ATOLL RESEARCH BULLETIN

NO. 421

LARGE-SCALE, LONG-TERM MONITORING OF CARIBBEAN CORAL REEFS: SIMPLE, QUICK, INEXPENSIVE TECHNIQUES

BY

RICHARD B. ARONSON, PETER J. EDMUNDS, WILLIAM F. PRECHT,
DIONE W. SWANSON, AND DON R. LEVITAN

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
AUGUST 1994

LARGE-SCALE, LONG-TERM MONITORING OF CARIBBEAN CORAL REEFS: SIMPLE, QUICK, INEXPENSIVE TECHNIQUES

BY

RICHARD B. ARONSON[1], PETER J. EDMUNDS[2], WILLIAM F. PRECHT[3], DIONE W. SWANSON[2] AND DON R. LEVITAN[4]

ABSTRACT

With coral cover and diversity declining on many coral reefs, a clearer understanding of large-scale reef dynamics is imperative. This paper presents a sampling program designed to quantify the sessile biotas of Caribbean reefs on large spatiotemporal scales. For each reef sampled, data are gathered along replicate, 25-m transects located within the habitat of interest. Herbivore impact is estimated by fish and echinoid censuses along the transects. High-resolution videotapes are used to estimate the percent cover of corals, algae, and other substratum occupants, and to estimate coral diversity. Finally, topographic complexity is measured along the transects. In at least some reef habitats, this index of three-dimensional structure provides a measure of the total disturbance regime, with flatter areas having been subjected to more intense, more frequent, and/or more recent sources of coral mortality. The techniques and statistical analyses described in this paper are simple, quick and inexpensive. Repeated sampling on multiple reefs will enable the investigator to detect changes in community structure and to test hypotheses of the causes of those changes.

INTRODUCTION

Coral reefs are complex, diverse, productive tropical ecosystems in which multiple physical and biological processes covary in space and time (Huston 1985). Discerning the contributions of those processes to the community structure of reefs has been and will continue to be extremely difficult. The question of the appropriate scales at which to search for pattern and process is fundamental to unraveling these multiple causal connections (Jackson 1991, 1992; Karlson and Hurd 1993). Are ecological parameters such as coral cover and diversity determined primarily by small-scale processes, such as the local level of herbivore activity (Sammarco 1980; Lewis 1986), or are larger-scale, regional disturbances more important? Such questions are becoming increasingly

---

[1] Marine Environmental Sciences Consortium, Dauphin Island Sea Lab, Dauphin Island, AL 36528; and Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.
[2] Department of Biology, California State University, Northridge, CA 91330.
[3] Reef Resources & Associates, 7310 Poinciana Court, Miami Lakes, FL 33014.
[4] Department of Biological Sciences, Florida State University, Tallahassee, FL 32306.

Manuscript received 14 October 1993; revised 22 July 1994

germane as we confront the possibility that human interference is altering coral reef ecosystems (e.g., Brown 1987).

Over the past two decades, the "health" of many coral reefs worldwide has deteriorated, as measured by indicators such as the diversity and abundance of reef-building corals (Rogers 1985; Dustan and Halas 1987; Hatcher et al. 1989; Grigg and Dollar 1990; Porter and Meier 1992; Ginsburg 1994). Hurricanes (Woodley et al. 1981; Rogers et al. 1982, 1991; Edmunds and Witman 1991; Hubbard et al. 1991; Bythell et al. 1993), coral bleaching (Oliver 1985; Brown and Suharsono 1990; Williams and Bunkley-Williams 1990; Glynn 1993), coral diseases (Gladfelter 1982; Rützler et al. 1983; Edmunds 1991), mortality of the sea urchin *Diadema antillarum* (Lessios et al. 1984; Levitan 1988; Lessios 1988; Carpenter 1990) and outbreaks of the seastar *Acanthaster planci* (Moran 1986; Endean and Cameron 1991) may all be involved. At present, it is unknown whether any or all of these problems are due to recent human activities, or whether they are part of natural, long-term trends or cycles (Brown 1987; Richards and Bohnsack 1990).

In addition, reefs are directly affected by human activities, particularly fishing, sedimentation, eutrophication and pollution (Brown 1987, 1988; Hatcher et al. 1989; Rogers 1990; Richmond 1993; Sebens 1994). These stresses reduce coral survivorship and growth and may promote macroalgal growth. Furthermore, marine pollution may increase the susceptibility of corals to disease (Brown 1988; Peters 1993).

Reef dynamics are governed by multiple causes operating on multiple scales (Grigg and Dollar 1990). For example, the recent decline in coral cover and increase in macroalgal cover on the well-studied reef at Discovery Bay, Jamaica appears to have resulted from a variety of interacting processes: Hurricane Allen (1980), which opened substratum for colonization; feeding by corallivorous snails, which increased the mortality of hurricane-fragmented corals; the *Diadema* dieoff, which reduced herbivory drastically; and a history of overfishing by humans, which had previously removed herbivorous reef fishes (Hughes et al. 1987; Knowlton et al. 1990; Hughes 1994). Likewise, the catastrophic effects of the 1982-83 El Niño event on eastern Pacific coral reefs were due to the interaction of physical changes and a variety of biological processes (Glynn 1990).

One of the greatest challenges to ecology is determining the relative importance of numerous causes to ecosystem structure and function (Quinn and Dunham 1983). Yet, even choosing the correct range of scales on which to understand coral reef dynamics seems a forbidding task. It is becoming increasingly clear that quadrat-scale observations (square meters or smaller) have less explanatory power than larger-scale observations (Jackson 1991). Those larger scales range from the landscape within a reef (hundreds of m^2 to hectares), to the area encompassing multiple reefs within a locality (hundreds of km^2), to an entire region such as the Caribbean.

