting population structure. Mortality rates were substantial, both on a chronic time scale and due to the hurricane, and mortality did not drop as sharply in relation to colony size as shown by *M. annularis*. These attributes may explain why *P. astreoides* dominates the shallow forereef, a zone where *M. annularis* is virtually absent and *D. strigosa* is an insignificant component of the community. Hughes and Jackson (1985) made the observation that more "mobile" species are favored in shallow, more disturbed habitats whilst more robust, massive species are often favored in deeper, less disturbed ones, despite the fact that the latter may be more resistant to physical perturbation from wave-action. This study suggests that even in shallow-water environments, the major causes of chronic mortality may be biological, not physical in origin

with predation by grazing parrotfishes being of major importance (Simpson 1979, Bak and Luckhurst 1980). *P. astreoides* is not resistant to these impacts (although more so than *M. annularis*), but the population is capable of sustaining itself by processes of sexual recruitment and colony fission. Interestingly *D. strigosa*, which appears to be resistant to these chronic effects, was moderately abundant on the south shallow forereef at Buck Island prior to Hurricane Hugo (whereas *M. annularis* was virtually absent but became dominant below approximately 6 m depth). The severe damage to *D. strigosa* populations in this area during the hurricane was perhaps a part of the ongoing historical process (Hughes 1989) which limits population development in this zone. *D. strigosa* populations may therefore be controlled by sporadic catastrophic events, whereas *M. annularis* is controlled largely by chronic disturbances. The near-absence of *M. annularis* in the shallow forereef may either be explained by physiological tolerances, mechanisms evolved to prevent larval recruitment in this unsuitable (e.g. hurricane damage-susceptible) environment, or rates of chronic mortality may increase in this shallow environment above a critical level to sustain population development.

Finally, the significant differences in mortality between sites, all of which are within a few hundred meters of each other, indicates that either disturbance levels or responses of individual species may vary dependent on relatively small differences in environmental conditions or community composition. The only reasonably assured method to determine the impact of anthropogenic or natural perturbations is therefore to have a long-term regular monitoring program in place prior to the impact (Brown and Howard 1985, Brown 1988, Rogers 1988).

References

- Antonius A (1981a) The "band" diseases in coral reefs. Proc 4th Int Coral Reef Symp 2:6-14
Antonius A (1981b) Coral reef pathology: A review. Proc 4th Int Coral Reef Symp 2:3-6

- Bak RPM, van Es YS (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* and *Porites astreoides*. Bull Mar Sci 30:883-887
- Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients at Curaçao. Oecologia 47:145-155
- Brown BE (1988) Assessing environmental impacts on coral reefs. Proc 6th Int Coral Reef Symp 1:71-80
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs 8:163-170
- Bythell JC, Gladfelter EH, Gladfelter WB, French KE, Hillis Z (1989) Buck Island Reef National Monument - Changes in modern reef-community structure since 1976. In: Hubbard DK (ed) Terrestrial and marine geology of St. Croix, U.S. Virgin Islands. West Indies Laboratory Spec Pub 8, pp 145-154
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1310
- Gladfelter WB (1982) White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull Mar Sci 32:639-643
- Connell, JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119-1144
- Edmunds PJ, Witman JD (1991) Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St. John, US Virgin Islands. Mar Ecol Prog Ser 78:201-204
- Gladfelter EH, Bythell JC, Gladfelter WB, Lewis SK, Woodbury M (1991) Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites. Part 1. U.S. Dept. Interior, National Park Service, Spec. Rept.
- Harriott VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. Mar Ecol Prog Ser 21:81-88
- Harper JL (1977) Population biology of plants. Acad Press, Lond.
- Highsmith RC, Riggs AC, D'Antonio CM (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322-329
- Hubbard DK, Parsons KM, Bythell JC, Walker ND (1991) The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, U.S. Virgin Islands - a preliminary assessment. J Coastal Res Spec Iss 8:33-48
- Hughes TP (1989) Community structure and diversity of coral reefs: The role of history. Ecology 70:275-279
- Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic

- consequences of partial mortality, fission and fusion. *Science* 209:713-715
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141-166
- Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. *Smithsonian Contrib Mar Sci* 31:25pp
- Knowlton N, Weil E, Weight LA, Guzman HM (1992) Sibling species in *Montastrea annularis*, coral bleaching, and the coral climate record. *Science* 255:330-333
- Loya Y (1976) The Red Sea coral *Stylophora pistillata* is an r strategist. *Nature* 259:478-480
- Porter JW (1974) Community structure of coral reefs on opposite sides of the Isthmus of Panama. *Science* 183:543-545
- Porter JW, Battey JF, Smith GJ (1982) Perturbation and change in coral reef communities. *Proc Natl Acad Sci USA* 79:1678-1681
- Rogers CS (1988) Recommendations for long-term assessment of coral reefs: U.S. National Park Service initiates regional program. *Proc 6th Int Coral Reef Symp*
- Rogers CS, Suchanek TH, Pecora FA (1982) Effects of hurricanes David and Frederick (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bull Mar Sci* 32:532-548
- Rogers CS, McClain LN, Tobias CR (1991) Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Mar Ecol Prog Ser* 78:189-199
- Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. *J Exp Mar Biol Ecol* 61:31-55
- Simpson G (1979) Predation on live coral by the parrotfishes *Scarus vetula* and *Sparisoma viride*. In: *Ecological Studies of Buck Island Reef National Monument*, US National Park Service, Spec Rept.
- Tunncliffe VJ (1981) Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc Natl Acad Sci* 78:2427-2431
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunncliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755

Relative effects of parrotfish grazing, tissue pigment loss and apparent disease on different morphological types of *Montastrea annularis* Ellis and Solander.

Chapter 5

John C. Bythell and Mary Bythell

Present address: Centre for Tropical Coastal Management, Department of Marine Sciences and Coastal Management, The University, Newcastle upon Tyne NE1 7RU.

Introduction

Species descriptions of scleractinian corals are based primarily on skeletal morphology (Vaughan and Wells 1943, Wells 1956). Skeletal structures have been shown to be highly variable within species, however, and may be influenced both by environmental conditions and genetic variation (Wijsman-Best 1972, Veron and Pichon 1976, Foster 1979, Graus and Macintyre 1982, Veron 1982). Microstructural and gross morphological traits of different species may even overlap (Foster 1982, Lang 1983).

The skeleton of *Montastrea annularis*, perhaps the most common Caribbean coral, has been shown to vary greatly in response to environmental conditions, particularly depth (Dustan 1975, Foster 1979). Recently, Knowlton et al. (1992), have suggested that *M. annularis* is a complex of at least three separate species from electrophoretic, behavioral and morphological studies (see also Szmant 1991). Two of the morphological variants described as separate species by Knowlton et al. (1992) have been described in several previous studies (see Colin 1978). These are the so-called Morph I, with colonies forming lobes or knobs of discrete tissues 5-20 cm in diameter and Morph II, consisting of mounding or plating colonies with continuous tissues up to several meters in diameter, often with distinctive raised ridges running vertically up the colony. Many believe that the Morph I morphology is a phenotypic response to high sedimentation levels (Hubbard and Pocock 1983), with the separate small lobes allowing sediment to be shed more easily via the intervening spaces.

In the present study, *Montastrea annularis* was one of three common Caribbean corals chosen for studies of organism-level responses and population dynamics at Buck Island Reef National Monument (Gladfelter et al. 1991 and Chapter 4, this volume). At two sites on the north forereef, the two morphs I and II were found to co-occur in sufficient numbers to examine differences in their responses. Here we describe the effects of various chronic impacts as well as injury caused by Hurricane Hugo (Gladfelter et al. 1991, Hubbard et al. 1991) on mortality and sub-lethal tissue damage in the two morphs.

Methods

Five sites, each containing approximately 25 heads of *Montastrea annularis* were originally established in Spring 1989. Within sites, individual coral heads were haphazardly located irrespective of morphology and semi-permanently marked with a numbered plastic tag attached to the adjacent substrate with a masonry nail and cable tie. Data are presented here from two of the five sites, where Morph I and Morph II were present in sufficient numbers to make a useful comparison. Both were forereef sites (depth ca. 10 m) on the north side of Buck Island, and are numbered sites 3 and 5 in Chapter 4 (this volume).

Colonies were monitored monthly for 26 months, during which time Hurricane Hugo, a major class V hurricane made direct landfall on the site causing extensive damage mainly on the south shallow forereef of the island (Gladfelter et al. 1991 and Chapter 1, this volume). During monthly surveys, cases of tissue necrosis, grazing damage (almost exclusively by parrotfishes), and discoloration, particularly reduced pigmentation or "bleaching" (Chapter 6) were noted by the observer. A ranked scale of severity of the condition was recorded, according to the total surface area of the colony affected: + = < 10%, ++ = 10% > 50%, and +++ = > 50%. Laminated photographs taken from various angles were taken into the field to identify colonies and locate areas of damage. After significant cases of mortality, the photographs were repeated to provide a baseline for future observations.

All colonies were photographed vertically in Spring/Summer 1989 and again, 26 months later in 1991. Transparencies were projected onto a 30 cm x 30 cm computer digitizing pad and planar surface areas determined with reference to a linear scale which was placed next to the tag in each photograph (Summagraphics II digitizer with Easydij 7.0 planimetering software). Changes between the 1989 and 1991 photographs were recorded, including the surface area of any tissue loss (partial mortality), total colony mortality, and cases of colony fission and fusion. These data were related to the monthly monitoring record to determine, where possible, the cause and time of any changes.

