

Temporal change in hard substrate communities 10-250 m, the Bahamas

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ABSTRACT

Fine-scale change in hard-substrate community structure was determined through repeat photography of natural substrates and artificial settling panels over a three year period and along a depth gradient of 10-250 m off Lee Stocking Island, the Bahamas. Indices were developed to address temporal changes in substrate components, including percent areas occupied and addition or loss of individuals or colonies. Overall values for change were relatively low at 10 m depth, increased to a maximum between 30 and 50 m, and then declined with increasing depth to 250 m. Numbers of fish grazing scars counted on artificial settling panels were positively correlated with the loss index and negatively correlated with algal cover, suggesting that fish are a major contributor to the observed temporal changes in the sessile community between 10-50 m. Dominant substrate components shifted from algae to corals to sponges with increasing depth. Although correlations between change indices and hard-substrate community structure suggest an association between intermediate values of change and high species diversity, a simple causal relationship between agents (wave action, fish grazing) of fine-scale change and community structure was not demonstrated. Instead, a complex interplay of abiotic and biotic disturbance forces, diminishing light levels, and changing phyletic dominance accompanied by shifting tradeoffs in competitive abilities occurs along the bathymetric gradient.

Keywords Temporal change, Disturbance, Reef communities, Bahamas, Hard substrates

Introduction

Work by Sale (1977) and Connell (1978) suggested that shallow reefs actually experience varying recruitment and moderate to high levels of disturbance and, as such, represent nonequilibrium systems. Although quantitative data on long-term changes in reef communities are lacking for many localities, results to date support the premise that shallow-reef communities are subject to moderate to high levels of both biotic and abiotic disturbance (Hughes et al. 1985, Liddell and Ohlhorst 1986, 1992, Dustan and Halas 1987, Jaap et al. 1988, Hughes 1989, Knowlton et al. 1990, Glynn and Colgan 1992). These observations have led to the widespread adoption of the Intermediate Disturbance Hypothesis (Grime 1973, Connell 1978) to explain the relatively high diversities exhibited by shallow-water coral reef communities.

Many of the agents of physical and biotic disturbance on coral reefs are strongly influenced by depth. The effects of storms are largely limited to less than 30 m to 40 m depth. In addition, grazing and bioerosion by fish and invertebrates are largely confined to the relatively shallow reef. Papers by Bak and Luckhurst (1980), Porter et al. (1981) and Hughes and Jackson (1985) appear to support the above observations and demonstrate that change over time in benthic communities is much greater in shallow coral assemblages (10 m to 20 m) than in deeper (30 m to 40 m) coral assemblages.

If the high diversity of shallow coral reef communities is dependent upon intermediate rates of disturbance and if disturbance levels are greater in shallow water than in deep, a logical prediction might be that deeper-water communities (> 30 m) would exhibit lower diversity. Despite significant differences in ambient environments, species compositions and, presumably,

disturbance frequency, data from Jamaica suggest that the diversity of deep-water communities remains relatively high from 15 m to near the limits of available hard substrata at approximately 100 m (Liddell and Ohlhorst 1988, Ohlhorst and Liddell 1988). Possible conclusions to be drawn from the above observations are: 1) alternate agents of disturbance, such as high or episodic sedimentation or detachment, may serve to maintain high diversity in deep-reef habitats; or 2) the patterns of diversity in deep-reef habitats are not adequately explained by intermediate levels of disturbance alone. Perhaps diversity in deep-reef settings is more dependent upon biotic interactions or life history phenomena.

Data on rates of change of community composition or spatial arrangement, frequently used as a surrogate measure of disturbance (Bak and Luckhurst 1980; Petraitis et al. 1989), in coral reef environments are lacking for depths below 40 m. The present study examines change occurring within benthic communities along a fairly extensive depth gradient (10 m to 250 m). The primary hypothesis addressed is that fine-scale change varies, in some general pattern, with depth. An assumption associated with this hypothesis is that disturbance (both biotic and abiotic) is a major contributor to this change.

Methods

Study site

The study was conducted from the Caribbean Marine Research Center laboratory on Lee Stocking Island, the Bahamas (23°46'N Lat., 76°06' W Long.). Data were collected along two permanent transects, "AB" and "BA", established by CMRC. Sites were located at 10 m, 20 m and 30 m (accessed by SCUBA) and at 50 m, 75 m, 100 m, 150 m, 200 m and 250 m (accessed by the submersible Nekton Gamma).

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Treatments

Data on fine-scale spatial change were gathered through repeat photography of permanently-marked natural substrate (control plots) and long-term settling panels.