The need for large-scale and long-term (>5 yr) monitoring programs for coral reefs has been emphasized over the past few years (Rogers 1988, 1990; Ogden and Wicklund 1988; D'Elia et al. 1991; Jackson 1991; Ray and Grassle 1991; Smith and Buddemeier 1992; Bythell et al. 1993; Glynn 1993; Hughes 1994), although less attention has been given to the hypotheses that should be driving the research (Hughes 1992). Few such studies have been undertaken, in part because hypotheses are so difficult to formulate and test (Hughes 1992). Such hypotheses might, for example, include an inverse relationship between the degree of disturbance and coral cover; the intermediate disturbance hypothesis (Connell 1978; Rogers 1993), which postulates that coral diversity should be highest at intermediate frequencies and intensities of disturbance; and complex relationships between herbivory, nutrients, coral and algal cover, and diversity (Littler et al. 1991; Knowlton 1992; Hughes 1994). However, with so many possible causes of community change, and with the ecological implications of each putative cause unknown, highly variable and/or controversial, it is hard to know which variables to monitor in order to test hypotheses adequately.

This paper outlines procedures for comparing coral reef community structure and disturbance regimes across space and through time, with a view toward eventually testing hypotheses such as those listed above. The methods were developed during continuing studies of four western Atlantic coral reefs: Carrie Bow Cay, on the Belizean Barrier Reef; Discovery Bay, Jamaica; and Conch and Carysfort Reefs, off Key Largo, Florida. Since funding for monitoring programs is difficult to obtain and since field time is usually limited, our goal was to create an accurate, relatively inexpensive, "rapid assessment" sampling program for Caribbean coral reefs, with sufficient statistical power to detect biologically meaningful differences. Video transects are used to describe the sessile biota, and fish and echinoid censuses provide estimates of the intensity of herbivory. Since the importance of each type of reef disturbance has not been conclusively demonstrated, we advocate combining them in a single disturbance index, topographic complexity. Topographic complexity reflects the total disturbance regime in at least some reef habitats, integrated on a time scale of years.

METHODS

1. Sampling Design

Any study that compares reefs must be standardized with respect to habitat. The design described here is for a common Caribbean fore-reef habitat: the spur-and-groove habitat of windward-facing reefs at 12-15 m depth. Ten 25-m long transects are sampled at each site. The transects are placed along the central axes of replicate, haphazardly chosen spurs. Sandy areas and the edges of the spurs are avoided. In the present study, each transect was placed on a different spur, except at Discovery Bay. A number of spurs at Discovery Bay were >25 m wide; 2 transects, spaced >10 m apart, were surveyed on some of those wide spurs. It is important to choose sites that will accommodate at least 25-30 transects, so that the transects sampled during different visits to a site will not be identical.

The use of band transects is dictated in this particular application by the elongate shape of the spurs, and in general by the desire to encompass as great an area as possible in each sample. The 25-m transect length was chosen to be as great as possible while still restricted to a narrow depth and habitat range on the spurs. A 25-m transect, when extended over a 3-m depth range, requires spurs that slope at angles of no more than 7°.

For each transect, scuba divers unreel a 25-m fiberglass surveyor's tape, laying it taught along the center of the spur. The tape is left undisturbed for 3-5 min, at which point the divers commence surveys of the mobile fauna.

2. Fish and Echinoid Censuses

Coral reef researchers have yet to agree on a single, reliable method for quantifying the activity of herbivores (Steneck 1983). The simplest measure is the abundance of herbivores, which correlates with their impact among habitats within reefs (Hay and Goertemiller 1983; Lewis and Wainwright 1985). Therefore, before the fish are disturbed further, a visual census is conducted along each transect. A diver swims along the tape at a standard slow speed, recording the number of parrotfish (Labridae, formerly Scaridae) and surgeonfish (Acanthuridae) within a visually-estimated 2 m on either side. The fishes are classified as small ($\leq$10 cm Standard Length), medium (10-25 cm), or large (>25 cm). The small transect width minimizes the underestimate of true fish population density inherent in the transect method (Sale and Sharp 1983). Divers then carefully explore the 100 m^2 area, recording the number and species identities of damselfish (Pomacentridae), as well as censusing *Diadema* and other regular echinoid species. The echinoids can be extracted from their shelters and measured (test diameter) with calipers. Size distributions of echinoid species can then be used to estimate their impacts on algal assemblages (Levitan 1988). It should be noted that daytime censuses underestimate echinoid densities; more accurate estimates can be obtained by censusing at night (e.g., Carpenter 1981, 1986).

An alternative approach is to examine the *process* of herbivory by counting the number of bites that parrotfish and surgeonfish take per unit time from small areas of algal turf (Steneck 1983). This technique is more time-consuming than counting fish. A more serious concern is that some habitats on some reefs are currently so overgrown with fleshy macroalgae that finding even a square meter of algal turf would be problematic. For example, at Discovery Bay in 1992 macroalgal cover was >90 %, coral cover was <3 %, and the cover of algal turfs, crustose coralline algae, and bare space combined was <6 % at 15 m depth (as assessed by the video technique described below; Table 1, p. 11). Large differences in the availability of algal turfs could lead to differences in fish foraging behavior, independent of fish abundance. It is important to recognize that both the abundance and bite frequency methods yield short-term "snapshots" of herbivory, which may not adequately reflect longer-term variability.

3. Percent Cover and Scleractinian Diversity

Photography provides the only practical means of sampling large areas underwater, given the time constraints of scuba diving. Littler (1980) discussed the advantages of photography over recording data *in situ*. High-resolution video technology makes the approach all the more attractive because videotaping is easier and less time-consuming than still photography. While still photographs provide better resolution than videotapes, the resolution of videotapes is adequate for work of the type described here. Videotapes enable the investigator to cover a far greater area per unit sampling effort. In addition, video exposures are automatic, continuous and do not require developing.

In this method, a diver swims slowly along the transect, videotaping a 40-cm wide swath of reef from a height of approximately 40 cm, using a high-resolution (Hi-8) video camera in an underwater housing, fitted with a wide-angle lens. A 15-cm gray plastic bar is attached to a rod that projects forward from the video housing. The bar, which is held at the level of the substratum during taping, provides scale in the videotaped images and also ensures that the camera is held a constant distance from the bottom.

Individual video frames are displayed on a high-resolution monitor in the laboratory. A clear plastic sheet with 10 random dots is laid over the monitor screen, and the sessile organisms underlying the dots are recorded (Sebens and Johnson 1991; see **Sample Sizes**, p. 8, for number of dots per frame). The videotape is then advanced to a new, non-overlapping position. Each 25-m transect yields 50 video "quadrats", for a total of 500 points per transect. The point count data are used to calculate percent cover and the Shannon-Wiener diversity index, H', for each transect. Since this and similar sampling methods tend to be biased against the inclusion of rare species, presence-absence data are also gathered for coral species by viewing the entire videotape of each transect (Chiappone and Sullivan 1991).

