PROCEEDINGS

OF THE

THIRTEENTH SYMPOSIUM

ON THE

NATURAL HISTORY OF THE BAHAMAS

Edited by
Jane Eva Baxter
and
Eric Stephen Cole

Conference Organizer
Thomas Rothfus

Gerace Research Centre
San Salvador Bahamas
2011

Cover photograph -- Amanda Rubasch and Anna Thomas of St. Olaf College

Printed at the Gerace Research Centre

ISBN 0-935909-93-3

SPATIAL PATTERNS OF EPIFAUNAL INVERTEBRATES IN TROPICAL NEAR SHORE REEFS: INFLUENCE OF ISLANDS, STORMS AND LAND-BASED SOURCES OF POLLUTION ON BENTHIC DIVERSITY

Kathleen Sullivan Sealey [1], Kathleen Semon[2] and Emily Wright[1]
[1]Department of Biology, P.O. Box 249118, Coral Gables, FL 33124 USA
[2] Fish and Wildlife Research Institute, St. Petersburg, FL USA

ABSTRACT

Benthic macrofauna have long been used to characterize marine communities such as coral reefs and seagrass beds, but these organisms are also used in impact assessment as indicators of ecological health and stability. Small differences in benthic macrofauna assemblage patterns can indicate shifts in marine communities over space and time. The assemblages of conspicuous marine benthic invertebrates were studied for near shore hard-bottom and patch reefs at two different islands that varied in size, history of hurricane disturbance and degree of coastal development over a five-year period. The greatest differences were found to be temporal in nature, and related to disturbance (e.g. hurricane or acute development events). Corals (Phylum Cnidaria: Scleractinia), echinoderms (Phylum Echinodermata), and sponges (Phylum Porifera) were most sensitive to disturbance, thus representing the best indicators of benthic habitat change over space and time. The results illustrate the importance of on-going monitoring of coastal system when attempting to segregate natural and anthropogenic stressors on near shore habitats. For large archipelagos such as The Bahamas, regional or island-specific baseline datasets are crucial for impact assessments.

INTRODUCTION

Over the past decade, researchers have focused efforts towards the use of proxies and indicator organisms to simplify the assessment of anthropogenic impacts on marine ecosystems (Burke and Maidens 2004). An important indicator group of marine ecosystem health is benthic macrofauna (Grall and Glémarec 1997, Simboura and Zenetos 2002, Perus et al. 2004). Members of benthic macrofauna communities including cnidarians, poriferans, echinoderms, crustaceans, molluscs, chordates and annelids, have many characteristics that make them ideal indicators. However, epifaunal invertebrates have clonal and aclonal life histories, different life spans and mobility. It is critical to understand how conspicuous benthic species respond to stress, particularly changes in water quality, extreme storm events and increased sedimentation rates. Their presence or absence can signal the state of health in the ecosystem (Zettler et al. 2007, Reiss and Kröncke 2005). Shallow, near shore marine habitats around islands in The Bahamas host unique assemblages of macro-invertebrate species that utilize consolidated and unconsolidated substrates. If these assemblages were well characterized and regularly monitored, they could serve as important indicators of impacts occurring over time and space, including shifts resulting from anthropogenic activities. The lack of baseline information as well as the tendency to assume uniformity in reef or benthic community composition across the archipelago restricts the ability to manage near shore marine resources.

While it is clear that benthos respond quickly to environmental changes and stress (Raffaelli et al. 2003, Dernie et al. 2003), there is a need to deduce what stressors can cause major changes in the coastal zone. The ability to distinguish natural stressors from anthropogenic stressors requires frequent and thorough study of habitats over time (Rosa and Bemvenuti 2006, Morrisey et al. 1992, Clarke and Warwick 2001, Lapointe et al. 2007). Benthic macrofauna respond physiologically and behaviorally to diurnal, lunar, and seasonal cycles (Nichols and Thompson 1985), and thus natural changes in species composition should occur in describable, cyclical patterns. Diversity and species composition are likely to change more rapidly and irreversibly with anthropogenic influences, a phenomenon described for coral reefs by Hughes (1994). However, early detection of catastrophic changes may be more difficult. Tropical marine benthic epifauna composition is a function of both stochastic recruitment events and additional filtering of smaller scale events (Carlton and Olson 1993). Frequent monitoring of the presence or absence, as well as the abundance of benthic macrofauna over time should elucidate of the rate and extent of community changes.

Although many studies have addressed temporal change in near shore benthic communities, research has traditionally focused on infaunal communities in subtropical and temperate lagoons and estuaries (Raut et al. 2005, Rosa and Benvenuti 2006, Duport et al. 2007, Hyland et al. 2006). Few studies have characterized the benthic epifauna in hard bottom reefal and non-reefal habitats, and there is a need for studies that characterize these communities over time. Exactly how temporal variability contributes to the long-term patterns and changes in benthic diversity and species assemblages in the Tropical Western Atlantic is currently unclear.

This study aimed to reveal the survey frequency required to characterize habitats and assess shifts in near shore benthic assemblages caused by complex stressors that can be linked to the geography and development of small island systems. Near shore benthic habitats from two different islands were examined to contrast temporal and spatial patterns of conspicuous epifauna across many phyla. Islands differed in size, history of hurricane events and intensity of coastal development. Study sites were surveyed over a five-year period. Temporal changes in these benthic assemblages were evaluated to determine a protocol for the detection of small changes in the invertebrate community. Key species and taxa indicative of major differences between benthic assemblages were identified.

The size of an island and extent of human development is critical for determining the scope and extent of anthropogenic stressors on near shore marine habitats. Presumably, larger islands may be able to sustainably support larger populations and infrastructure of tourism development. However, the type of development and infrastructure in place may mitigate land mass limitations. The Bahamian archipelago has less than 330,000 people, with a wide range of islands varying in size and population density. The islands cover 1200 kilometers, thus representing a range of natural disturbance events (e.g. hurricanes, tropical storms and frontal systems). The archipelago provides an ideal location to contrast spatial patterns of benthic invertebrate community composition under varying coastal environments and human development regimes.