Results

Size-frequency distributions

The differences between Morph I and Morph II are clearly shown in the size-frequency distributions of physiologically isolated colonies (Kolmogorov-Smirnov two-sample test, $p < 0.001$, Fig. 1). Individual lobes of Morph I rarely exceeded 500 cm^2 in surface area, whereas colonies greater than 2000 cm^2 were commonly seen in Morph II. When whole heads were measured, the differences were less obvious and the distributions were not significantly different (Kolmogorov-Smirnov, $p > 0.8$), although colonies greater than 2000 cm^2 surface area were more common in Morph II (Fig. 2). In this latter case, heads were believed to consist only of clonal tissues, and were distinguished in the field by the proximity and morphological similarity of separate lobes. The sizes of whole heads of the two forms suggest that their population structure may be similar, despite the formation of smaller physiologically isolated colonies in Morph I. This assumes that the radial extension rates of whole colonies of the two forms are similar (see Hughes and Jackson 1985).

Monthly observations

In general, Morph I was affected by tissue damage and discoloration more frequently than Morph II throughout the study period. Grazing scars from parrotfish were extremely common in Morph I, but not in Morph II (Fig. 3). Rates appeared to be suppressed following Hurricane Hugo (September 1989) and subsequently rose to a peak in October 1990-March 1991. Morph II did not show these obvious changes, with grazing scars appearing in only approximately 1 colony in 10 over any 6-month period throughout the study. Severe grazing (i.e. $> 10\%$ surface area affected) did not occur in Morph II, but was seen in Morph I, particularly in the year following Hurricane Hugo.

Tissue loss without a visible grazing scar occurred in both morphs, with consistently higher levels in Morph I (Paired samples t-test, $0.05 > p > 0.01$; Fig. 4). Tissue loss of this

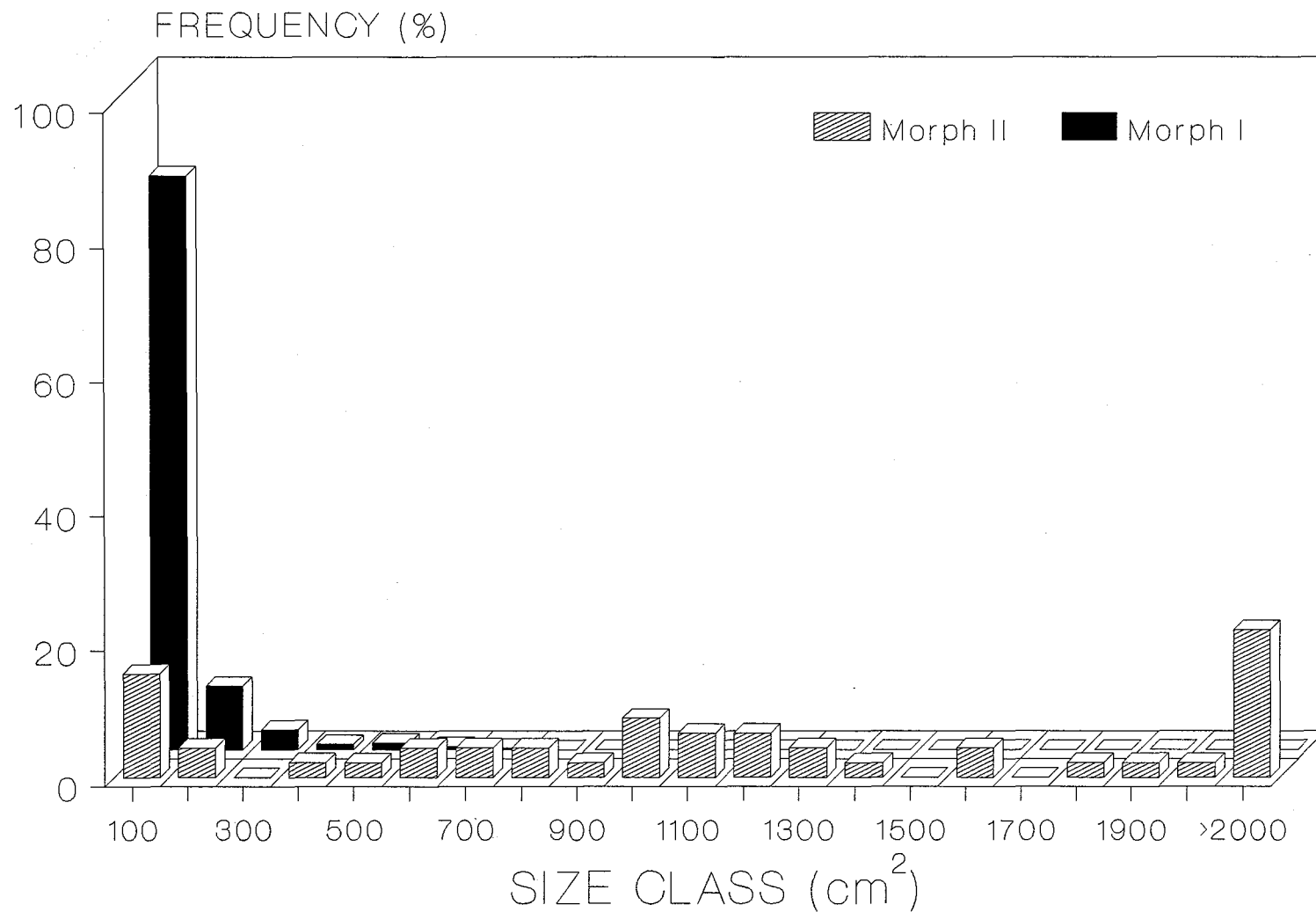


Figure 1. Size-frequency distributions based on planar surface areas of physiologically isolated colonies of *Montastrea annularis* Morph I and morph II. Areas determined by computer digitization of vertical photographs of tagged colonies (five separate sites, n=512 and n = 46 for Morph I and Morph II, respectively).

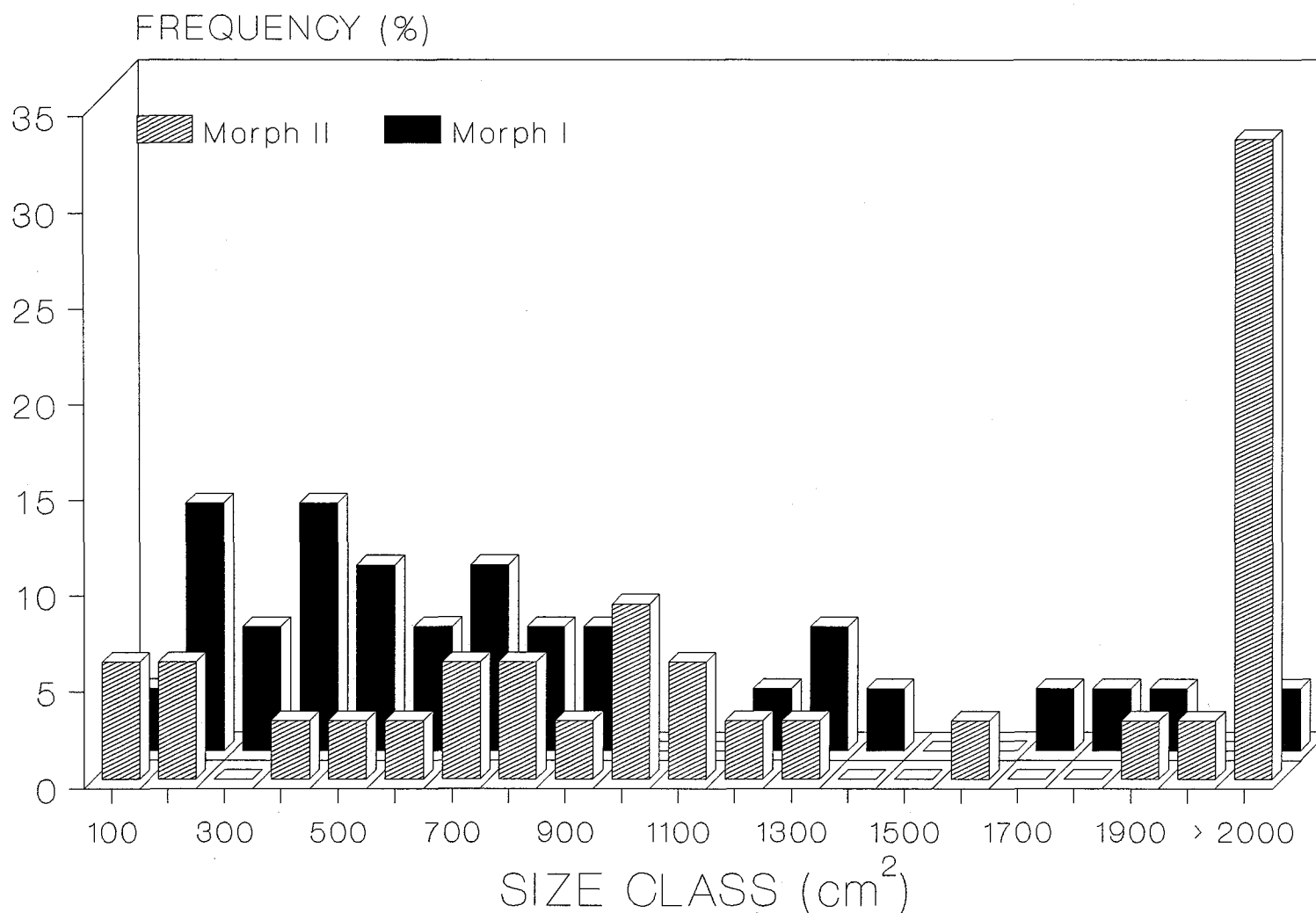


Figure 2. Size-frequency distributions based on planar surface areas of whole coral heads, including physiologically isolated tissues believed to have arisen from a single settlement of *Montastrea annularis* Morph I and morph II. Areas determined by computer digitization of vertical photographs of tagged colonies (five separate sites, n = 31 and n = 33 for Morph I and Morph II, respectively).