By holding the camera perpendicular to the substratum, swimming slowly along the transect, and using a pair of video lights (50 or 100 watts each), it is possible to produce clear stop-action images. Corals, sponges, and some gorgonians and macroalgae can be identified to species, down to a diameter of approximately 5 cm. A drawback of this method is the difficulty of distinguishing fine algal turfs, crustose coralline algae and bare space from the tapes; these are lumped into a single category, which can be resolved by closeup, still photography if desired.

Ecologists have devoted a great deal of effort to developing and comparing methods for quantifying coral reef community structure, with variable results (e.g., Loya 1978; Dodge et al. 1982; Ohlhorst et al. 1988; Chiappone and Sullivan 1991; Porter and Meier 1992). Porter and Meier (1992) examined some of the biases introduced to surface area estimates by photographic and video techniques. Such errors include non-orthographic projection, in which coral heads that stick up above the surrounding substratum are closer to the camera lens and therefore artificially enlarged, and parallax. These problems are difficult to correct (Porter and Meier 1992).

Whorff and Griffing (1992) found that point counts from video frames overestimated the percent cover of intertidal barnacles and bivalves, compared to computer image-processing of the video frames. More dots per frame yielded better percent cover estimates. On the other hand, Foster et al. (1991) concluded that point counts from photographs underestimated cover in multilayered, temperate subtidal assemblages, compared to point counts done in the field. The point count method is not as accurate as planimetry of the individual colonies in each frame or fully-automated image processing. However, planimetry is so time-consuming as to be impractical. Image processing is also difficult at present because subtle color and pattern differences must be detected; most corals and algae are quite similar in color, and reasonably-priced, hand-held video lights provide limited color saturation. The point count method is capable of detecting significant among-site differences in percent coral cover and diversity (see Sample Sizes, p. 8). Video has its problems and biases like other techniques, but it remains a simple, cost-effective comparative method.

Another concern is the seasonality of macroalgal growth (Carpenter 1981; Hughes et al. 1987). Seasonal changes within a site could change estimates of coral cover, as more or less living coral is obscured by the algae (J. C. Lang, personal communication). The constraints of time, logistics and funding do not always permit the investigator to standardize sampling by season, and the error in coral cover estimates caused by seasonal variations in algal growth are unknown. In the present study, Carrie Bow Cay was sampled in the late spring, Discovery Bay in the winter, and Conch and Carysfort Reefs in the fall of 1992. If algal growth is maximal in the summer and algal destruction by storms is maximal in the winter, then, all other things being equal, macroalgal cover, and the error in coral cover estimates due to macroalgal cover, should have been greatest in Florida (after the summer's algal growth), intermediate at Carrie Bow Cay (before the summer's growth), and least at Discovery Bay (during the stormy season). In fact, macroalgal cover was highest at Discovery Bay, intermediate at Conch Reef and Carrie Bow Cay, and lowest at Carysfort Reef (Table 1, p. 11). In this study, differences in macroalgal cover among sites apparently outweighed any error in coral cover estimates associated with seasonal differences.

The species diversity of scleractinian corals is evaluated as species richness, S, and as the Shannon-Wiener index, H'. S is measured for each site as the asymptote of the rarefaction curve (cumulative species numbers plotted against number of transects videotaped). Species richness is not calculated for each transect since reefs with lower coral cover are expected to have lower S per transect simply because fewer colonies are sampled (Magurran 1988). The Shannon-Wiener index is calculated for each transect as $H'=-\Sigma(p_i[\ln p_i])$, where p_i is the proportion of the ith species in the sample. Vast size differences among coral colonies and colony fragmentation and fusion obscure the meaning of H' calculated from numbers of "individuals". Unless the investigator is prepared to establish the genetic identity of all ramets, we recommend H' indices based on areal coverage for a general characterization of reef communities.

4. An Integrated Measure of Disturbance

Historical records of disturbance do not exist for most coral reefs. Even where such records are available, there is no obvious way to sum the different disturbances to reflect the total disturbance regime; one cannot simply score three disturbance points for a hurricane and two for a bleaching event. We present topographic complexity as a technique for measuring disturbance, along with its rationale and sources of error, so that the individual investigator can decide whether or not it will be useful.

Topographic complexity is measured by carefully conforming a 5-m length of fine brass chain to the substratum adjacent to the central part of each transect tape. The chain is conformed to the finest topographic features that the 17-mm links permit; it is carefully inserted into small cavities and into the spaces within thickets of foliose and branching corals. The 5-m chain length was chosen so that the procedure could be completed in a reasonable length of time (10-15 min); the chain must be carefully straightened before it is conformed to the substratum. A complexity index, C, is calculated as $C=1-d/l$, where d is the horizontal distance covered by the conformed chain (measured against the transect tape) and l is its length when fully extended (e.g., Risk 1972; Rogers et al. 1982; Aronson and Harms 1985; Hubbard et al. 1990; Connell and Jones 1991).

Disturbances that lead to the partial or complete mortality of coral colonies decrease this topographic complexity. Hurricanes decrease complexity directly by toppling branching and head corals (e.g., Rogers et al. 1982; Kaufman 1983), although this is not true in all reef habitats (Rogers et al. 1991; see below). In addition, once dead coral skeletons are exposed by a disturbance of any sort, they are colonized by bioeroders, including bivalves, sponges, sipunculans, polychaetes and echinoids, which break down the reef framework (Hutchings 1986). Disturbances that cause partial to complete mortality of coral colonies, provide fresh substratum for bioeroders, and in fact lead to increased bioerosion rates include hurricanes (Moran and Reaka-Kudla 1991), El Niño-induced coral bleaching (Glynn 1990) and damselfish territoriality (Kaufman 1977), although damselfish can have a negative effect on bioerosion by excluding echinoids from their territories (Eakin 1988; Glynn 1990). Naturally and artificially high levels of nutrients on reefs also increase bioerosion rates (Highsmith 1980; Tomascik and Sander 1987; Hallock 1988). Overfishing off the coast of Kenya increased bioerosion and decreased topographic complexity as well, by releasing burrowing echinoids from predation (McClanahan and Shafir 1990). Furthermore, coralline algae, which are important in cementing the reef framework (and thus important in maintaining topographic complexity), are suppressed by macroalgae, which are promoted by nutrient input and the removal of herbivores (Littler and Littler 1985; Lewis 1986; Carpenter 1990). Coral growth, by contrast, generally increases topographic complexity at the scale under consideration (Dahl 1976). To a first approximation *in certain situations*, the topographic complexity index should be inversely related to total disturbance, with lower values indicating flatter terrain and suggesting more frequent, more recent and/or more intense disturbance.