Control plots

At each study site four to eight control plots (35 cm x 55 cm) were selected as representative of the surrounding substrate and marked. Shallow plots (10 m to 30 m) were generally located on roughly horizontal surfaces. Plots located below 30 m were oriented vertically.

Settlement panels

Long-term settlement panels consisted of 5 cm x 25 cm x 45 cm slabs composed of Bahamian Portland Cement mixed with local carbonate sand. These panels were affixed to the bottom for the duration of the study (c.f. Hirata 1992). A minimum of four panels were established at each depth site. Shallow panels were generally oriented horizontally. Panels deployed below 30m were oriented vertically.

Panels and plots were photographed at approximately 1:15 scale with 35 mm transparency film (approx. 0.2 m² area ea.), allowing the resolution of objects as small as 1 mm. Photography of controls and panels began in 1993 and was repeated in 1994, 1995 and 1996. Photography of the panels allowed a coarse evaluation of recruitment and succession on substrates lacking a prior "biotic history" (Hughes 1989). As such, the results of this treatment might represent the response of the local community to "extreme" or "severe" disturbance events (community set back to "zero").

Data analysis

Control plots

All transparencies were digitally scanned with a Polaroid slide scanner and saved as tagged-image file format (TIFF) files (3.5 to 8 megabytes). Sequential transparencies were adjusted as necessary to match scales in Adobe Photoshop 3.0 and then analyzed for changes such as addition or loss of individual organisms or colonies or growth or shrinkage in areal coverage.

The following Indices of change were established:

$$\begin{aligned}\text{Change Index } I_C &= (C + L + G)/(O \times F) \\ \text{Loss/gain Index } I_{L,G} &= 2(L + G)/(N \times F \times Y) \\ \text{Loss Index } I_L &= 2L/(N \times F \times Y)\end{aligned}$$

Where: C = number of observed growths or shrinkages of individuals or colonies

L = number of observed losses of individuals or colonies

G = number of observed gains of individuals or colonies

O = total number of individual observations

N = number of loss observations

F = fraction of overlapping area in common with all images in a series

Y = number of years in time span

Settlement panels

Because the settling panels represented bare patches of substrata where recruitment and successional processes must necessarily dominate the observed changes, the data were treated differently from that of the natural control plots. Data obtained from panels include: 1) percent cover (filamentous and non-filamentous); 2) yearly changes in non-filamentous percent cover; 3) numeric additions (N_{add}), numeric losses (N_{loss}) and replacements (N_{repl}). Losses were counted if an individual present one year was absent the next. If the exact location of a lost individual was occupied by an individual of a different species, it was counted as a replacement.

The degree of fish grazing was determined by counting all distinct linear grazing scars visible on each panel and then determining an average number of grazing scars for the four panels at each depth site.

Results

For the sake of brevity, not all data discussed are contained herein. The reader is referred to Avery (1998) to view the complete data set.

Control plot trends

Change indices were positively correlated with depth (Spearman Rank Correlation, SRC, $p < 0.05$) from 10 m to 30 m and then negatively correlated with depth from 30 m to 200 m (Table 1, Fig. 1). This general pattern held for the loss index as well, though a sharper decline occurred between 30 m and 50 m for losses. From 10 m to 75 m, the majority of observed changes were losses or gains of macroalgae. Corals contributed to change between 20 m and 50 m and coralline algae contributed to change between 30 m and 50 m. Below 75 m the majority of observed changes were losses or gains of sponges. Miscellaneous invertebrates, such as hydroids and polychaetes, also made a small contribution to observed change below 75 m.

Settlement panel trends

Settlement panel change data include percent cover (filamentous and non-filamentous), yearly changes in non-filamentous percent cover, numeric additions, losses and replacements (Table 2). Change observations on the panels followed the same bathymetric pattern as those of the natural control plots. In general, change was positively correlated with depth from 10 m to between 20 m and 50 m, and then negatively correlated with increasing depth (SRC, $p < 0.05$). Changes in percent cover (considering only macroalgae, coralline algae and invertebrates) observed on the settling panels increased from 1993 to 1996. The greatest increases in percent cover occurred between 20 m and 75 m depth. Maximum observed changes in cover increased with both depth and time. The Greatest change from 1993 to 1994 occurred at the 20 m site. The greatest change from 1994 to 1995 occurred at the

30 m site. The greatest absolute change in cover overall cover were not noted on panels until 1996 and these occurred between 1995 and 1996 at the 50 m site. Losses in occurred only at the 10 m and 20 m sites.

Table 1 Control plot change indices, Lee Stocking Island, 1993-1996. Means with 95% confidence intervals in parentheses, S = species number, H' = Shannon Weiner, J' = evenness. Diversity data from Liddell et al. (1997).