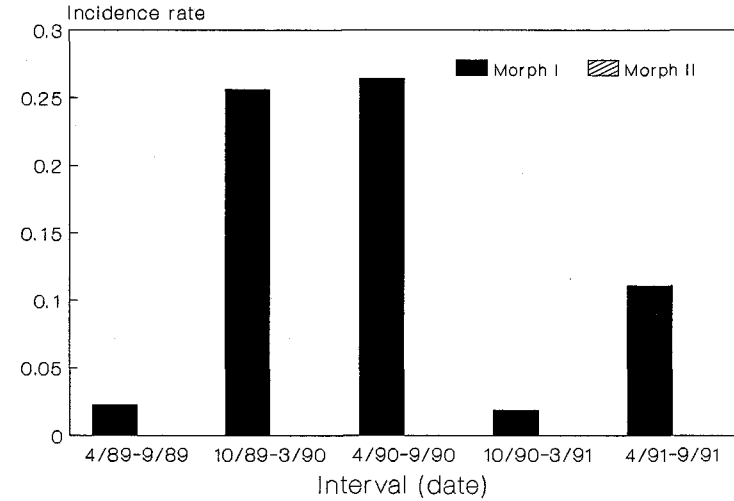
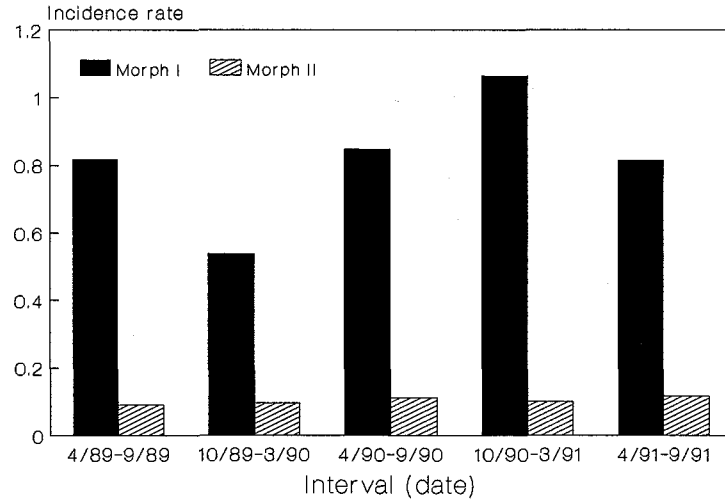


Figure 3. Incidence rates over consecutive six-month periods of parrotfish grazing, including fresh and partially healed or algal fouled scars. Incidence rates were calculated as the number of colonies showing grazing scars out of the total population in each month over the given period. Incidence rates (per colony) may exceed 1 since each colony may be affected more than once. Rates were calculated irrespective of the severity of grazing (left panel) and only for serious cases (> 10% of colony surface area affected; right panel).

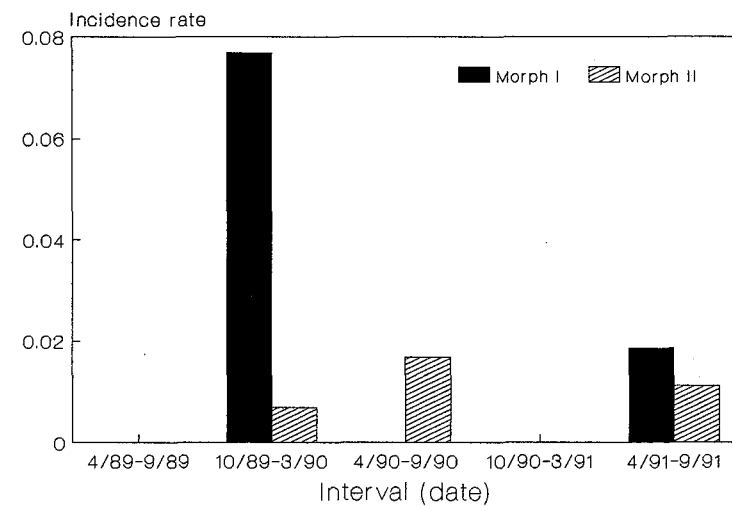
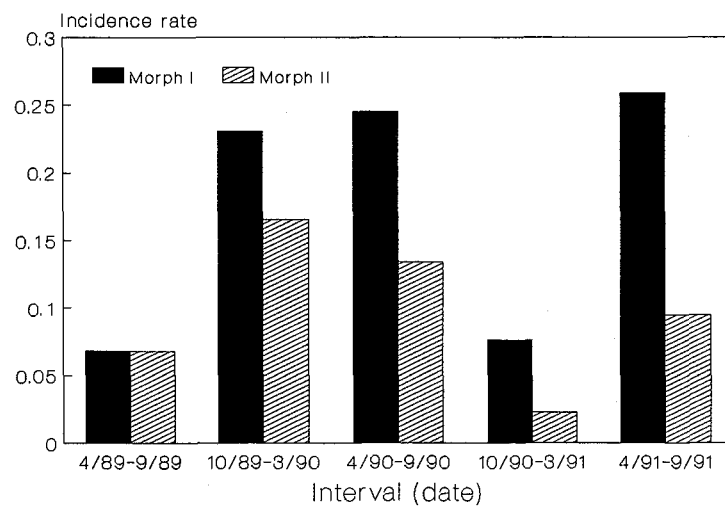


Figure 4. Incidence rates over consecutive six-month periods of fresh tissue loss without a visible scar. Incidence rates were calculated as for Fig. 3, irrespective of the severity of tissue loss (left panel) and only for serious cases (> 10% of colony surface area affected; right panel). During the study, tissue loss without a visible scar was seen to occur due to necrosis and disease, but not due to invertebrate predation (eg. by the gastropod *Coraliophilia* sp., as reported in other studies (Knowlton et al. 1990).

type was seen to occur due to sloughing of the tissues from the skeleton and often in close proximity to clumps of blue-green algae. No cases of invertebrate grazing were observed, although this has been reported elsewhere (Knowlton et al. 1990). Severe cases of tissue loss occurred in both morphs, but most frequently in Morph I (Paired samples t-test, $0.05 > p > 0.01$; Fig. 5). Also in the case of partial bleaching (but in none of the other conditions) frequency of occurrence in Morph I was significantly correlated with that in Morph II (Pearson $R = 0.97$, $p < 0.05$). This indicates that similar processes may have been causing changes in occurrence over time in the two morphs, but Morph I was consistently more severely affected. Total loss of pigmentation again appeared to be more frequent in Morph I (Fig. 6), but was less consistent and was not significantly different between the two morphs (Paired samples t-test, $p > 0.3$).

Mortality, fission and fusion

No cases of total genet (whole-head) mortality were observed at the two sites analyzed here. Mortality of separate lobes (physiologically isolated colonies) of Morph I was relatively common, but did not occur in Morph II (Table 1). Rates of colony fission and fusion were low in both morphs, with a slightly higher frequency of fission in Morph I, while fission and fusion rates cancelled each other out in Morph II. Thus, out of 38 colonies of Morph II, initially tagged in 1989, 38 were present after 26 months. Of 32 initial colonies of Morph I, 15 were killed and two produced by fission, leaving 19 colonies.

Surface area losses, including both partial and whole colony mortality, were greater in Morph I than Morph II (Table 1b). Even accounting for the greater initial surface area of Morph II, due to larger mean colony size, there was a 10-fold greater loss of tissue in Morph I. Parrotfish grazing accounted for more than half of the losses in Morph I, but was not responsible for any detectable amount of tissue loss in Morph II. Hurricane losses were also high in Morph I and undetected in Morph II, but most of the losses were unaccounted for in Morph II. Most of the losses in Morph II were probably so small that they were overlooked by the observer, since only approximately 20 cm² was lost over 26 months from an initial sample size of over 6.5 m² planar surface area.