No measure of disturbance is free of bias, including topographic complexity. One source of error is that coral mortality does not lead to the immediate loss of structure because bioerosion takes time. In addition to this time lag, the relationship between coral mortality and physical complexity is not always direct. Some coral species can survive breakage in storms and even reproduce asexually as a result (*Acropora* spp.: Highsmith et al. 1980; Tunnicliffe 1981); low complexity accompanied by high coral cover is a possible consequence. Conversely, bioerosion following partial or complete mortality of massive coral heads could initially increase complexity rather than decrease it.

While these problems introduce error to estimates of disturbance, that error should be minimal in the spur-and-groove down to 15 m depth. Throughout Florida and the Caribbean, those habitats are now or were formerly (before disturbance) dominated by branching or other delicate coral species, including *Acropora cervicornis* (Belize, Jamaica, the Florida Keys and many other localities), branching *Porites* spp. (some reefs in St. Croix, U. S. Virgin Islands), and *Agaricia tenuifolia* (Belize). For all of these corals, complexity in their habitats should decline rapidly following mortality. Topographic complexity would not be as useful an indicator of disturbance in certain other reef habitats, such as shallow-water hardground areas, which are characterized by isolated head corals on limestone pavements. Similarly, deep-reef areas dominated by corals with a plating morphology could have high coral cover but low topographic complexity.

Another potential complication in separating disturbance and herbivory effects is an observed positive correlation of fish abundance and topographic complexity. Herbivorous (and other) fish avoid low-relief areas, including those which have been disturbed (Hay and Goertemiller 1983; Kaufman 1983). Areas with fewer herbivores may experience increased algal cover, decreased coral cover, and increased bioerosion, leading to even flatter topography (reviewed in Hutchings 1986). This feedback loop does not appear to be a problem in the reefs studied (see **Sample Sizes**).

SAMPLE SIZES

The techniques outlined above are intended for testing hypotheses on large scales, ranging from a landscape scale (among spurs in the spur-and-groove habitat within reefs), to a subregional scale (among reefs within an area such as the Florida Keys), to a regional scale (among reefs throughout the Caribbean). In order to determine the appropriate sample sizes for statistical comparisons among reefs, preliminary surveys were conducted during 1992-93 in the spur-and-groove habitats of the four sites mentioned in the **Introduction**. Ten transects were completed at each site, and an additional 10 transects were videotaped only (see comments below on species richness). Two investigators can sample a site in 3-4 days, assuming 2-3 "full" transects per dive and 2 dives per day. Where funding and equipment are available, the use of nitrox diving techniques increases bottom time substantially, increasing the number of transects that can be completed per dive.

Percent cover and *H'* are estimated by point counts from each of 10 video transects per site. Fifty non-overlapping, video frame "quadrats" cover most of the length of the transect videotape. The question is how many random dots to use per video frame. For each of the 50 frames in each of the 10 Carrie Bow Cay and 10 Discovery Bay transects that were analyzed, the substratum occupants under 25 random dots were recorded, in groups of 5 dots. The means and standard deviations of percent cover of hard corals and *H'* for scleractinians remained virtually unchanged when the number of dots used was ≥ 10 (Figs. 1, 2). Therefore, an appropriate sampling protocol is 50 video frame "quadrats" per transect and 10 random dots per video frame. Each 500-dot data set constitutes a single sample, requiring 2-3 hours for trained personnel to extract from the videotaped transect. Because each video transect is a single sample, increasing the number of random dots per frame yields no advantage in terms of statistical power.

The only parameter for which more than 10 video transects per reef are required is species richness, *S*. Plots of cumulative *S* for Conch Reef and Discovery Bay reach their asymptotes after 9 and 15 transects, respectively, and the curves for Carysfort Reef and Carrie Bow Cay both asymptote after 13 transects (Fig. 3). The difference in sample sizes required to estimate *H'* and *S* is due to rare species, which add little to the coral cover from which *H'* is calculated. We recommend 20 transects to estimate species richness for a site.

The percent cover and topographic complexity data were arcsine-transformed and the fish census data logarithmically transformed, so that they conformed to the assumptions of parametric statistics (Sokal and Rohlf 1981). The square root transformation, often recommended for data in the form of counts (Sokal and Rohlf 1981), was not used on the census data. This transformation assumes that the data in question are Poisson distributed, but count data are not necessarily so distributed. Transformation of the *H'* data was unnecessary because *H'* is normally distributed (Magurran 1988) and the data collected in this study were homoscedastic. (See Clarke and Green [1988] for a detailed discussion of data transformations.)

A one-way analysis of variance (ANOVA) on the arcsine-transformed percent coral cover data showed significant among-site differences ($p<0.0005$; Table 1). Tukey HSD multiple comparisons revealed the following differences between sites, listed in order of increasing cover (<, significantly less than; =, not significantly different from at $\alpha=0.05$):

Discovery Bay < Conch Reef < Carrie Bow Cay = Carysfort Reef.