METHODS AND MATERIALS

Six study sites were chosen to characterize two different near shore benthic habitat types (non-reef hard bottom or "hardbar" and patch reef) on two islands (Great Exuma and Guana Cay, Abaco) in The Bahamas. Great Exuma is a large island located in the southern Bahamas and the study sites around this island are located in Elizabeth Harbour (Figure 1A). Great Guana Cay is a very small offshore cay near Abaco Island (Figure 1B). Survey sites were selected based on 1.) Size of the island, 2.) Proximity to the shoreline, and 3.) Condition of the shoreline in terms of vegetation and development. Most sites were relatively protected from exposure to open ocean currents, resulting in low to medium wave energy. One site on each island, Tombola Beach (BBC5) on Great Guana Cay, and Fowl Cay (FC) off Great Exuma, were adjacent to channels open to the western Atlantic Ocean and represented reefs furthest from island-based impacts. All of the sites in this study are shallow (maximum depth 6 meters), and each site is located within 500 meters of the study island shoreline. Throughout the Bahamian archipelago, coastal areas experience semi-diurnal microtides (range 1.9 meters in Abaco island group, 1.6 meters in Exuma Cays), with the annual tidal range increasing from the southern to the northern extent of the archipelago.

"Hardbar" habitats are characterized by nearshore, non-reefal hard bottom areas dominated by either algae or soft corals with smaller heads of stony corals. Hardbar habitats are created by natural processes of cementation (mixed facies of oolite with coralline skeletal consolidated sediments) (Sealey 2006). Patch reefs are isolated, nearshore clusters of coral colonies normally located adjacent to seagrass beds on the leeward side of an island.

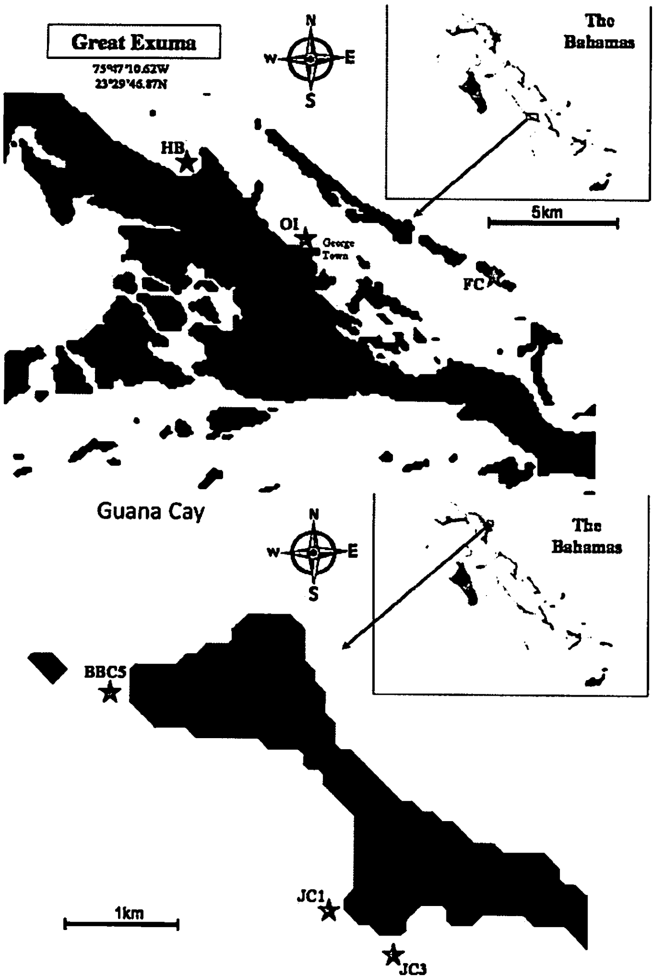

Figure 1: Top is 1A, a map of Great Exuma Island and associated reef study sites, Bottom is 1B, a map of Great Guana Cay in the northern Abacos, with associated reef study sites.

To better understand the nature of change and variability in near shore marine habitats, the two islands were selected based on the proxy indicators for threats to coral reefs in the "Reefs at Risk" analyses compiled by Burke and Maidens (2004). The parameters measured for coastal development that correspond to land-based threat sources include the number of cities (settlements), ports, airports, dive tour centers and coastal population of the island (Table 1).

Sampling methods

Each site was surveyed two to four times between March 2004 and July 2006, resulting in a total of 18 surveys at the six sites. Roving diver surveys were completed over an area of 2500 m^2, measured by underwater transect tape. Survey times ranged from 1-2 hours per survey event. Conspicuous benthic macrofauna were identified on site to the most specific taxonomic level possible and recorded on underwater paper. Species abundances were recorded using geometric abundances: 1 individual = single; 2-10 individuals = few; 11-100 individuals = many; >100 individuals = abundant. Invertebrate and coral identification guides for the Caribbean (Humann and DeLoach 2002), underwater photos, drawings and descriptions were used as aides following each survey to confirm species identifications.

The probability of Type 2 errors with the misidentification of species was reduced by referencing field guides, verification by laboratory identification and experience. References on Bahamian distribution of the surveyed species (Appendix 2) served to confirm the presence of each species on the different islands. Very rare or questionable species (outliers) were also removed from the dataset. Transect tapes were used to estimate areas and define the limits of the survey area.

Data analysis

Univariate diversity indices (Shannon Diversity, number of species present, species richness and Peilou's evenness) were calculated with the species data from each survey event using the PRIMER v5 package (Clarke and Gorley 2001) to measure assemblage diversity and species equitability. Multivariate analyses also were performed on the assemblage data using the PRIMER v5 package to elucidate differences in near shore benthic assemblages by island, year and habitat. Raw data from the surveys, including presence/absence and geometric abundance of species, was sorted and outliers were removed. Data did not require transformation because use of the geometric abundance system normalized the dataset. A Bray-Curtis similarity matrix was composed to show similarities between the surveyed communities. The Bray-Curtis Index is not affected by joint absences and is based on quantitative data, reflecting differences in relative abundances of species between samples (Clarke and Warwick 2001).