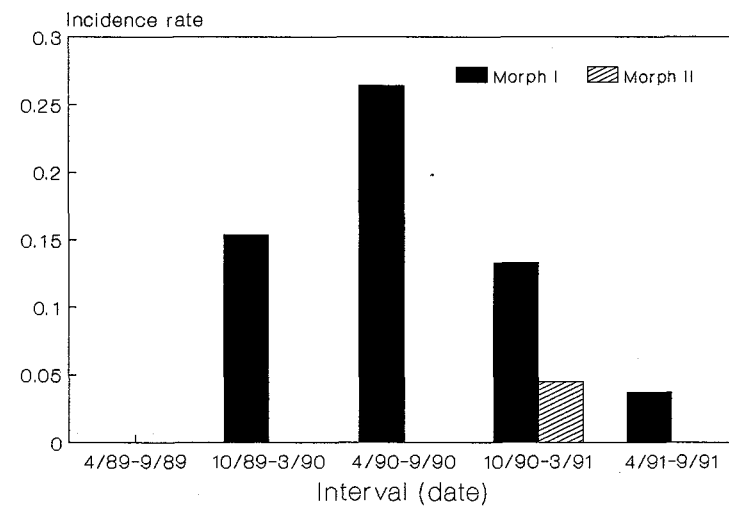
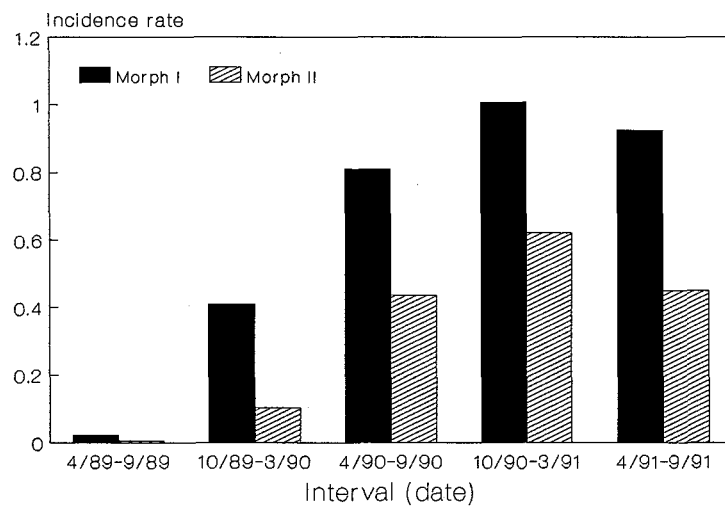


Figure 5. Incidence rates over consecutive six-month periods of pale (partially bleached) tissues. Incidence rates were calculated as for Figure 3, irrespective of the severity of paling (left panel) and only for serious cases (> 10% of colony surface area affected; right panel). Tissue paling is believed to indicate the loss of algal symbionts in response to environmental stress (Brown 1990).

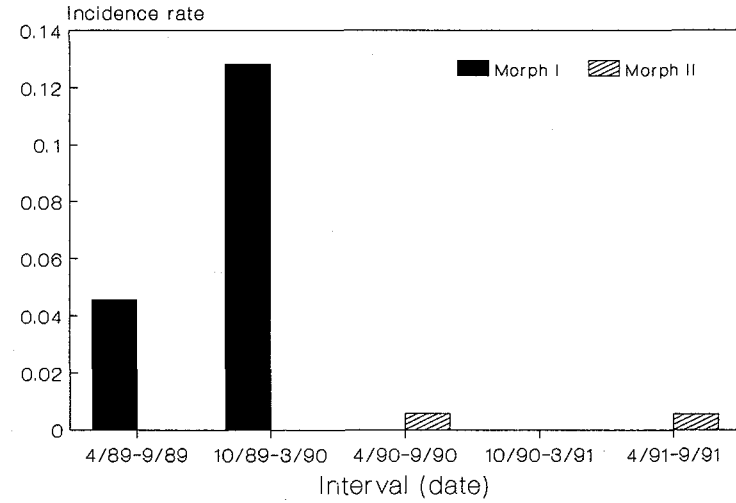
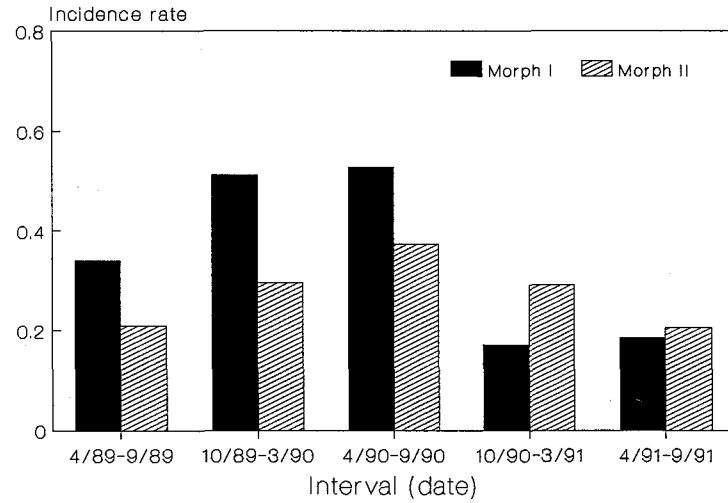


Figure 6. Incidence rates over consecutive six-month periods of apparently transparent (bleached) tissues. Incidence rates were calculated as for Figure 3, irrespective of the severity of bleaching (left panel) and only for serious cases (> 10% of colony surface area affected; right panel). Complete loss of pigment was believed to indicate a more severe depletion of algal symbionts than reduced pigmentation (cf. Fig. 5)

Table 1. Summary statistics of mortality data for *Montastrea annularis* Morph I and II at sites 3 and 4 (cf. Chapter 4) on the north forereef at Buck Island, where the two forms coexist in close proximity. Data are presented for cases of colony fission, fusion and mortality as a percent of the original (1989) population sampled. The "colony" here refers to physiologically isolated tissues; no cases of total genet (i.e. whole coral head) mortality were recorded. Planar tissue surface area loss (both partial and whole colony mortality) is presented as a percent of the original surface area of the colonies, and the causes of mortality, if known, shown as a percent of those losses. Duration of the study was 26 months.

	MORPH I	MORPH II
(a) Frequency of colony fission, fusion and mortality		
N	32	38
Fission (%)	6.2	2.6
Fusion (%)	0	2.6
Mortality (%)	46.9	0
(b) Planar tissue surface area losses over 26 mo.		
Initial surface area (cm ²)	474	67581
Total tissue mortality (%)	45.5	0.03
Hurricane Hugo (% of losses)	21.3	-
Parrotfish grazing (% of losses)	54.3	-
Tissue necrosis/disease (% of losses)	24.4	12.4
Unknown (% of losses)	-	87.8

Discussion

This study shows well-defined biological and ecological differences between two morphological types of *Montastrea annularis* (Morph I and II, Knowlton et al. 1992). This supports morphological, ecological and electrophoretic evidence that they should be classified as separate species.

Hughes and Jackson (1985) showed a clear relationship between colony size and mortality rate of foliaceous corals, a primary function of their population dynamics. This was confirmed for the massive species *Diploria strigosa* and *Montastrea annularis* and the plating-mounding form of *Porites astreoides* (Bythell et al. 1991 and Chapter 4). Morph II of *M. annularis* forms much larger colonies than Morph I at Buck Island and this may account for the different susceptibilities to tissue damage seen in the two forms. However, since the size-frequency distributions for whole heads of the two morphs were similar, we have assumed that their population age structure is similar and the smaller physiologically isolated colonies in Morph I are therefore a morphological trait. Since smaller colonies experience higher mortality rates, the tendency to form smaller colonies or lobes in Morph I would appear to be an anti-adaptive trait.

The effect of colony size on mortality can be explained on probabilistic grounds (Jackson 1979) or by size-dependent differences in the abilities of colonies to recover from insult (Connell 1973). Colonies of larger size may be more likely to receive a given impact, but the impact is less likely to result in whole-colony mortality. This type of effect may be coupled, in larger colonies, with greater energy and material reserves to repair the damage or resist disease (Jackson 1979). The latter argument may also explain why fecundity in corals is size-dependent rather than age-dependent (Szmant 1985). In a short-term 58 d study it was shown that it was the rate of impact, rather than rate of repair that resulted in the observed differences in tissue loss (Bythell et al. 1991). Also, although differences in resource reserves could account for the different levels of disease and necrosis, this could not account for the effects of an extrinsic effect like parrotfish grazing. On purely probabilistic grounds, the larger Morph II colonies may be expected to receive greater impact from grazing than Morph I, and

this therefore suggests that the parrotfish are preferentially grazing on Morph I.

Different susceptibility to damage may also explain the morphologic variation in the two morphs. Production of separate lobes or physiologically isolated colonies of clonal coral occurs by partial mortality of tissues intervening the isolates (Hughes and Jackson 1985). Different susceptibility to damage may therefore largely account for different rates of partial colony mortality and hence fission rates leading to separate lobes in Morph I. It has been suggested that the Morph I morphology is a phenotypic response to sedimentation. The smaller lobes may be cleared of sediment more effectively by random ciliary action (Hubbard and Pocock 1983), and the sediment is then voided via the intervening channels between the lobes. However, the two morphs often co-occur directly adjacent to one another (pers. obs.), suggesting that although sedimentation tolerance may account for the evolution of the separate morphologies, there is distinct genetic variation underlying it. Also, in general there appears to be a distinct separation between the Morph I and II morphologies, rather than a gradual variation between the two, which might be expected if the morphologies were a response to environmental variables.

In conclusion, the differences in population dynamics, susceptibility to intrinsic factors (disease) and extrinsic factors (parrotfish grazing) point to species with two very different life-history strategies. Morph II exhibits population dynamics more similar to *Diploria strigosa*, another species which produces large colonies with continuous sheets of tissues and is also highly resistant to chronic impacts (Bythell et al. 1991). The implications of this are important as many studies of Caribbean corals have centered on *Montastrea annularis* (Dustan 1975, Foster 1980, Szmant 1985, Hudson 1981, for example). Researchers carrying out studies on *M. annularis* should take these differences into account when reviewing the literature and planning their experimental design.