The ANOVA results were used to estimate the minimum detectable difference, δ, in transformed percent cover at a significance level of $\alpha=0.05$ with a power of $1-\beta=0.90$ (Zar 1984; Clarke and Green 1988). For an ANOVA comparing 4 sites, $\delta=0.13$. This calculated δ was then used to estimate the range of the minimum detectable difference in actual (untransformed) percent cover by the following procedure:

1. adding δ to the (transformed) lowest mean, back-transforming that value to actual percent cover, and taking the difference between the back-transformed value and

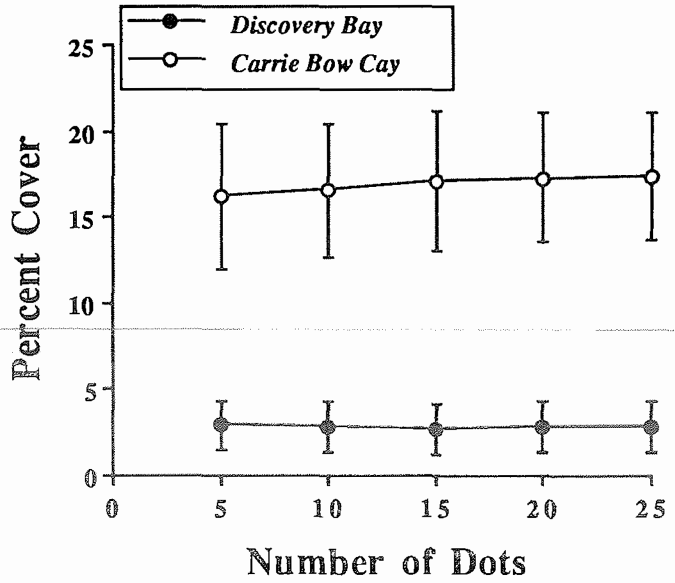

Fig. 1. Percent cover of hard corals as a function of the number of random dots used per video frame in transsects from Discovery Bay, Jamaica and Carrie Bow Cay, Belize. Fifty frames were analyzed in each of 10 transects for each site. Error bars represent standard deviations.

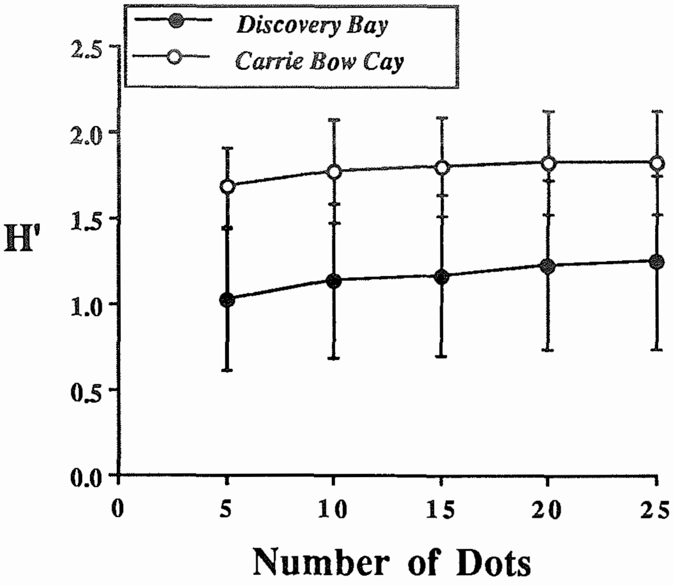

Figure 2. Shannon-Wiener diversity of Scleractinia, *H'*, as a function of the number of random dots per video frame in transects from Discovery Bay and Carrie Bow Cay. Sample sizes as in Fig. 1. Error bars represent standard deviations.

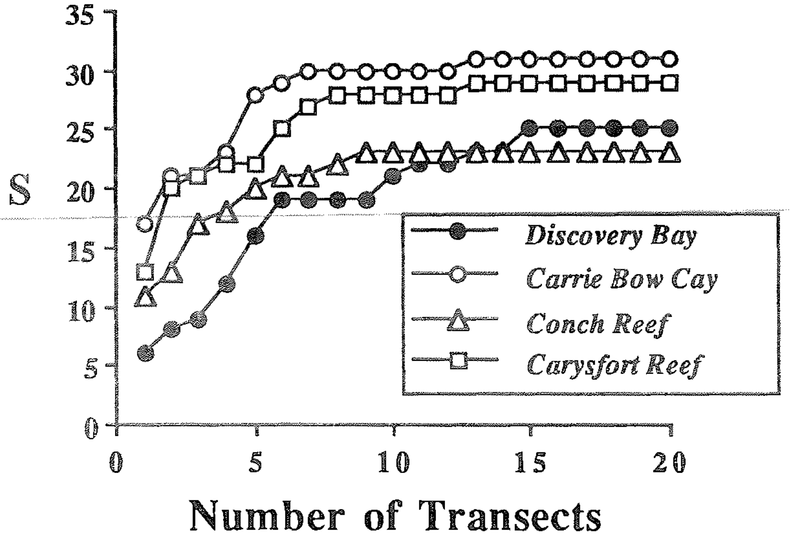

Figure 3. Cumulative species richness curves for scleractinian corals in video transects from the four sites surveyed.

Table 1. Means ± standard deviations of parameters measured in 1992 at four coral reef sites.

	Field Site			
Parameter	Discovery Bay	Carrie Bow Cay	Conch Reef	Carysfort Reef
A. Percent Cover				
Hard corals	2.8±1.5	16.7±3.8	6.4±4.0	21.2±7.7
Macroalgae	91.2±4.3	63.2±6.9	65.7±8.8	40.9±12.0
B. Scleractinian Diversity				
H'	1.22±0.28	1.81±0.29	1.04±0.55	1.21±0.58
C. Integrated Disturbance Index				
C	0.184±0.078	0.403±0.089	0.194±0.077	0.335±0.106
D. Fish Abundance (number/transect)				
Parrotfish	31.5±10.0	24.6±7.4	17.0±8.3	34.2±15.8
Damselfish	7.5±4.5	38.5±7.9	58.5±14.2	18.5±7.8

the observed (untransformed) lowest mean, and

2. subtracting δ from the (transformed) highest mean, back-transforming that value to actual percent cover, and taking the difference between the observed (untransformed) highest mean and the back-transformed value.

The minimum detectable difference ranged from 5.2 % where coral cover is minimal (a few percent cover) to 9.8 % at high values of coral cover (approximately 20 % cover; Table 1). In fact, *a posteriori* comparisons after ANOVA on the arcsine-transformed percent cover data detected a significant difference between the sites with the two lowest means, Discovery Bay and Conch Reef, which differed by only 3.6 % cover (Table 1). If the study were expanded to include surveys of 10 sites instead of just 4, the minimum detectable difference would range from 6.3 to 11.1 % cover.

A one-way ANOVA on the H' data also revealed significant differences among sites ($p<0.005$), which are listed in the same format as for percent coral cover:

Conch Reef = Carysfort Reef = Discovery Bay < Carrie Bow Cay.