From the Bray-Curtis similarity matrix, CLUSTER dendrograms were created to eliminate outliers, then show potential groupings by island, year and habitat type. To visualize the groupings of surveys, ordination by non-metric multidimensional scaling (MDS) was carried out to produce two-dimensional ordination plots of the Bray-Curtis similarities between surveys. Distance on MDS plots between samples corresponds to the relative similarity between factors (in this case, species presence/absence and abundance) such that samples that are far apart are more dissimilar than those that are closer together. Analysis of Similarities (ANOSIM) was used to test for significant differences between community assemblages. Similarity percentages (SIMPER) highlighted which species contributed to the differences between groups of surveys that showed clustering (similar species composition and abundance patterns).

RESULTS

In the 18 surveys of six benthic macrofauna assemblages in Great Exuma and Guana Cay, 142 total invertebrate species were recorded. Seven phyla were represented (Figure 2). Benthic cnidarians, including hard and soft corals, anemones, and hydroids showed the highest richness (61 species). Other represented phyla including mollusca, porifera and echinodermata may not have been less speciose, but certainly less detectable in this survey method (2-20 species). The crustaceans and annelids are often cryptic on tropical reefs, and thus require special collection methods. Only large and conspicuous species are represented in this survey (e.g. *Spirobranchus giganticus*). Tunicates were also limited to a few conspicuous species (<15 species).

Proxy indicators for land-based impacts on nearshore marine communities (Table 1) highlight the differences in size and development of Great Exuma compared to Guana Cay. Univariate diversity indices for each island (Table 2) indicate that while Great Exuma is more developed, the average benthic macrofauna assemblage there has higher species richness and higher Shannon diversity than at Guana Cay. Figure 3 shows the Shannon diversities for each site surveyed at the islands, with 95% confidence intervals that represent the range of temporal variability in the benthic assemblages at those sites. While diversity varied little by island, the confidence intervals imply that the assemblages at Guana Cay were more variable over time than those at Great Exuma.

Initial non-hierarchical clustering verified the need to exclude Tombola Beach (BBC5) off Guana Cay as an outlier, as this one site was less than 5% similar to any other site surveyed. This site was distinctly different in its species composition, and was the most dissimilar site. The removal of this site helped elucidate more differences in the other survey events over space and time (Gauch 1982).

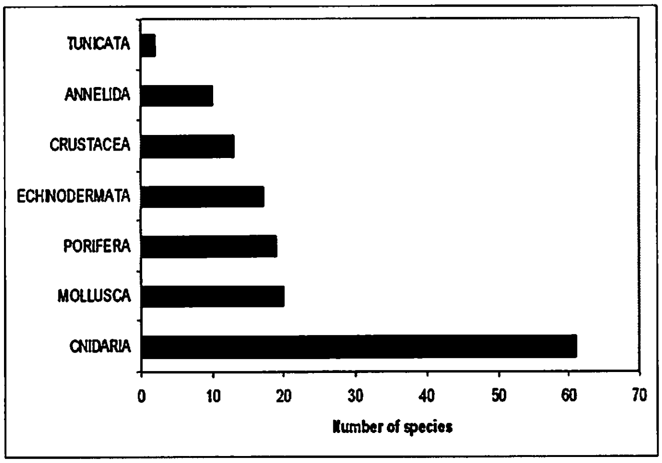

Figure 2: Benthic macrofauna composition of near shore reefs habitats in Great Exuma and Guana Cay, Abaco based on 18 surveys of 6 sites sampled in 2004, 2005 and 2006.

Univariate diversity indices averaged for all surveys by year indicate few major differences between the three years of this study. Closer inspection of the Shannon diversities over time (Figure 4.) exposed greater differences in the assemblages from year to year at a single site. The Great Exuma sites show temporal changes due to micro-scale proximity impacts, with large diversity differences observed at Hooper's Bay (HB), smaller differences at Out Island Inn (OI), and minimal differences at Fowl Cay (FC). Each of these sites is affected by different amounts of land-based development; HB is the closest to a large development under construction and FC is more than 5 kilometers away from the nearest development center.

The sites on Guana Cay presumably show similar temporal changes to each other due to proximity and larger scale disturbance (e.g. three hurricanes). The outlier site, Tombola Beach (BBC5), demonstrated increased Shannon diversity over time while the sites near Joe's Creek (JC1, JC3) demonstrated decreased diversity. BBC5 is exposed to more ocean currents due to its location in a channel, while JC1 and JC2 are close to the island in the Sea of Abaco.

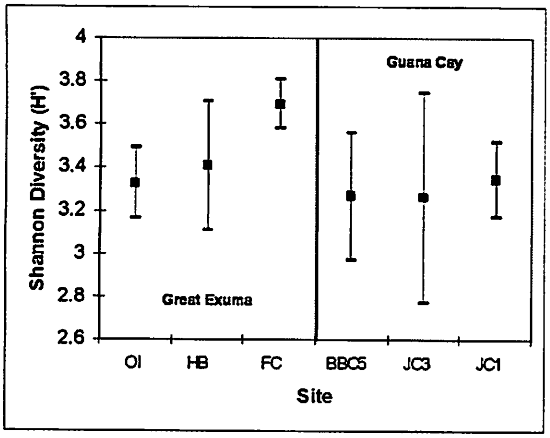

Figure 3: Mean Shannon diversities with 95% confidence intervals for each benthic macrofauna assemblage by site. Note that the length of the whiskers represents the range of temporal variability for each site. Guana Cay experienced hurricanes in both 2004 and 2005, while Exuma was not impacted by a major hurricane over the course of this study.