References

- Bythell JC, Gladfelter EH, Lewis SK, Woodbury M (1991) Impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix U.S. Virgin Islands: II. Organism level processes and their potential effect on the population dynamics of the three dominant

- reef building corals. In: U.S. National Park Service Special Report: Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites, Part I.
- Colins PL (1978) Caribbean Reef Invertebrates and Plants. TFH Publications, 512p
- Connell JH (1973) Population ecology of reef-building corals. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, Vol. 2. Academic Press, New York, pp 205-245
- Dustan P (1985) Growth and form in the reef-building coral *Montastrea annularis*. Mar Biol 33:101-107
- Foster AB (1979) Phenotypic plasticity in the reef corals *Montastrea annularis* and *Siderastrea siderea*. J Exp Mar Biol Ecol 39:25-54
- Foster AB (1980) Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea siderea*. Bull Mar Sci 30:678-709
- Foster AB (1982) Species overlap in reef-corals and its evolutionary significance. Geological Society of America, Abstracts with programs 14:491
- Graus RR, Macintyre IG (1982) Variation in growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): a quantitative evaluation of growth response to light distribution using computer simulation. In: Rutzler K, Macintyre IG (eds.) The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Contributions to the Marine Sciences, No 12. Smithsonian Institution Press, Washington DC, 539p
- Hubbard JAEB, Pocock YP (1983) Scleractinian functional morphology: a key to paleoecological reconstruction. In: Oliver WA, Sando WJ, Cairns SD, Coates AG, Macintyre IG, Bayer FM, Sorauf JE (eds) Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids), No 54. Paleontological Research Institution, Ithaca, pp 523-530
- Hudson HJ (1981) Growth rates of *Montastrea annularis*: a record of environmental change in Key Largo National Marine Sanctuary, Florida. Bull Mar Sci 31:444-459
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Mongr 55:141-166
- Jackson JCB (1979) Morphological strategies of sessile animals. In: Rosen B, Larwood G (eds). Biology and systematic of colonial animals. Academic Press, New York, pp 499-555
- Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. Smithsonian Contributions to the Marine Sciences, No 31. Smithsonian Institution Press, Washington DC
- Lang JC (1983) Whatever works: the variable importance of skeletal and of non-skeletal

- characters in scleractinian taxonomy. In: Oliver WA, Sando WJ, Cairns SD, Coates AG, Macintyre IG, Bayer FM, Sorauf JE (eds) Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids), No 54. Paleontological Research Institution, Ithaca, pp 18-44
- Szmant AM (1985) The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis*. Proc 5th Int Coral Reef Symp 4:295-300.
- Szmant AM (1991) Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa*. Mar Ecol Prog Ser 74:13-25
- Vaughan TW, Wells JW (1943) Revision of the suborders families and genera of the Scleractinia. Geological Society of America, No 44. 363p
- Veron JEN (1982) The species concept in 'Scleractinia of Eastern Australia'. Proc 4th Int Coral Reef Symp 2:183-186
- Veron JEN, Pichon M (1976) Scleractinia of Eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. Australian Institute of Marine Science Monograph Series, Vol 1. 86p
- Wells JW (1956) Scleractinia. In: Moore RC (ed) Treatise on invertebrate paleontology Part F Coelenterata. Kansas University Press, Kansas 498p
- Wijsman-Best M (1972) Systematic and ecology of New Caledonian Faviinae (Coelenterata-Scleractinia). Bijl Dierk 42:1-90

A record of coral bleaching at Buck Island Reef National Monument between 1989 and 1991: Post-hurricane and seasonal correlates.

Chapter 6

Mary Bythell and John C. Bythell

Present address: Centre for Tropical Coastal Management, Dept of Marine Sciences and Coastal Management
The University of Newcastle upon Tyne NE1 7RU,UK

Introduction

Recently, much attention has been focussed on wide-scale coral bleaching events. Most notably, the 1982-83 El-Niño related Pacific event, which caused widespread coral mortality (Glynn 1985; Brown and Suharsono 1990) and the 1987-88 Caribbean event. Although the Caribbean event did not appear to cause the same dramatic colony mortality rates (Porter et al. 1989; Goreau and Macfarlane 1990), it did affect reproduction and physiological responses, the long-term effects of which are as yet unknown (Szmant and Gassman 1990; Porter et al. 1989).

The tissue of most corals is transparent, with the zooxanthellae providing the pigment that causes the apparent coloration of the coral tissues. Bleaching, the loss of this coloration, is a result of two factors: expulsion of the symbiont and/or decrease in chlorophyll content of the zooxanthellae (Szmant and Gassman 1990; Porter et al. 1989).

Bleaching is believed to occur as a generalized stress response (Jokiel and Coles 1990), signalling the breakdown of the delicate balance of the symbiosis. Whether this is a response primarily of the host or of the symbiont is unclear (Porter et al. 1989), though it appears that there may be a combined effect of the two (D'Elia et al. 1991). Environmental parameters known to illicit bleaching include increased water temperature (Porter et al. 1989; Jokiel and Coles 1990; D'Elia et al. 1991), reduced water temperature (Steen et al. 1987), reduced salinity (Goreau 1964), increased UV light (Lesser et al. 1990), and increased sedimentation (Rogers 1983). Initiation of the bleaching response has been shown to be related to the severity and duration of the stress, and different types of stresses may act synergistically (Jokiel and Coles 1990).

In spite of the attention paid to wide-scale severe bleaching events, where entire colonies are affected throughout the reef, bleaching of small parts of coral colonies occurs on a routine basis (Gates 1990). Unlike the severe bleaching events, this routine bleaching does not appear to lead to colony mortality (Gladfelter et al. 1991). Various grades of pigment loss can occur, with apparently colorless tissues showing lower levels of chlorophyll than pale (reduced pigment) tissues (Jokiel and Coles 1990).

This chapter examines bleaching frequency and severity in *Porites astreoides*, *Diploria strigosa* and two morphological variants of *Montastrea annularis* at several sites at Buck Island in order to follow temporal patterns in bleaching over a 34 month period. Nine months into the study, Hurricane Hugo passed over St. Croix, severely impacting some of the study sites. Here we attempt to relate seasonal changes in bleaching with temperature data and both the immediate and longer-term impact of the hurricane.

Methods and Materials

Fifteen study sites at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands were selected in areas of locally high coral population densities, adjacent to permanently marked cross-reef transects. At each site, an approximately circular haphazard swim was executed and each colony of either *Diploria strigosa*, *Porites astreoides* or *Montastrea annularis* encountered was tagged. These three species are dominant in many areas at Buck Island (Bythell et al. 1989), and represent 22%, 10% and 12% of live coral cover respectively, averaged between zones. Tags were attached by a plastic cable tie to a masonry nail that had been driven into the dead substrate adjacent to the colony. Many tagged heads included more than one physiologically isolated colony, especially in *M. annularis*. Maps were made of the sites so that the tagged corals could be easily relocated.

Thirteen of the fifteen original sites were used in this analysis (two sites completely destroyed during Hurricane Hugo were excluded). Of the *D. strigosa* sites used in this analysis two were situated north of the island, one on the backreef just west of the underwater trail and one on the inshore pavement. The depth of these sites ranged between 1 and 4 m. Three *M. annularis* sites were located on the forereef, one south and two north of the island. Two *M. annularis* sites were located on the backreef, one on the southeast and the other on the north of the island. The depth of the backreef sites ranged between <1 m and 4 m, while the depth of the forereef sites fell between 6 m and 10 m. Two of the *P. astreoides* sites were located on the forereef, one north of the island and the other on the southeast side between 4 m and 8 m depth. One of the backreef sites was located just west of the underwater trail,

at a depth of approximately 4 m, while the other was located further west on the north reef, again at approximately 4 m depth (Gladfelter et al. 1991).

Recent evidence indicates that the two obvious morphs of *M. annularis* are actually three separate species (Knowlton et al. 1992). Using the descriptions by Knowlton et al. (1992) it was found that the *M. annularis* colonies in this study included both their morph I (the "knobby" form, which forms small 5-20cm diameter heads) and morph II (larger colonies with continuous sheets of tissue). No colonies of the morphological type III had been tagged. The monitoring data for *M. annularis* has been categorized by morph type and analyzed separately.

A total of 63 morph I and 37 morph II colonies of *M. annularis* were tagged. 103 *D. strigosa* and 101 *P. astreoides* colonies were tagged. *M. annularis* colonies with both a morph I and morph II colony under the same tag were excluded from the analysis.

The definition of bleaching in field observations is subjective due to the natural variability in pigmentation. Here we discuss only cases of "complete" bleaching i.e.; where the tissues appeared completely colorless (allowing the whiteness of the skeleton to show through) on either part or over the entirety of a colony.

Completely colorless tissues in *Porites astreoides* were rarely encountered in this study. This species has a much more porous skeleton than *D. strigosa* or *M. annularis* and the tissue is ramified throughout it (Bak et al. 1980). When the tissue is tightly retracted, bare skeleton is exposed which appears white between the polyps, while the polyps themselves retain a dark coloration. This was interpreted by some observers as "bleached" tissue leading to some confusion in the monitoring data for this species.

Beginning in December 1988 to March 1989 (depending on the study site), and ending in September 1991, each colony was monitored monthly using either SCUBA or snorkel. The percentage of the surface area of the colony that was bleached was noted as: I. < 10%, II. 10 - 50% or III. > 50%. In the following analyses, "general" bleaching refers to all cases of bleaching, while "severe" bleaching refers only to bleaching over 10% (categories II and III, combined). Monitoring was incomplete in October 1989 and no monitoring was done in November 1989 due to operational difficulties caused by the hurricane.

Temperature data was collected using a Ryan Tempmentor thermograph that was attached to a cement block at the base of the forereef at a depth of 30 feet to the east of the Underwater Trail. Because the thermograph had to be removed occasionally to download the data to a computer, an incomplete data record was collected for July and August, 1990, and April 1991. No data was collected from mid-July 1989 to mid-December 1989. Only data through April 1991 was available for this analysis.