Depth (m)	Change (IC)	Loss/Gain (IL/G)	Loss (IL)	S	H'	J'
10	0.27 (0.08)	0.39 (0.12)	0.15 (0.06)	55	2.67	0.67
20	0.34 (0.08)	0.38 (0.14)	0.20 (0.14)	44	2.74	0.72
30	0.54 (0.09)	0.49 (0.24)	0.27 (0.12)	36	1.96	0.55
50	0.39 (0.21)	0.21 (0.16)	0.08 (0.08)	38	2.03	0.56
75	0.04 (0.04)	0.05 (0.08)	0.04 (0.05)	39	2.19	0.60
100	0.01 (0.04)	0.03 (0.07)	0.00 (0.00)	19	1.47	0.50
150	0.01 (0.01)	0.01 (0.02)	0.00 (0.00)	11	1.38	0.58
200	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	5	1.04	0.65

Table 2 Change on settlement panels, Lee Stocking Island, 1993-1996. Means with standard deviations in parentheses.

Percent Cover		Non-filamentous Change (%)			Counts			
Depth (m)	Non-fil.	Filamentous	93 to 94	94 to 95	95 to 96	N add	N repl	N loss
10	16.73 (12.90)	trace	14.48 (10.08)	7.75 (5.20)	-5.5 (18.49)	12.33 (6.06)	0.00 (0.00)	9.75 (7.42)
20	20.00 (14.80)	trace	21.85 (24.24)	7.67 (17.61)	-9.5 (14.15)	7.33 (4.74)	5.00 (0.00)	6.25 (4.02)
30	47.00 (27.10)	trace	10.90 (7.97)	21.58 (32.34)	14.53 (15.00)	10.33 (3.28)	8.00 (9.70)	6.00 (7.38)
50	71.50 (4.85)	28.50 (4.70)	5.90 (0.33)	16.00 (13.22)	57.15 (2.98)	10.11 (5.35)	4.00 (3.09)	0.00 (0.00)
75	19.00 (9.70)	81.00 (23.00)	6.58 (3.04)	6.33 (3.86)	6.10 (6.55)	15.75 (5.93)	5.00 (3.41)	0.00 (0.00)
100	5.54 (2.53)	6.76 (2.30)	4.20 (2.31)	0.48 (4.94)	0.86 (2.98)	16.08 (5.54)	0.00 (0.00)	2.28 (1.80)
150	1.90 (1.00)	trace	1.00 (0.00)	0.88 (1.00)		5.38 (0.70)	0.00 (0.00)	0.00 (0.00)
200	1.00 (0.00)	0.00	0.50 (0.49)	0.50 (0.49)		1.88 (0.88)	0.00 (0.00)	0.00 (0.00)
250	0.30 (0.50)	0.00	0.00 (0.00)	0.33 (0.53)		0.17 (0.30)	0.00 (0.00)	0.00 (0.00)

At certain depths, panels exhibited a mixed-filamentous algal turf. This growth was not included in the above description of cover and was a negligible contributor to percent cover at depths below 50 m. Percent cover of filamentous turf was significantly

correlated with depth (Table 2). At 50 m and 75 m the otherwise bare surfaces of the settlement panels were filled in with varying degrees of this mixed algal turf. Percent cover of filamentous turf declined abruptly between 75 m and 100 m and was insignificant below 100 m.

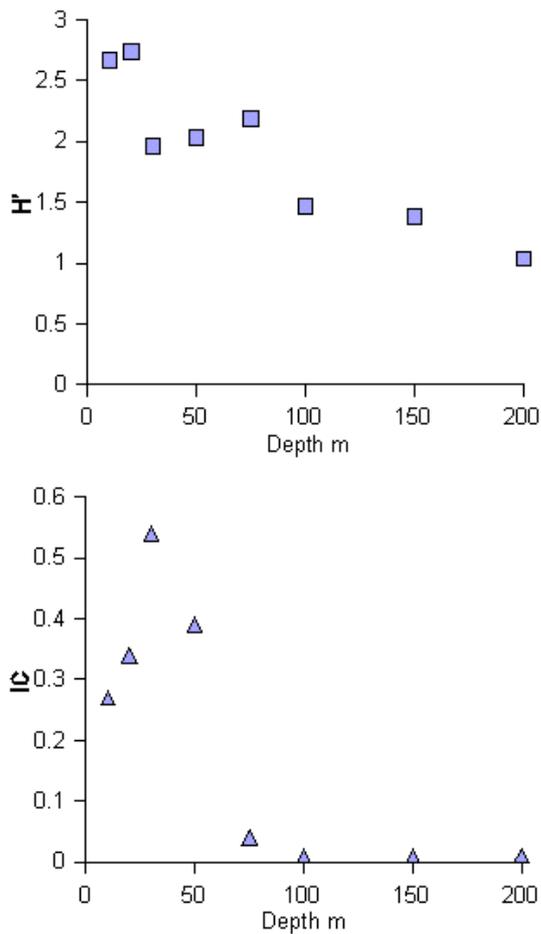


Fig. 1 Bathymetric patterns of diversity (H') and change (IC) for Lee Stocking Island, 1993-1996.