Multivariate analyses for all surveys by year show significant temporal effects on benthic macrofauna assemblages (Figure 6 and 7). MDS shows a grouping of surveys from 2004 and 2005 and another grouping of surveys from 2006, with little overlap between the two major clusters. A pairwise comparison of the three years using ANOSIM indicated that this grouping was likely not produced by chance and that there is a difference between the assemblages by year (R=0.197, 1.6% significance). SIMPER analysis (Table 4) indicated that corals, echinoderms and sponges contributed fairly equally to the differences in benthic assemblages by year. Inspection of SIMPER analyses between 2005 and 2006 (Table 4B) and 2004 and 2006 (Table 4C) shows that echinoderms represent half (5/10) of the species contributing to the largest differences between the years shown in the MDS plot.

Univariate indices of the benthic assemblages show no clear patterns in species richness, evenness or diversity by habitat type (Figure 5). However, the confidence intervals of the mean Shannon diversities by habitat type (Figure 6) illustrate that patch reef assemblages varied more over time than hardbar assemblages. Multivariate analyses indicated habitat effects on macrofauna assemblages (Figure 6 and 7). MDS exhibited grouping of hardbar surveys and grouping of patch reef surveys with some overlap. The more compacted grouping of hardbar surveys compared to the spread of the patch reef surveys again suggests that patch reef assemblages show more variability than hardbar assemblages. ANOSIM confirmed a strong difference in benthic macrofauna assemblages between the two habitats (R=0.178, 2.6% significance). SIMPER analysis (Table 5) revealed that soft and hard corals are the most common taxa (10/15) among the top contributing species for differences in benthic macrofauna assemblages across the habitat types.

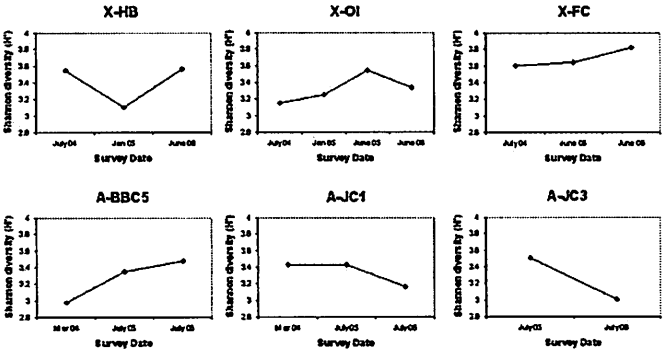

Figure 4: Year to year changes in benthic macrofauna diversity (Shannon index) for each site in Great Exuma and Guana Cay, Bahamas. The prefix X- denotes a site in Exuma and A- denotes a site in Guana Cay, Abaco.

DISCUSSION

Relatively common and conspicuous epifauna, in addition to the stony corals, can vary dramatically between survey sites and over time. Sponges and echinoderms appear to be particularly likely to change in both occurrence and abundance over time. Stressors, both abiotic and biotic, induce changes in marine communities (Fabricius and De'ath 2004); ideally there would be changes in the benthos that could be indicative of high sedimentation rates (e.g. loss of corals); increased pathogens (e.g. loss of sponges or echinoderms) or increased physical damage from storms (e.g. increased occurrence of weedy or encrusting benthos).

The population density for Great Exuma was twice as high as that of Guana Cay (but well below the highest population density in the Bahamian archipelago of 290 people per hectare on North Bimini). Great Exuma is more developed, having more and larger resorts, settlements, marinas and dive centers than Guana Cay. These results suggest potentially greater anthropogenic influence on the near shore communities at Great Exuma than at Guana Cay.

Natural stressors (hurricanes and frontal systems) and anthropogenic stressors (coastal alterations associated with development) may have produced local impacts, including coastal eutrophication and increased turbidity. Although Great Exuma sites overall were more diverse than sites at Guana Cay, there were greater differences between sites on Great Exuma. The least diverse sites (HB and OI), exhibiting the least stability and greatest change over time, occurred immediately adjacent to a hotel and filled coastal areas under construction. The site FC, furthest from developed coastal areas, exhibited the highest diversity and changed the least over years. The proximity of coastal alterations can impact both the diversity and stability of benthic invertebrate communities, even when water quality changes are not detectable or obvious (Sealey 2004). Changes at the two near-development sites were attributed to the loss of the stony corals *P. furcata* and *M. annularis* and loss of the soft corals *Psuedopterogorgia* spp. combined with the increase in the occurrence of the encrusting sponges *C. nucula* and *A. varians* and weedy fire coral *M. alcicornis.*

Generally, all benthic sites off Guana Cay contained fewer species in lower abundances that those sites surveys off Great Exuma. Both hard bottom habitat types appear to have greater invertebrate species diversity and species richness off Great Exuma compared to Guana Cay. The importance of latitudinal gradients along the archipelago are critical in making island to island comparisons, as Great Exuma may have naturally greater diversity of reefal invertebrates in the absence of cold fronts and temperature extremes experienced by northern Guana Cay. Weak differences found in the macro-invertebrate assemblages in these two islands elucidate the importance of habitat and locations when making benthic assessments.

The variability seen over time in benthic macrofauna assemblages may be influenced by acute anthropogenic impacts, such as in Great Exuma, and acute storm events, such as in Guana Cay. Guana Cay experienced three large hurricane events, concurrent with a decrease in diversity and evenness. Specifically, there was a loss of soft coral species *P. homomalla*, and *Psuedopterogorgia spp.*, as well as an increase in sea anemones such as *Condylactis gigantean* and *Stichodactyla helianthus*. Some hard corals decreased in abundance (*M. annularis*, *S. siderea* and *P. furcata*) as well. Increased monitoring of near shore marine systems over longer periods of time will clarify responses to specific stressors such as hurricane events or major dredging/ development activities.

The differences observed in benthic epifauna assemblages over time indicated that assemblages in 2004 and 2005 were similar to each other and yet both different from assemblages in 2006. One possible explanation for this pattern is that the hurricane impacts caused by Wilma in October 2005 were more damaging than those caused by the hurricanes in the fall of 2004. It is important to note that sampling of benthic invertebrate assemblages on annual or semiannual time frames can allow researchers to miss important changes; quarterly sampling may be required in areas with rapid development changes taking place or large active construction project to pinpoint major disturbance events (Nichols and Thompson 1985).