Results

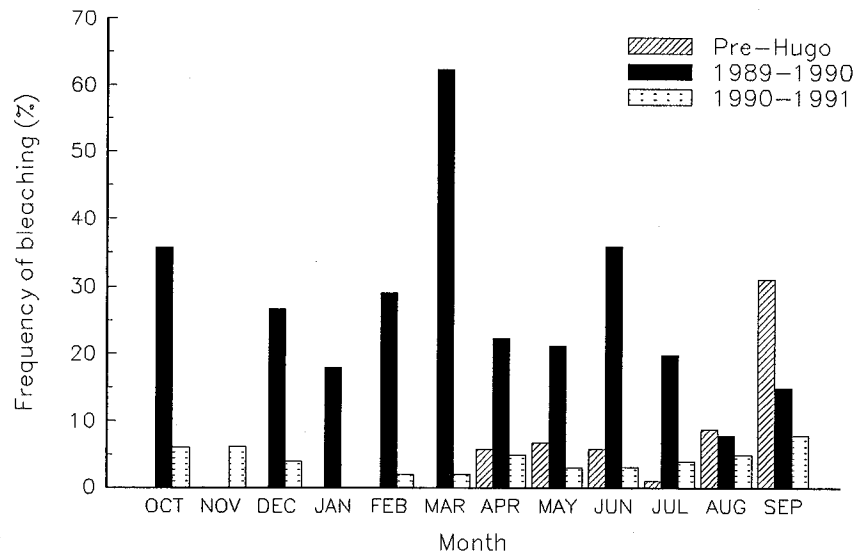
General Observations

Most cases of bleaching involved only small parts ($< 10\%$) of colonies. Colonies that entirely bleached were rarely encountered. A short bleaching event was noted in the fall of 1990, when several colonies were seen to be totally bleached or with a large percentage of the surface area bleached. This apparently did not significantly increase the frequency of bleached colonies within the study sample (Fig. 1).

Temperature and bleaching

No relationship between average seawater temperature (Fig.2) and frequency of bleaching was found, except in Morph II of *Montastrea annularis* ($p < 0.01$). A relationship between the prevalence rate of general bleaching and average monthly seawater temperature was tested using Kendall's rank correlation coefficient. A non-parametric test was used because the bleaching data was non-normal and angular transformations were unsuccessful (Sokal and Rohlf 1981). Attempts to show a relationship between average seawater monthly temperature and the prevalence rate of bleaching for October 1990-April 1991 (the months of the second post-hurricane year for which temperature data are available) using the same test were unsuccessful.

A



B

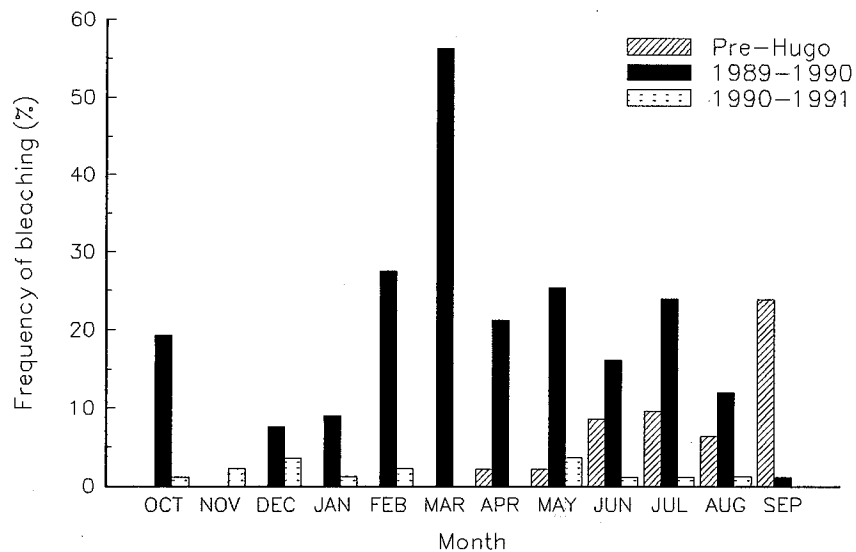
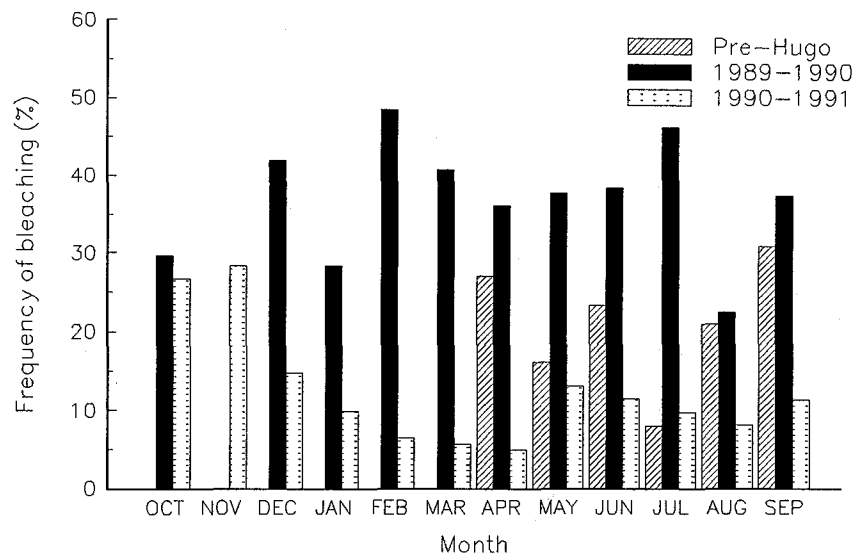


Figure 1a, b. Frequency of occurrence of bleaching in the entire sample for each month. Only completely white-appearing tissues were counted as bleached for this analysis, but all classes of severity (proportion of the surface area of the colony affected) were included. a. *Diploria strigosa*. b. *Porites astreoides*.

C



D

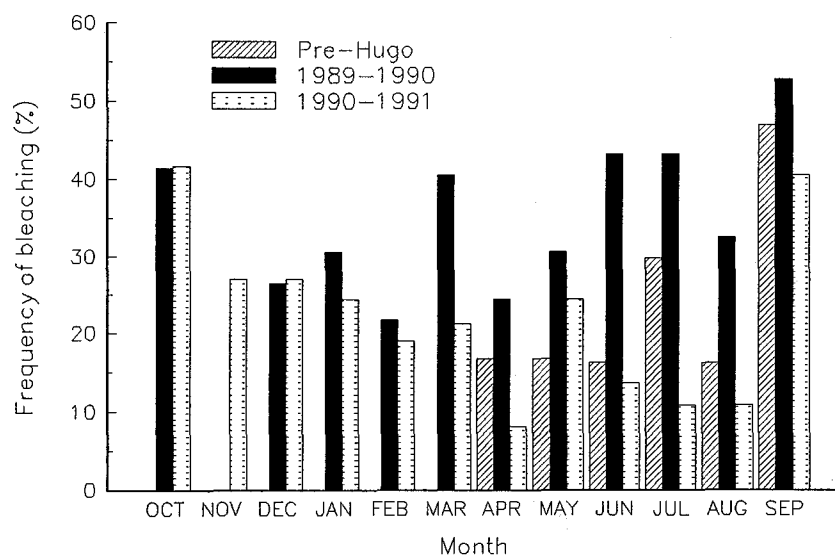


Figure 1c, d. Frequency of occurrence of bleaching in the entire sample for each month. Only completely white-appearing tissues were counted as bleached for this analysis, but all classes of severity (proportion of the surface area of the colony affected) were included. c. *Montastrea annularis* Morph I. d. *M. annularis* Morph II.