As would be expected during the first year of deployment, the greatest number of additions at all sites (with one exception, 30 m) occurred in the period from 1993 to 1994 and then, for most sites, declined over the next two years. Numeric additions of individuals were high at the 10 m depth, then declined with depth to 50 m and finally increased again from 50 m to 100 m. Losses of individuals did not occur until the 1994 to 1995 time period and then increased the following year. Numeric losses were generally greatest in shallow water (10 m), declined with depth to 30 m, dropped to zero between 50 m and 75 m and occurred again only at 100 m. Observed replacements occurred only during the last two time periods (1994 to 1995 and 1995 to 1996) and only between 20 m to 75 m.

Major contributors to the changes observed on panels included macroalgae between 10 m and 20 m, macroalgae and coralline algae between 30 m and 50 m, sponges between 50 m and 200 m and polychaetes between 50 m and 250 m.

Species richness increased from 1993 to 1996 at all

sites. Shallow sites (10 m to 50 m) approached an asymptote more rapidly than deeper sites (75 m to 250 m), which took longer to level off. The greatest observed panel diversity occurred within the depth range of 30 m to 100 m.

Fish grazing

The number of fish grazing scars observed per panel increased significantly from 10 m to 30 m and declined significantly between 50 m and 75 m. No evidence of fish grazing was observed below 75 m. The abundance of fish grazing scars was negatively correlated with the percent cover of filamentous algal turf (natural log-transformed SRC, $p < 0.02$) and positively correlated with the loss index (SRC, $p < 0.001$).

Discussion

General trends

The various methods of measuring change in the benthic hard-substrate community at LSI revealed highly consistent bathymetric patterns. In general, each index began at a relatively low value at 10 m, increased to a maximum value between 20 m and 50 m (most frequently 30 m) and then declined with increasing depth beyond 50 m. Other studies using similar methods have also observed an inverse relationship between micro-scale spatial change and depth, although over a more limited bathymetric range (Connell 1973, Bak and Luckhurst 1980, Porter et al. 1981, Hughes and Jackson 1985).

Disturbance or change?

Previous work has established a precedent of using measurements of differences in species composition or relative abundance between sample locations or sample times as surrogate measurements for disturbance (Connell 1973, 1978, Sousa 1979, Paine and Levin 1981, Menge and Sutherland 1987, Pickett et al. 1989). The extent to which the change indices presented here represent disturbance is debatable. Part of the difficulty lies in the definition of disturbance. Pickett et al. (1989) defined disturbance as a change in the minimal structure (of an assemblage or other object) caused by a factor external to the level of interest. This would exclude growth or overgrowths, which may alter percentage cover or relative abundance within an assemblage. Following this definition, change, addition or loss/gain indices, which include internal influences, would be inappropriate surrogate indicators for disturbance. On the other hand, loss indices may provide a better representation of disturbance. The loss index derived from control plot data shows the same general pattern for all indices mentioned above and indicates that disturbance may increase from 10 m to a maximum at 30 m and then decline rapidly with depth. Furthermore, loss data obtained from settlement panels suggest that maximum disturbance may occur between 10 m and 20 m. As the assemblages on these panels must be considered early-successional and some of the losses may be due to succession-related or internal forces, the loss index obtained from the natural substrate

control plots is likely a better indicator of disturbance.

Disturbance forces may be divided into abiotic forces and biotic forces. Abiotic forces include wave energy, storm surges, tidal currents and sedimentation and (with the possible exception of sedimentation) decline logarithmically with depth (Stowe 1983). If the loss index presented here is representative of disturbance to the benthic community and abiotic disturbance decreases with depth, then biotic disturbances must be significant between 10 m to 30 m, where losses actually increase with depth.