A power analysis gave $\delta=0.81$ for an ANOVA comparing 4 sites and $\delta=0.93$ for an ANOVA comparing 10 sites, at $\alpha=0.05$ and $1-\beta=0.90$. *A posteriori* comparisons detected a significant difference between the sites with the two highest means, Carrie Bow Cay and Discovery Bay, which actually differed in mean H' by only 0.57. The video method thus provides a statistically powerful tool for detecting differences in coral cover and diversity among sites.

The estimates of percent cover and H' for Discovery Bay were compared to estimates obtained independently at the same time (during the winter of 1992) by the linear point-intercept (LPI) method (Ohlhorst et al. 1988). A 10-m surveyor's tape was positioned randomly at 15 m depth, and the sessile organisms underlying the tape were recorded every 10 cm, for a total of 100 points per transect. The LPI method gave a higher estimate of coral cover (mean 4.4±0.9 SD, based on 5 transects) than the video transects (Table 1), but the two estimates were not significantly different by Student's t-test ($t_s=2.207$, df=13, $0.05<p<0.10$). In contrast, the LPI method underestimated H' (mean 0.72±0.18 SD) compared to the video transects ($t_s=3.577$, df=13, $p<0.005$). The significant difference in species diversity obtained by the two methods is largely an artifact of the number of points used to calculate H'. Since coral cover was so low at Discovery Bay, the H' value calculated for each 100-point LPI transect was based on a maximum of only 5 points overlying coral. With 5 times as many points per sample, undersampling corals was not a problem in the video transects (Fig. 2).

Hughes (1994) employed line-intercept transects to document reef dynamics at Discovery Bay at 10 m depth. Using a 10-m surveyor's tape, he recorded the lengths of tape overlying different species. His value for coral cover in 1993, approximately 3 %, agrees with the mean reported for 15 m depth in Table 1. In addition, Hughes (1994) monitored permanent photoquadrats at a site near Discovery Bay. In 1993, he obtained values of coral and macroalgal cover at 15-20 m depth that are nearly identical to those listed in Table 1 for Discovery Bay.

Analysis of the topographic complexity data showed that the chain method is capable of detecting significant differences among sites (ANOVA, $p < 0.0005$):

Discovery Bay = Conch Reef < Carysfort Reef = Carrie Bow Cay.

Interestingly, the four sites display the same qualitative differences in topographic complexity that they do in coral cover. Jackson (1991) used coral cover as a proxy for disturbance, with higher coral cover indicating a lower level of disturbance. Our suggested measure of disturbance, topographic complexity, agrees with Jackson's (1991) for the reefs studied. We prefer the complexity index, because it avoids the circularity of using Jackson's (1991) method to test for a causal relationship between disturbance and coral cover.

The log-transformed abundance of damselfish differed from site to site (ANOVA, $p < 0.0005$):

Discovery Bay < Carysfort Reef < Carrie Bow Cay = Conch Reef.

Apart from damselfish, which actually promote algal growth, parrotfish were by far the most abundant herbivorous fishes in the spur-and-groove habitat (Lewis and Wainwright 1985); 82-98 % of the herbivores were parrotfish in censuses at the four sites. Surgeonfish and echinoids were virtually absent, and they were ignored in this analysis. Among-site differences were also detected in log-transformed parrotfish abundance (ANOVA, $p < 0.0005$):

Conch Reef < Carrie Bow Cay = Discovery Bay = Carysfort Reef.

Multiplying parrotfish abundance in the three size classes by average length to calculate "biomass" did not alter these patterns. As suggested in the section on fish and echinoid censuses, parrotfish and surgeonfish abundance can be highly variable, and counts of these mobile herbivores should be interpreted with caution.

For long-term studies of particular reefs, our protocol has distinct advantages over the traditional approach of permanent transects or quadrats. The marine environment is highly variable, and independent sampling during each site visit (factorial, with time as a factor; Green 1979) encompasses more of that variation than a permanent transect approach (repeated measures). While it is true that independent sampling makes it more difficult to detect significant effects, conclusions are not bound to the particular histories of individual organisms and the particular areas of reef framework on which they live. An independent/factorial approach thus gives investigators increased scientific confidence in the signals detected, but less statistical power to detect those signals, than a permanent/repeated measures approach. Furthermore, since the independent sampling approach avoids the expensive and time-consuming procedures involved in permanently marking study areas, it is more practical for reef monitoring in developing countries.

CONCLUSION

The methods outlined in this paper were developed to combine logistical ease, low cost and statistical power. The point-count data extracted from the videotapes can be taken beyond univariate statistical treatments to more sophisticated, multivariate ordinations and tests. Differences in species composition among reefs can then be considered in light of differences in geomorphology and oceanography as well as differences in disturbance regime.

Coral reefs have been central to the development of ecological theory (Connell 1978), yet we still need basic information on their dynamics (Jackson 1991; Ginsburg 1994). As reef ecosystems become increasingly threatened, commitment to large-scale management is growing in the United States and abroad. However, effective management policy cannot be created without an understanding of reef dynamics and the effects of disturbance. The methods described in this paper can provide the necessary information. Large-scale and long-term data collected now will be of particular value if and when conditions change (e.g., recovery of *Diadema* populations, future hurricanes).

ACKNOWLEDGEMENTS

This research was supported by the Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) Program and by NOAA's National Undersea Research Center at the University of North Carolina, Wilmington (NURC-UNCW). Additional support was provided by the Institute of Marine and Coastal Sciences (IMCS) at Rutgers University, the Smithsonian Institution Women's Committee and Northeastern University's East/West Program. Sony Corporation of America generously provided an underwater video system, and S. L. Miller lent us his personal video equipment. G. Sternschein invented a superb little device to hold the video scale rod and manufactured it in his machine shop in Glasgow, Scotland. We thank M. A. Buzas, J. C. Bythell, J. H. Connell, G. D. Dennis III, P. Dustan, C. M. Eakin, L.-A. Hayek, J. C. Lang, M. M. Littler, J. B. C. Jackson, I. G. Macintyre, S. L. Ohlhorst, S. R. Smith and R. S. Steneck for their advice and comments. We are also grateful to S. L. Miller and the staff of NURC-UNCW's Florida Research Program, K. Ruetzler, and J. D. Woodley for providing laboratory space and logistical support in the Florida Keys, Belize, and Jamaica, respectively. Research in the Florida Keys was conducted under National Marine Sanctuary Permits KLNMS-19-92 and FKNMS-14-93. This is CCRE Contribution No. 417, IMCS Contribution No. 94-21, and Contribution No. 560 of the Discovery Bay Marine Laboratory, University of the West Indies.