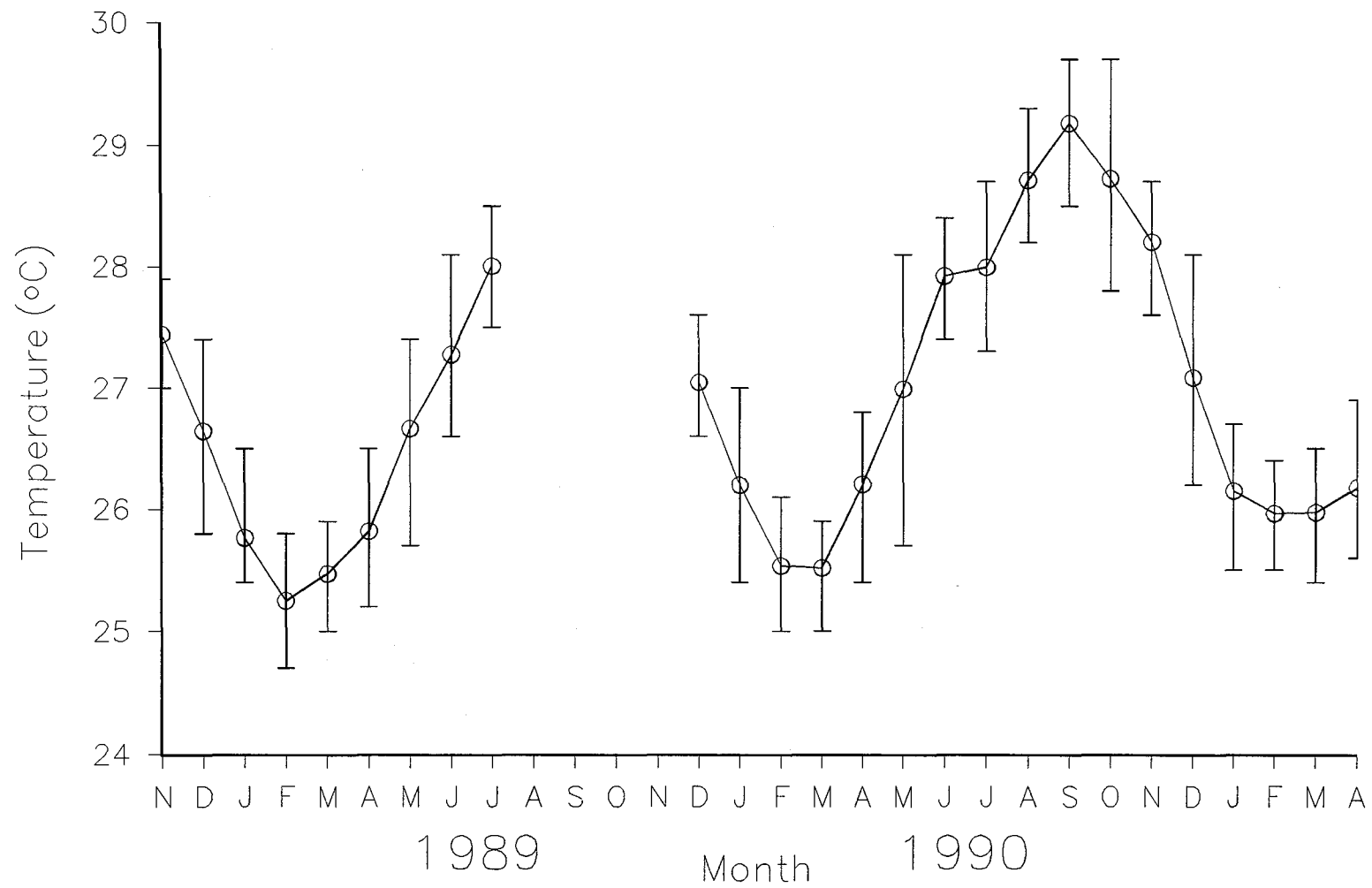


Figure 2. Average monthly seawater temperature recorded by the Ryan Thermograph located at a depth of 10 m, eastern forereef, Buck Island.

Prevalence rates of general bleaching in 1989/90 and 1990/91

Prevalence rates of bleaching of all severities for the 6 months before the hurricane, for October 1989-September 1990 (the year immediately following Hurricane Hugo) and October 1990-September 1991 are shown in Figure 1. Distribution of rates over the two twelve-month periods following the hurricane were all significantly different. (Kolmogorov-Smirnov two-sample test, *Diploria strigosa*, *Porites astreoides*, and morph I of *Montastrea annularis* $p < 0.01$, Morph II $p < 0.05$). The bleaching frequencies for the year following Hurricane Hugo are generally consistently higher for the same month of either the 6 months before the hurricane or the second year following the hurricane.

Incidence rates of general and severe bleaching

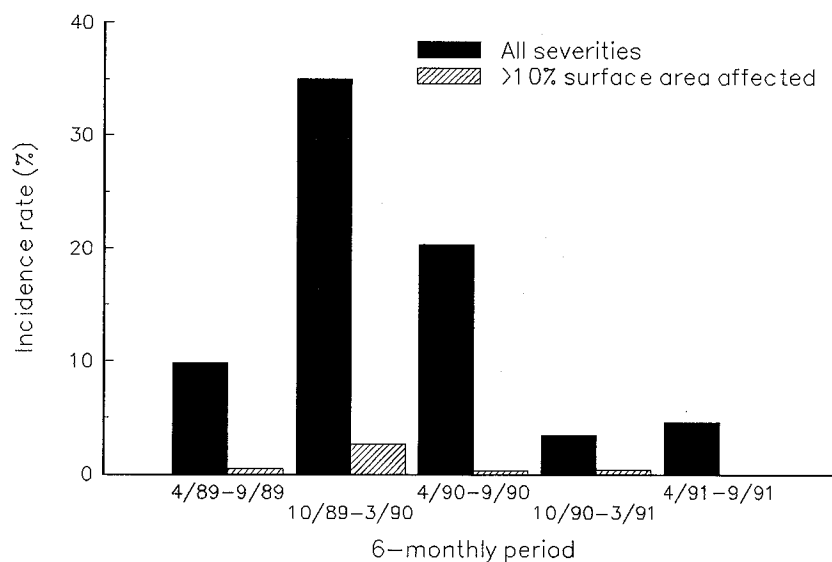
Incidence rates calculated as:

#of cases of bleaching during the x month period

$x * (\text{avg \# of cases per month})$

(Rustagi 1985) for general and severe bleaching for the four species/morphs are shown in Figure 3. Since no monitoring was carried out in November 1989, the period immediately following Hurricane Hugo was calculated using a 5-month interval, whereas all other periods were of 6-months duration. It appears that there was an elevation in bleaching levels following the hurricane in all species/morphs. Levels seem to have returned to their pre-hurricane state 12 months after the storm. In *D. strigosa* and *P. astreoides*, levels appear to decrease after the initial post-hurricane increase. The percent of Morph I of *M. annularis* bleached remained at similar levels for the two 6-month periods following the storm, while Morph II appeared to continue to increase during these periods. Differences between periods were highly significant for all species/morphs (log likelihood ratio chi-square, morph II general $p < 0.006$, severe $p < 0.029$, all others $p < 0.001$).

A



B

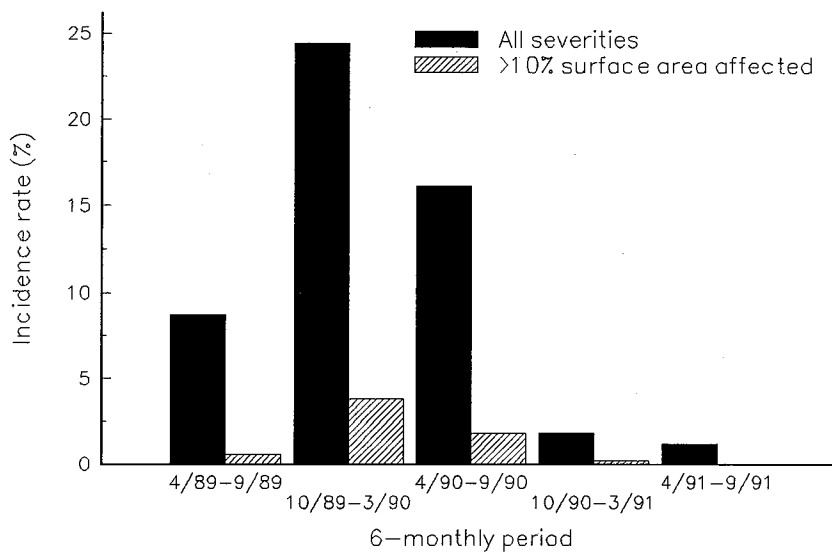
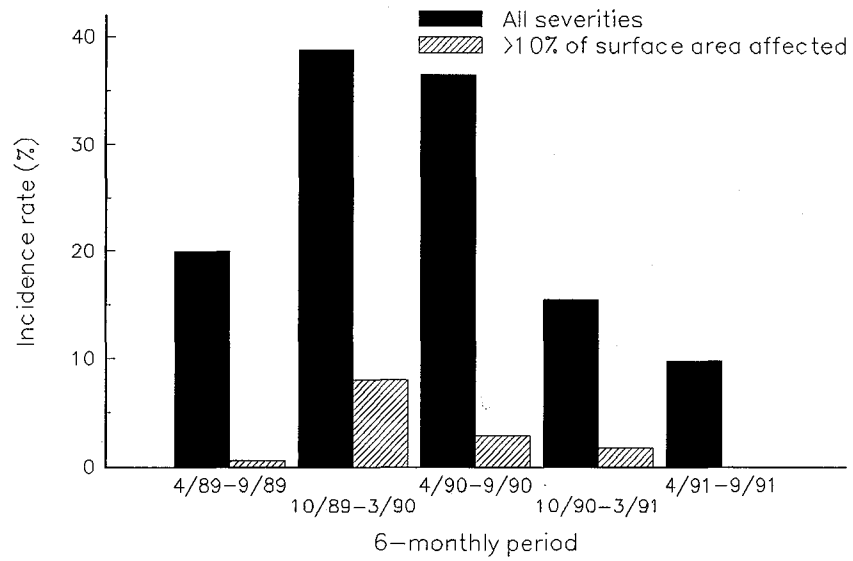


Figure 3a, b. Incidence rates of bleaching over consecutive six-month periods. Incidence rates were calculated as the number of colonies showing bleached areas of tissue out of the total population in each month over the given period. Incidence rates (per colony) may exceed 1 since each colony may be affected more than once. Rates were calculated irrespective of the severity (black bars) and only for serious cases (>10% of colony area affected; hatched bars). A. *Diploria strigosa* B. *Porites astreoides*.