Estuarine macrofauna communities in Brazil show seasonal variability with water temperature variations. Communities there are denser in the summer months due to high levels of recruitment following the patterns of high water temperature and salinity (Rosa and Benvenuti 2006). Sfriso et al. (2001) found seasonal changes in macrofauna communities in a Venice lagoon due to seasonal changes in environmental variables such as oxygen and temperature levels. Buchanan et al. (1978) found some of the largest changes in benthic macrofauna abundances to occur after unpredictable natural disturbances such as storms, which were likely the cause of the major changes seen in the assemblages in Guana Cay following the hurricanes of 2004 and 2005. Higher frequency surveys will allow a more complete characterization of the marine community and will the assessment of species assemblage response to specific stressors on the system.

The two most common hard bottom benthic habitats in the Bahamian archipelago are the non-reefal hardbar and patch reefs (Sealey 2002). These two habitats are often described as containing corals and sponges, but are distinct in their epifauna species composition. Patch reefs are more diverse, but have a higher dissimilarity over time compared to hardbar sites. It is not clear if patch reefs naturally have a higher species turnover of the benthos or are more susceptible to change from disturbance events. Disturbance regimes and wave energy in marine systems not only influence diversity levels, but also determine the distribution of habitat types (Dernie et al. 2003). In the same way, the physical characteristics facilitating a patch reef in a given location could contribute to the increased level of change in the benthic community over time from localized water flow rates, substratum diversity, topographic complexity, depth, surrounding habitat, and the age of the site (Sale and Douglas 1984). Differences in benthic invertebrate assemblages by habitat type may also indicate acute micro-scale (10 to 100's of meters) stressors such as disease outbreaks or local overfishing. Near shore reefs may change more over time because they are more susceptible to these stressors. Patch reefs should be chosen for long-term monitoring rather than hardbar sites because of the higher benthic diversity and the likelihood to show noticeable shifts over time.

Stony and soft corals appear to be the best indicators of differences in assemblages between island and between habitat. Corals have been described as good indicators of variability in physical parameters and ecosystem health in other studies (Shinn 1966, Negri and Heyward 2000, Okamoto et al. 2000). Benthic surveys that include echinoderms, sponges and soft corals will be more sensitive to temporal changes in benthic assemblages. Echinoderms have been previously found to be sensitive indicators of contamination in coastal marine environments (Burd and van Poppelen 2004, Atkinson et al. 2003). Diaz et al. (2004) found that sponges can give insight to the directionality of community shifts. Use of a relatively short checklist of less than 50 benthic invertebrates could be developed (specific for an island group) to reduce survey time in future research of near shore ecosystem health.

Many benthic organisms surveyed in this study may have the ability to handle some levels of stress and harmful impacts, both natural and anthropogenic. Life history strategies of benthic organisms are reflected in response times to disturbance (Thistle 1981), and rapid recovery has been measured in benthic shallow-water communities of temperate estuary systems (Dernie et al. 2003) and subtropical estuaries (Raffaelli et al. 2003). Shallow near shore habitats may support benthic organisms adapted to deal with seasonal changes and impacts from processes occurring on land due to their vicinity to the shore or the stability of the bottom type in hardbar and patch reef habitats. De La Rosa et al. (2006) studied a decapod community in the Inner Bay of Cádiz in Spain and found the diversity, species richness and evenness of the assemblage to be stable over a two year period, despite high levels of anthropogenic impacts on the bay. The researchers suggested that the diversity and stability of this community may have been due to the specific characteristics of the bottom type.

The frequency of disturbances, including the storm history of an island, is critical to any near shore ecological assessment. Connell (1978) proposed that physical disturbances are important in the maintenance of diversity, and that a direct relationship exists between the frequency of these disturbances and the species richness in a community. The proximity of this study's sites to land and their shallow depth lead to higher levels of disturbances than habitats offshore, including frequent salinity changes due to fresh water runoff after precipitation and changes in temperature and light during the tidal cycle. Shallow, near shore communities, like those in this study, are most susceptible to land-based stressors caused by coastal development (Sealey 2004).

Shallow, near shore hardbar and patch reef habitats require protection to maintain high diversity and ecological function, and management and research plans must take into account the differences present between communities in different island groups and in different habitats over time. Consistent, frequent surveys will enable full characterizations of tropical near shore invertebrate communities in terms of health and stability, and will contribute information when relating changes over time ity, and disturbances such as hurricanes, or anthropogenic impacts.

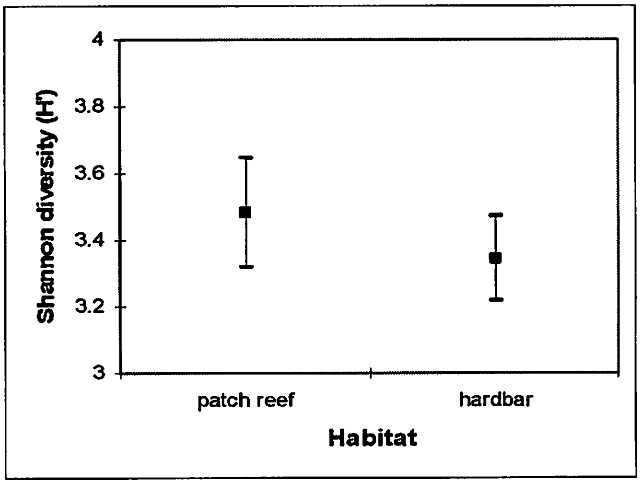

Figure 5. Mean Shannon diversities with 95% confidence intervals for benthic macrofauna communities in patch reef and hardbar sites in The Bahamas. Note that the length of the whiskers represents the range of temporal variability for each habitat type.