The abundance of fish grazing scars is highly correlated with the pattern of loss and is negatively correlated with the presence of filamentous algae. At LSI the fish bite marks consisted of pronounced, linear scrapes 1 to 3 mm in width and 1 to 3 cm in length. Other studies, in which fish bite marks were counted as a measure of grazing intensity, attributed most of the bite marks to parrotfish (Scaridae) and, to a lesser degree, damselfish (Pomacentridae) and surgeonfish (Acanthuridae) (Hixon and Brostoff 1996). Though no quantitative data on fish species and abundance were gathered in the present study, important grazers such as damselfish and parrotfish were observed at all sites from 10 m to 30 m and occasionally viewed from the submersible at 50 m. Dennis (1996) found most abundant species of fish were split between shallow and deep regions near the "wall" with a significant decline in abundance below 150 m. It is likely that fish grazing is a major force of biotic disturbance from 10 m to 50 m off Lee Stocking Island and contributed significantly to the observed fine-scale change in the benthic community.

Evidence of both abiotic and biotic disturbance declined significantly below 50 m. Under conditions of low disturbance and low productivity (reduced light levels with greater depth), it is thought that life history patterns, such as recruitment rates and relative competitive abilities, may determine community structure and diversity (Menge and Sutherland 1987). Colonization of the panel surfaces, though not significantly correlated with depth, remained strong to depths of 100 m. This is consistent with recruitment data from this locality. Filamentous algae, sponges, corals, polychaetes, bryozoans and tunicates settled in significant numbers to 100 m (Avery and Liddell 1997). Increases in species richness on panels occurred most rapidly between 50 m and 100 m. Percent cover of natural substrates also remained relatively high to depths of 100 m. This suggests that within the depth range of 10 m to 100 m, community structure and diversity is probably not limited by recruitment rates. The maintenance of high community diversity (S, H') to a depth of 100 m is likely due to tradeoffs in the ability of the taxa present to compete for space.

As competition for space on hard substrata necessarily involves species acquiring physical space, replacement counts (individuals of one species replaced by individuals or portions of colonies of another species) may indicate competition for space on the panels. If this can be used as an indicator of competition, then the data suggest that competition for space may have been detected from 20 m to 75 m with the greatest magnitude occurring between 30 m and 50 m.

When change/loss indices from the present study are compared to measures of community diversity (Table 1, Fig. 1), it appears that the highest diversity is associated with intermediate levels of change, lower diversity is associated with high change, and the lowest diversities with very low change. This pattern is similar to that observed by Connell (1978), relating diversity to percent cover of coral (a proposed surrogate measure of disturbance intensity). This led to the Intermediate Disturbance Hypothesis (IDH) as an explanation for community diversity that has been widely applied to aquatic and terrestrial ecosystems.

Because of the magnitude of the abiotic and biotic changes occurring along the depth gradient from 10 m to 250 m, an attempt to explain the variations in community structure and diversity with just one variable (i.e., disturbance) is inappropriate. Huston (1985) proposed a modification to the IDH that incorporated both disturbance and light availability and seems to come somewhat closer to representing the situation along the bathymetric gradient at LSI. The factors influencing the bathymetric patterns in community structure at LSI include abiotic disturbance, biotic disturbance, light availability and space-acquiring competitive abilities (associated with a shift in phyletic dominance from macroalgae to corals to sponges and finally to a suite of other filter-feeding invertebrates).

In general, abiotic forces associated with wave and storm energy are strong in shallow waters (less than 10 m). From 10 m to 30 m this source of disturbance is reduced logarithmically. Fish grazing appears to be concentrated at 20 m and 30 m and may contribute to high total disturbance to the benthic community even as abiotic disturbance is reduced. Light levels decline logarithmically with depth to the 1% level (compensation point where respiration = photosynthesis) at approximately 100 m (Stowe 1983, Valiela 1995). Competitive dominance capability shifts from algae to corals to sponges from 20 m to 75 m and each group "senses" disturbance and optimal light levels differently. Algae are competitively dominant in bright shallow waters, but are attacked by grazers. Hermatypic corals are calcareous and less apt to be attacked by algae-grazing fish but are slower growing than algae. However, hermatypic corals are filter feeders as well as photosynthetic and so are not entirely dependent upon light. Sponges (with exceptions) are primarily filter feeders and generally independent of light. Change, possibly resulting from competitive interactions, rather than disturbance forces, was observed at 50 m and 75 m. Finally, both diversity and change declined dramatically below 100 m, presumably due to the very low light levels and, possibly, high sedimentation associated with decreasing slope angle. Explanations for community structure and diversity patterns from 10 m to 250 m must necessarily take into account the full range of the above phenomena.

Acknowledgments We wish to express our appreciation to the Caribbean Marine Research Center, which funded this project and provided facilities. In particular we would like to thank George Dennis (formerly CMRC) for his support and the staffs of Lee Stocking Island (CMRC) and

Seacoast Engineering Resources, which operated the submersible Nekton Gamma.

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