LITERATURE CITED

Aronson, R. B. and C. A. Harms. 1985. Ophiuroids in a Bahamian saltwater lake: the ecology of a Paleozoic-like community. Ecology 66:1472-1483.

Brown, B. E. 1987. Worldwide death of corals--natural cyclic events or man-made pollution? Mar. Poll. Bull. 18:9-13.

Brown, B. E. 1988. Assessing environmental impacts on coral reefs. Proc. 6th Int. Coral Reef Symp., Australia 1:77-80.

Brown, B. E. and 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, J. C., M. Bythell and E. H. Gladfelter. 1993. Initial results of a long-term coral reef monitoring program: impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. J. Exp. Mar. Biol. Ecol. 172:171-183.

Carpenter, R. C. 1981. Grazing by *Diadema antillarum* Philippi and its effects on the benthic algal community. J. Mar. Res. 39:749-765.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56:345-363.

Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population dynamics and coral reef algal communities. Mar. Biol. 104:67-77.

Chiappone, M. and K. M. Sullivan. 1991. A comparison of line transect versus linear percentage sampling for evaluating stony coral (Scleractinia and Milleporina) community similarity and area coverage on reefs of the central Bahamas. Coral Reefs 10:139-154.

Clarke, K. R. and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser. 46:213-226.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell, S. D. and G. P. Jones. 1991. The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. J. Exp. Mar. Biol. Ecol. 151:271-294.

Dahl, A. L. 1976. Generation of photosynthetic surface area by coral reef algae. Micronesica 12:43-47.

D'Elia, C. F., R. W. Buddemeier and S. V. Smith. 1991. Workshop on coral bleaching, coral reef ecosystems and global change: report of proceedings. Maryland Sea Grant College, College Park, MD.

Dodge, R. E., A. Logan and A. Antonius. 1982. Quantitative reef assessment studies in Bermuda: a comparison of methods and preliminary results. Bull. Mar. Sci. 32:745-760.

Dustan, P. and J. C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974-1982. Coral Reefs 6:91-106.

Eakin, C. M. 1988. Avoidance of damselfish lawns by the sea urchin *Diadema mexicanum* at Uva Island, Panama. Proc. 6th Int. Coral Reef Symp., Australia 2:21-26.

Edmunds, P. J. 1991. Extent and effect of Black Band Disease on a Caribbean reef. Coral Reefs 10:161-165.

Edmunds, P. J. and J. D. Witman. 1991. Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St. John, U. S. Virgin Islands. Mar. Ecol. Prog. Ser. 78:201-204.

Endean, R. and A. M. Cameron. 1991. *Acanthaster planci* population outbreaks. Pages 419-437 in Z. Dubinsky, ed. Ecosystems of the world 25: coral reefs.

Elsevier, Amsterdam.

Foster, M. S., C. Harrold and D. D. Hardin. 1991. Point versus photo quadrat estimates of the cover of sessile marine organisms. J. Exp. Mar. Biol. Ecol. 146:193-203.

Ginsburg, R. N., compiler. 1994. Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL. 420 pp.

Gladfelter, W.B. 1982. White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull. Mar. Sci. 32:639-643.

Glynn, P. W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. Pages 55-129 in P. W. Glynn, ed. Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier, Amsterdam.

Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12:1-17.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York, NY. 257 pp.

Grigg, R. W. and S. J. Dollar. 1990. Natural and anthropogenic disturbance on coral reefs. Pages 439-452 in Z. Dubinsky, ed. Coral reefs: ecosystems of the world 25. Elsevier, Amsterdam.

Hallock, P. 1988. The role of nutrient availability in bioerosion: consequences to carbonate buildups. Palaeogeogr. Palaeoclimatol. Palaeoecol. 63:275-291.

Hatcher, B. G., R. E. Johannes and A. I. Robertson. 1989. Review of research relevant to the conservation of shallow tropical marine ecosystems. Oceanogr. Mar. Biol. Annu. Rev. 27:337-414.

Hay, M. E. and T. Goertemiller. 1983. Between-habitat differences in herbivore impact on Caribbean coral reefs. Pages 97-102 in M. L. Reaka, ed. The ecology of deep and shallow coral reefs. NOAA Symp. Ser. Undersea Res., Vol. 3, Rockville, MD.

Highsmith, R. C. 1980. Geographic patterns of coral bioerosion: a productivity hypothesis. J. Exp. Mar. Biol. Ecol. 46:177-196.

Highsmith, R. C., A. C. Riggs and C. M. D'Antonio. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322-329.

Hubbard, D. K., A. I. Miller and D. Scaturo. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): applications to the nature of reef systems in the fossil record. J. Sedim. Petrol. 60:335-360.

Hubbard, D. K., K. M. Parsons, J. C. Bythell and N. D. Walker. 1991. The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, U. S. Virgin Islands--a preliminary assessment. J. Coast. Res., Spec. Issue 8:33-48.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551.

Hughes, T. P. 1992. Monitoring of coral reefs: a bandwagon. Reef Encounter 11:9-12.

Hughes, T. P., D. C. Reed and M.-J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. J. Exp. Mar. Biol. Ecol. 113:39-59.

Huston, M. A. 1985. Patterns of species diversity on coral reefs. Ann. Rev. Ecol. Syst. 16:149-177.

Hutchings, P. A. 1986. Biological destruction of coral reefs: a review. Coral Reefs 4:239-252.

Jackson, J. B. C. 1991. Adaptation and diversity of reef corals. BioScience 41:475-482.

Jackson, J. B. C. 1992. Pleistocene perspectives of coral reef community structure. Amer. Zool. 32:719-731.

Karlson, R. H. and L. E. Hurd. 1993. Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12:117-125.

Kaufman, L. S. 1977. The three spot damselfish: effects on benthic biota of Caribbean coral reefs. Proc. 3rd Int. Coral Reef Symp., Miami 1:560-564.