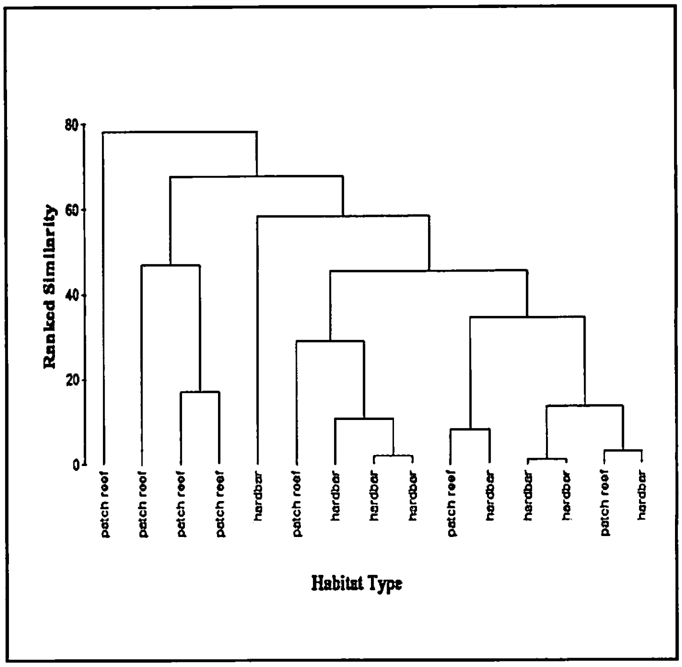

Figure 6. Multivariate analyses for habitat effects on macrofauna assemblages ranked similarities of all benthic macrofauna assemblages surveyed. calculated using PRIMER v5. CLUSTER dendrogram showing the Bray-Curtis.

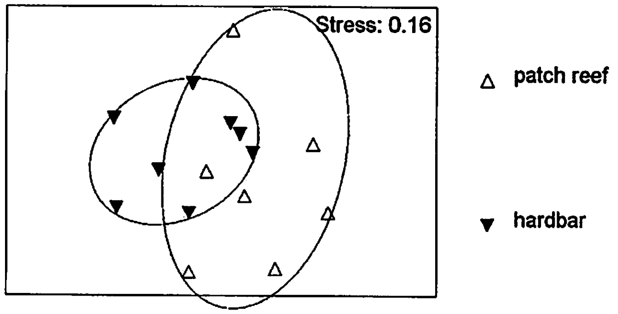

Figure 7. Two-dimensional non-metric MDS plot based on Bray-Curtis similarities for all benthic macrofauna assemblage surveys taken at each site in The Bahamas showing habitat type as the factor.

ACKNOWLEDGMENTS

Funding for this work came from University of Miami Honors Programme, Earthwatch Institute (Coastal Ecology of The Bahamas project), Exuma Education Resource Foundation, and Discovery Land Company. The assistance of Earthwatch expedition volunteers and staff is gratefully acknowledged

REFERENCES

Allee, R. J. et al. 2000. Marine and estuarine ecosystem and habitat classification. NOAA Technical Rept. NMFS-F/SPO 43.

Atkinson S., M. Atkinson, and A. Tarrant. 2003. Estrogens from sewage in the coastal marine environment. Environmental Health Perspectives 111:531–5.

Bayer, F. M. 1961. The shallow-water Octocorallia of the West Indian region. Studies on the Fauna of Curação and other Caribbean islands 12:1-373.

Baisre, J. A., W. Blanco, I. Alvarez, and M. E. Ruiz de Quevedo. 1978. Distribution and relative abundance of lobster larvae (Panulirus argus) in the Caribbean Sea and Bahamas. Revista Cubana de Investigaciones Pesqueras 3:1-20.

Bell, L. J. 1992. Reproduction and larval development of the West Indian topshell, Cittarium pica (Trochidae), in the Bahamas. Bulletin Of Marine Science 51(22):250-266.

Buchanan, J. B., M. Sheader, and P. F. Kingston. 1978. Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971-1976. Journal of Marine Biological Association of the United Kingdom 58:191-209.

Bunt, J. S., W. T. Williams, and B. E. Chalker. 1981. Coral associations at depths of 45 to 125 feet in the Bahamian region. In The Reef and Man: Proceedings of the Fourth International Coral Reef Symposium, Volume 1, eds. E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh Jr, and R. T. Tsuda, 707-714. Quezon City, Philippines: Marine Sciences Center, University of the Philippines.

Burd, B. J., and P. van Poppelen. 2004. Review and Update of the Indicator-and-Trigger Approach to Managing Discharges into Marine Receiving Environments. 2003 Georgia Basin/Puget Sound Resarch Conference Proceedings, 1-6.

Burke, L., and J. Maidens. 2004. Reefs at Risk in the Caribbean. Washington, D.C.: World Resources Institute.

Cairns, S. D. 1977. Guide to the Commoner Shallow-water Gorgonians (Sea Whips, Sea Feathers and Sea Fans) of Florida, the Gulf of Mexico, and the Caribbean Region. Florida: University of Miami Sea Grant Field Guide Program, Series 6.

Carlton, D.B. and R.R. Olson 1993 Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals J. Exp. Mar. Biol. Ecol., 173: 247-263.

Chiappone, M., K. M. Sullivan, and C. Lott. 1996. Hermatypic scleractinian corals of the southeastern Bahamas: a comparison to western Atlantic reef system. Caribbean Journal of Science 32:1-13.

Clarke, K. R., and R. N. Gorley. 2001. PRIMER v5: User manual. United Kingdom: PRIMER-E Ltd., Plymouth.

Clarke, K. R., and R. M. Warwick. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd ed. United Kingdom: PRIMER-E Ltd., Plymouth.

Colin, P. L. 1978. Caribbean Reef Invertebrates and Plants. New Jersey: T. F. H. Publishing.

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

Debrot, A. O. 1986. Comparative coastal ecology of the tropical rocky-intertidal snail Cittarium pica in the Exuma Islands, Bahamas. Journal of Shellfish Research 7:114-115.