C



D

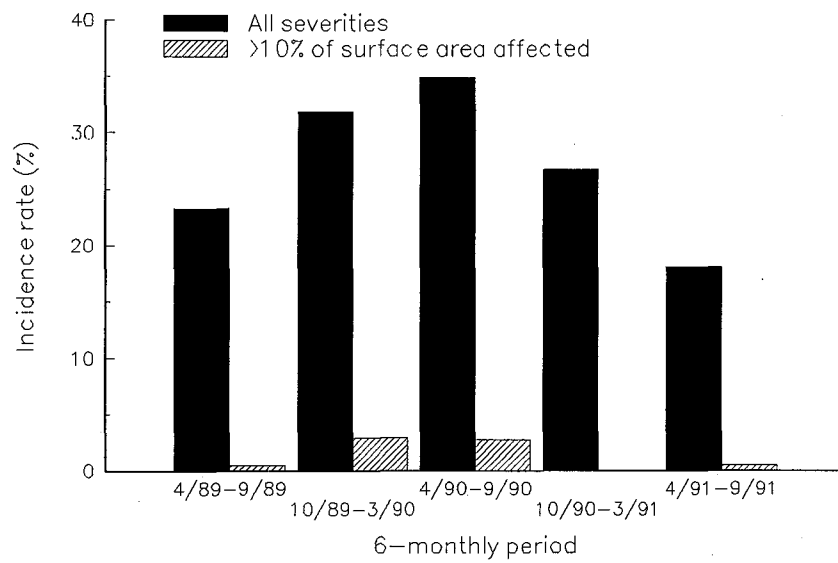


Figure 3c, d. Incidence rates of bleaching over consecutive six-month periods. Incidence rates were calculated as in Figs 3a, b. C. *Montastrea annularis* Morph I D. *M. annularis* Morph II.

Discussion

This study shows that Hurricane Hugo was followed by a prolonged bleaching episode. Unlike many previous accounts (Glynn et al. 1990; Goenaga et al. 1989) no whole colonies were killed during this bleaching, and only one colony exhibited partial mortality. We hypothesize that the increased frequency of bleaching could have been due to several factors; 1) a massive stress due directly to impact of the hurricane itself, even in areas that were not obviously affected 2) a stress indirectly resulting from the hurricane 3) a stress caused by a factor totally unrelated to the hurricane or 4) a combination of these factors.

Immediate effects of hurricanes and other storms are often obvious, such as severe scouring or mechanical destruction of localized areas. A sub-lethal effect associated with the increased water motion of a severe storm may be abrasion of the coral tissues. Recovery of this abraded tissue could account for the initial rise in the occurrence of bleaching due to the long repigmentation process. It has been shown by Bythell et al. (1991) that parrotfish grazing scars can be covered by tissue in as little as two days. The total recovery and repigmentation of this tissue, however, can take more than 58 days. Bak et al. (1980) showed that the size of lesion areas on *P. astreoides* is a major factor in the corals ability to regenerate the damaged tissues. In this light, it is possible that large areas of tissue which were damaged in the storm could have taken several months to regain their normal complement of zooxanthellae.

In the course of the study, bleaching was noted under macro algae and blue-green algae. Immediately following the storm, massive blooms of the fleshy macrophyte *Liagora* spp. were noted. This occurred on newly opened substrate, possibly fuelled by nutrients from land runoff and death and decay of organisms due to the storm (Gladfelter 1991). Shading by this algae and other opportunistic species could have caused spots of bleached tissue, though the bloom was short-lived and is therefore is unlikely to be the sole cause of the elevation.

One factor, localized to the south reef may have been the alteration of oceanographic conditions associated with the virtual bulldozing of the shallow forereef and the creation of the rubble rampart 30 m inshore of the previous reef crest. The reef crest in this area was previously more open, allowing a greater exchange of water between the backreef and the

forereef. Two of the sites used in this analysis were located in this area, a shallow *M. annularis* backreef site and a relatively shallow *P. astreoides* forereef site.

Freshwater input during storms has been implicated in mass bleaching (Goreau 1964). However, rainfall estimates for St. Croix during Hurricane Hugo have been remarkably low (Hubbard et al. 1991). Like the effects of a sharp temperature change, immediate sharp increases in bleaching with a gradual recovery would be expected. This does not agree with the long duration of the increase following the storm.

There were no significant increases in benthic area cover of sediment following the hurricane (Bythell et al. in press). Also, no obvious sedimentation was observed, with the exception of the rubble rampart that was created on the south reef. This lack of sedimentation is probably due to several factors. Buck Island is a small, offshore island with no natural watercourses. Prevailing northeasterly winds tend to flush any runoff towards the west, away from the reef. Any runoff from the east end of St. Croix is usually retained within the bank barrier system there, with suspended sediments tending to be flushed out to the west, downstream from Buck Island. Therefore, it seems unlikely that smothering by terrestrial sediment runoff acted to induce the prolonged bleaching.

Because we do not have temperature data for August-November, 1989, it cannot be said with certainty that an elevated seawater temperature occurrence did not cause, or act synergistically with the stress of the hurricane to produce the prolonged bleaching. If in fact a sharp increase or decrease in temperature did occur in association with the storm, a sharp rise in bleaching frequency would be expected, rather than the sustained, slightly elevated rates seen. There was an increase in prevalence rates of general bleaching in *D. strigosa*, *P. astreoides* and morph II *M. annularis* of in March 1990 which coincides with the coldest water temperatures of the year. It is possible that the decrease in water temperature exacerbated the already stressed corals leading to an immediate increase in bleaching levels though attempts to correlate bleaching frequency with seawater temperature in these species was unsuccessful.

Low levels of bleaching were present in all species in almost every month monitoring was performed. Although only morph II of *M. annularis* showed a correlation between average monthly temperature and the prevalence rate of bleaching, the 1990-91 data in all

species shows what appears to be a seasonal response, with higher frequencies of bleaching during months of increased water temperature, similar to what Gates (1990) found in Jamaica. However, because the analysis is based primarily on temperature data from the year following Hurricane Hugo, any relationship between water temperature and bleaching would probably have been masked by the effects of this impact and other factors that may have been responsible for the increased bleaching.

The fact that Morph II of *M. annularis* did show a correlation between seawater temperature and frequency of bleaching suggests that this species may have a different life history strategy than the other species. Bythell et al. (1991) suggest that this morph may divert relatively more of its resources to the resistance of chronic conditions rather than to repair. It could be that this resistance, at least to reduction in pigmentation, is affected by water temperature, hence the correlation.

In conclusion, the year immediately following the hurricane, 1989-90, showed significantly higher frequencies of bleaching than the six months prior to Hugo and 1990-91. Evidence points to an immediate impact, most likely tissue abrasion, which led to a prolonged recovery period and increased susceptibility to other stresses such as perhaps the increase in algal cover immediately following the storm and the low seawater temperatures in February and March of 1990. These additional stressors could have acted either to divert resources from repair of hurricane damage or could represent significant stresses in their own right, in either case delaying the recovery process further. Thus the post-hurricane bleaching episode may have been a series of contiguous stress events rather than a single event related to the hurricane.

References

- Bak RPM, Steward-Van Es Y (1980) Regeneration of superficial damage in scleractinian corals *Agaricia agaricites* f. *purpurea* and *Porites astreoides*. Bull of Mar Sci 30(4):883-887
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs 8:163-170
- Bythell JC, Gladfelter EH, Lewis SK, Woodbury M (1991) Impact of Hurricane Hugo at Buck

- Island Reef National Monument, St Croix U.S. Virgin Islands: II. Organism level processes and their potential effect on the population dynamics of the three dominant reef building corals. In: U.S. National Park Service Special Report: Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites, Part I.
- D'Elia CF, Buddemeier RW, Smith SV (1991) Workshop on coral bleaching, coral reef ecosystems and global change: Report on Proceedings. Maryland Sea Grant Publication, 49p
- Gates RD (1990) Seawater temperature and sublethal coral bleaching in Jamaica. *Coral Reefs* 8:192-197
- Gladfelter EH, Bythell JB, Archer S, Lewis SK, Woodbury M (1991) Impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands: I. Effect on coral community structure and diversity relative to changes in the system since 1976. In: U.S. National Park Service Special Report: Ecological studies of Buck Island Reef National Monument St. Croix, U.S. Virgin Islands: A quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites, Part I.
- Glynn PW, D'Croz L (1990) Experimental evidence for high temperature stress as the cause of El-Niño-coincident coral mortality. *Coral Reefs* 8:181-191.
- Glynn PW, Peters EC, Muscatine L (1985) Coral tissue microstructure and necrosis: relation to catastrophic coral mortality in Panama. *Dis Aquat Org* 1:29-37
- Goenaga C, Vincente VP, Armstrong, RA (1989) Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: A precursor of change in the community structure of coral reefs? *Carib J Sci* 25:59-65
- Goreau TF (1964) Mass expulsion of zooxanthellae from Jamaican reef communities after hurricane Flora. *Science* 145:383-386
- Goreau TJ, Macfarlane AH (1990) Reduced growth rate of *Montastrea annularis* following the 1987-1988 coral-bleaching event. *Coral Reefs* 8:211-215
- Hubbard DK, Parsons KM, Bythell JC, Walker NB (1991) The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, U.S. Virgin Islands - A preliminary assessment. *J Coastal Res Spec Issue No 8 Impacts of Hurricane Hugo: September 10-22, 1989*, 33-48
- Knowlton N, Weil E, Weight LA, Guzman HM (1992) Sibling species in *M. annularis*, coral bleaching, and the coral climate record. *Science* 225:330-333
- Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155-162

- Lesser MP, Stochaj WR, Tapley DW, Shick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8:225-232
- Porter JW, Fitt WK, Spero HJ, Rogers CS, White MW (1989) Bleaching in reef corals: Physiological and stable isotopic responses. *Proc Natl Acad Sci USA* 86:9342-9346
- Rogers CS (1983) Sub-lethal and lethal effects of sediments applied to common Caribbean corals in the field. *Mar Poll Bull* 14:3