Kaufman, L. S. 1983. Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. Coral Reefs 2:43-47.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. Amer. Zool. 32:674-682.

Knowlton, N., J. C. Lang and B. D. Keller. 1990. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Smithson. Contrib. Mar. Sci. 31: 1-25.

Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Ann. Rev. Ecol. Syst. 19:371-393.

Lessios H. A., D. R. Robertson and J. D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226:335-337.

Levitan, D. R. 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U. S. Virgin Islands. J. Exp. Mar. Biol. Ecol. 119:167-178.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol. Monogr. 56:183-200.

Lewis, S. M. and P. C. Wainwright. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. J. Exp. Mar. Biol. Ecol. 87:215-228.

Littler, M. M. 1980. Southern California rocky intertidal ecosystems: methods, community structure and variability. Pages 565-608 in J. H. Price, D. E. G. Irvine and W. F. Farnham, eds. The shore environment. Volume 2: ecosystems. Systematics Assoc. Spec. Vol. 17A, Academic Press, London.

Littler, M. M. and D. S. Littler. 1985. Factors controlling relative dominance of primary producers on biotic reefs. Proc. 5th Int. Coral Reef Cong., Tahiti 4:35-39.

Littler, M. M., D. S. Littler and E. A. Titlyanov. 1991. Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. Coral Reefs 10:199-209.

Loya, Y. 1978. Plotless and transect methods. Pages 197-217 in D. R. Stoddart and R. E. Johannes, eds. Coral reefs: research methods. Unesco Monogr. on Oceanogr. Methodology 5, Paris.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ. 179 pp.

McClanahan, T. R. and S. H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83:362-370.

Moran, D. P. and M. L. Reaka-Kudla. 1991. Effects of disturbance: disruption and enhancement of coral reef cryptofaunal populations by hurricanes. Coral Reefs 9:215-224.

Moran, P. J. 1986. The *Acanthaster* phenomenon. Oceanogr. Mar. Biol. Annu. Rev. 24:379-480.

Ogden, J. C. and R. Wicklund, eds. 1988. Mass bleaching of reef corals in the Caribbean: a research strategy. NOAA Natl. Undersea Res. Progr. Res. Rep. 88-2. 51 pp.

Ohlhorst, S. L., W. D. Liddell, R. J. Taylor and J. M. Taylor. 1988. Evaluation of reef census techniques. Proc. 6th Int. Coral Reef Symp., Australia 2:319-324.

Oliver, J. 1985. Recurrent seasonal bleaching of corals on the Great Barrier Reef. Proc. 5th Int. Coral Reef Cong., Tahiti 4:201-206.

Peters, E. C. 1993. Diseases of other invertebrate phyla: Porifera, Cnidaria, Ctenophora, Annelida, Echinodermata. Pages 393-449 in J. A. Couch and J. W. Fournie, eds. Pathobiology of marine and estuarine organisms. CRC Press, Boca Raton, FL.

Porter, J. W. and O. W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. Amer. Zool. 32:625-640.

Quinn, J. F. and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. Am. Nat. 122:602-617.

Ray, G. C. and J. F. Grassle. 1991. Marine biological diversity. BioScience 41:453-457.

Richards, W. J. and J. A. Bohnsack. 1990. The Caribbean Sea: a large marine ecosystem in crisis. Pages 44-53 in K. Sherman, L. M. Alexander and B. D. Gold, eds. Large marine ecosystems: patterns, processes, and yields. AAAS, Washington, DC.

Richmond, R. H. 1993. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. Amer. Zool. 33:524-536.

Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull. 153:1-6.

Rogers, C.S. 1985. Degradation of Caribbean and Western Atlantic coral reefs and decline of associated fisheries. Proc. 5th Int. Coral Reef Cong., Tahiti 6:491-496.

Rogers, C. S. 1988. Recommendations for long-term assessment of coral reefs: U. S. National Park Service initiates regional program. Proc. 6th Int. Coral Reef Symp., Australia 2:399-403.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation.

Mar. Ecol. Prog. Ser. 62:185-202.

Rogers, C. S. 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. Coral Reefs 13:127-137.

Rogers, C. S., L. N. McLain and C. R. Tobias. 1991. Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. Mar. Ecol. Prog. Ser. 78:189-199.

Rogers, C. S., T. H. Suchanek and F. Pecora. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U. S. Virgin Islands. Bull. Mar. Sci. 32:532-548.

Rützler, K., D. L. Santavy and A. Antonius. 1983. The Black Band Disease of Atlantic reef corals. III. Distribution, ecology and development. P. S. Z. N. I: Mar. Ecol. 4:329-358.

Sale, P. F. and B. J. Sharp. 1983. Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37-42.

Sammarco, P. W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. 45:245-272.

Sebens, K. P. 1994. Biodiversity of coral reefs: what are we losing and why? Amer. Zool. 34:115-133.

Sebens, K. P. and A. S. Johnson. 1991. Effects of water movement on prey capture and distribution of reef corals. Hydrobiologia 226:91-101.

Smith, S. V. and R. W. Buddemeier. 1992. Global change and coral reef ecosystems. Ann. Rev. Ecol. Syst. 23:89-118.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd edition. Freeman, San Francisco, CA. 859 pp.

Steneck, R. S. 1983. Quantifying herbivory on coral reefs: just scratching the surface and biting off more than we can chew. Pages 103-111 in M. L. Reaka, ed. The ecology of deep and shallow coral reefs. NOAA Symp. Ser. Undersea Res., Vol. 1, Rockville, MD.

Tomascik, T. and F. Sander. 1987. Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Mar. Biol. 94:53-75.

Tunnicliffe, V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. Proc. Natl. Acad. Sci. U.S.A. 78:2427-2431.

Whorff, J. S. and L. Griffing. 1992. A video recording and analysis system used to sample intertidal communities. J. Exp. Mar. Biol. Ecol. 160:1-12.

Williams, E. H., Jr. and L. Bunkley-Williams. 1990. The world-wide coral reef bleaching cycle and related sources of coral mortality. Atoll. Res. Bull. 335:1-71.

Woodley, J.D. and 19 others. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214:749-755.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice Hall, Englewood Cliffs, NJ. 718 pp.