De La Rosa, I. L., A. Rodríguez, and J. E. G. Raso. 2006. Seasonal variation and structure of a decapod (Crustacea) assemblage living in a Caulerpa prolifera meadow in Cádiz Bay (SW Spain). Estuarine, Coastal and Shelf Science 66(3-4):624-633.

Dernie, K. M., M. J. Kaiser, and R. M. Warwick. 2003. Recovery rates of benthic communities following physical disturbance. Journal of Animal Ecology 72(6):1043-1056.

Diaz, M. C., K. P. Smith, and K. Rutzler. 2004. Sponge species richness and abundance as indicators of mangrove epibenthic community health. Atoll Research Bulletin 518:1-17.

Duport, E., F. et al. 2007. Benthic macrofauna and sediment reworking quantification in contrasted environments in the Thau Lagoon. Estuarine, Coastal and Shelf Science 72(3):522-533.

Eckelbarger, K. J., and R. Larson. 1992. Ultrastructure of the ovary and oogenesis in the jellyfish Linuche unguiculata and Stomolophus meleagris, with a review of ovarian structure in the Scyphozoa. Marine Biology 114(4):633-643.

Eggleston, D. B., R. N. Lipcius, L. S. Marshall Jr., and S. G. Ratchford. 1998. Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. Marine Ecology Progress Series 174:33-49.

Fabricius, K. E., and G. De'ath. 2004. Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications 14(5):1448-1465.

Garth, J. S. 1978. Marine biological investigations in the Bahamas. Part 19 Decapoda, Brachyura. Sarsia 63:317-334.

Gauch, H. G. Jr. 1982. Multivariate analysis in community ecology. New York: Cambridge University Press.

Gendron, R. P., and K. Mayzel. 1976. Association of Thalassoma bifasciatum with Condylactis gigantea in the Bahamas. Copeia 1976(2):382-384.

Grall, J., and M. Glémarec. 1997. Using biotic indices to estimate macrobenthic community pertubations in the Bay of Brest. Estuarine, Coastal and Shelf Science 44 (Suppl. A):43-53.

Herrnkind, W., G. Stanton, and E. Conklin. 1976. Initial characterization of the commensal complex associated with the anemone Lebrunia danae at Grand Bahama. Bulletin Of Marine Science 26:65-71.

Hess, S. C. 1978. Guide to the commoner shallow-water asteroids (starfish) of Florida, the Gulf of Mexico, and the Caribbean Region. Florida: University of Miami Sea Grant Program.

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

Humann, P., and N. DeLoach. 2002. The Reef Set: Florida, Caribbean, Bahamas; Reef Creature Identification and Reef Coral Identification. Florida: New World.

Hyland, J., C. et al. 2006. The soft-bottom macrobenthos of Gray's Reef National Marine Sanctuary and nearby shelf waters off the coast of Georgia, USA. Journal of Experimental Marine Biology and Ecology 330(1):307-326.

Jones, R. L. 1996. Spatial Analysis of Biological and Physical Features Associated with the Distribution of Queen Conch, Strombus gigas, Nursery Habitats. Thesis. Florida Institute of Technology, Melbourne, Florida.

Kaplan, E. H. 1988. A Field Guide to Southeastern and Caribbean Seashores. Massachusetts: Houghton Mifflin Company.

Lyons, W. G. 1981. Comments on chitons Mollusca Polyplacophora of the Bahama islands Atlantic ocean. American Malacological Bulletin 50:38-39.

Matthai, G. 1928. A monograph of the recent meandroid Astraeidae. Catalogue of the Madreporarian corals of the British Museum (Natural History), 7. British Museum, London.

McClintock, J. B., and K. R. Marion. 1993. Predation by the king helmet (Cassis tuberosa) on six-holed sand dollars (Leodia sexiesperforata) at San Salvador, Bahamas. Bulletin Of Marine Science 52(3):1013-1017.

McConnaughey, R. A., and S. D. Sulkin. 1984. Measuring the effects of thermoclines on the vertical migration of larvae of Callinectes sapidus (Brachyura: Portunidae) in the laboratory. Marine Biology 81(2):139-145.

Morrisey, D. J., A. J. Underwood, L. Howitt, and J. S. Stark. 1992. Temporal variation in soft-sediment benthos. Journal of Experimental Marine Biology and Ecology 164(2):233-245.

Mosher, C. 1980. Distribution of Holothuria arenicola in the Bahamas with observations on habitat behavior and feeding activity Echinodermata Holothuroidea. Bulletin of Marine Science 30:1-12.

Multer, H. G. 1977. Field guide to some carbonate rock environments. Florida Keys and western Bahamas. Iowa: Kendall-Hunt Publishing Company.

Negri, A. P., and A. J. Heyward. 2000. Inhibition of fertilization and larval metamorphosis of the coral Acropora millepora (Ehrenberg, 1834) by petroleum products. Marine Pollution Bulletin 41(7):420-427.

Nero, V. L. 2005. Abiotic and biotic influences on the composition of nearshore marine communities of The Bahamas. Thesis. University of Miami, Florida.

Nero, V.L. and K. Sullivan Sealey. 2005 Characterization of tropical near shore fish communities by coastal habitat status on spatially complex island systems. Environmental Biology of Fishes (2005) 73:437-444.

Nero, V.L. and K. Sullivan Sealey. 2007. Island-specific Responses of Bahamian Benthic Flora to Environmental Features. Caribbean Journal of Science (2007) 42(3).

Nichols, F. H., and J. K. Thompson. 1985. Time scales of change in the San Francisco Bay benthos. Hydrobiologia 129(1):121-138.

Okamoto, M., T. Sato, and S. Morita. 2000. Basic coral distribution data for long term monitoring at Sekesei Lagoon. OCEANS 2000 MT S/IEEE Conference and Exhibition 2:1383-1387.

Opresko, L., R. Thomas, and F. M. Bayer. 1976. A guide to the larger marine gastropods of Florida, the Gulf of Mexico, and the Caribbean Region. Florida: University of Miami Sea Grant Program.

Perus, J. et al. 2004. Coastal marine zoobenthos as an ecological quality element: a test of environmental typoloty and European Water Framework Directive. Coastline Reports 4(2004):27-38.

Pomponi, S. A. 1976. An ultrastructural study of boring sponge cells and excavated substrata. Florida Scientist 39(Suppl):11-12.

Raffaelli, D., M. Emmerson, M. Solan, C. Biles, and D. Paterson. 2003. Biodiversity and ecosystem processes in shallow coastal waters: and experimental approach. Journal of Sea Research 49(2):133-141.

Raut, D., T. Ganesh, N. V. S. S. Murty, A. V. Raman. 2005. Macrobenthos of Kakinada Bay in the Godavari delta, East coast of India: comparing decadal changes. Estuarine, Coastal and Shelf Science 62(4):609-620.

Reiss, H., and I. Kröncke. 2005. Seasonal variability of benthic indices: an approach to test the applicability of different indices for ecosystem quality assessment. Marine Pollution Bulletin 50(12):1490-1499.

Robertson, R. 1994. Two new tropical western Atlantic species of Epitonium, with notes on similar global species and natural history. Nautilus 107(3):81-93.

Robertson, R. 1986. The marine mollusks of the Bahama Islands: identification, systematics, zoogeography and natural history. American Malacological Bulletin 4:113.

Rosa, L. C., and C. E. Bemvenuti. 2006. Temporal variability of the estuarine macrofauna of the Patos Lagoon, Brazil. Revista de Biología Marina y Oceanografía 41(1):1-9.

Sale, P. F., and W. A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65(2):409-422.

Sánchez, J. A., C. S. McFadden, S. C. France, and H. R. Lasker. 2003. Molecular phylogenetic analyses of shallow-water Caribbean octocorals. Marine Biology 142(5):975-987.

Schriever, G. 1978. In situ observations on the behaviour and biology of the tropical spider crab Stenorhynchus seticornis Herbst (Crustacea, Decapoda/Brachyura). European Marine Biology Symposium 12:297-302.

Sealey, N. E. 2006. Bahamian Landscapes: An Introduction to the Geology and Physical Geography of The Bahamas, 3rd ed. Nassau, Bahamas: Macmillan Caribbean.

Sfriso, A., T. Birkemeyer, and P. F. Ghetti. 2001. Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds. Marine Environmental Research 52(4):323-249.

Shinn, E. A. 1966. Coral growth-rate, an environmental indicator. Journal of Paleontology 40(2):233-240.

Simboura, N., and A. Zenetos. 2002. Benthic indicators to use in ecological quality classification of Mediterranean soft bottom marine ecosystems, including a new biotic index. Mediterranean Marine Science 3:77-111.

Squires, D. F. 1958. Stony corals from the vicinity of Bimini, Bahamas, British West Indies. Bulletin of the American Museum of Natural History 115:215-262.

Sullivan Sealey, Sealey, K.. 2002. An ecoregional plan for the Bahamian Archipelago. Florida: Taras Oceanographic Foundation. 278 pp.

Sullivan Sealey, K. 2004. Large scale ecology impacts of development on tropical island systems: comparison of developed and undeveloped islands in the Central Bahamas. Bull. Mar. Sci. 75(2): 295–320.

Thistle, D. 1981. Natural physical disturbances and communities of marine soft bottoms. Marine Ecology Progress Series 6:223-228.

Turball, T. L. 1982. A study of the symbiotic relationship between the palaemonid shrimp Periclimenes pedersoni Chace (Crustacea, Decapoda, Caridea) and certain species of Serranid fishes in the Bahamas. Dissertation Abstracts International Biological Sciences and Engineering 42:4656.

Vaughan, W. 1915. The geologic significance of the growth-rate of the Floridian and Bahaman shoal-water corals. Journal of the Washington Academy of Sciences 5:591-600.

Wiedenmayer, F. 1977. Shallow-water sponges of the western Bahamas. Switzerland: Birkhauser Verlag.

Wells, J. W. 1974. Two new hermatypic scleractinian corals from the West Indies. Bulletin of Marine Science 23:925-932.

West, J. M., C. D. Harvell, and A. M. Walls. 1993. Morphological plasticity in a gorgonian coral (Briareum asbestinum) over a depth cline. Marine Ecology Progress Series 94:61-69.Whitlatch, R. B. et al. 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. Hydrobiologia 375-376(0):217-226.

Zeiller, W. 1974. Tropical Marine Invertebrates of Southern Florida and the Bahamas Islands. New York: Wiley.

Zettler, M. L. , D. Schiedek, and B. Bobertz. 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. Marine Pollution Bulletin 55(1-6):258-270.

Table 1. Comparison of proxy indicators for anthropogenic impacts (coastal development and marine threats) on Great Exuma and Guana Cay, Bahamas.

PARAMETER	GREAT EXUMA (Moss Town to Rolletown)	GUANA CAY, Abacos
Area (ha)	**2270.8**	**251.2**
Number of people	**3,571**	**170**
Population density (persons/ hectare)	**1.57**	**0.68**
Number of airports	**1**	**0**
Number of resorts/hotels	**7**	**3**
Number of major settlements (25 buildings or more)	**10**	**1**
Number of marinas and major anchorages	**14**	**7**
Number of Dive Tour Centers	**2**	**2**

Table 2. Univariate diversity indices (calculated with the DIVERSE function in PRIMER v5) for all surveys over time. Indices shown are the number of species present (S), species richness (d), Pielou's evenness (J'), and Shannon diversity (H').

Island	Survey Site Code	Date	Habitat	S	d	J'	H'
Exuma	OI	July 04	patch reef	24	5.573	0.9941	3.159
Exuma	OI	Jan 05	patch reef	27	6.252	0.9873	3.254
Exuma	OI	June 05	patch reef	36	7.686	0.9892	3.545
Exuma	OI	June 06	patch reef	30	6.738	0.983	3.343
Exuma	HB	July 04	hardbar	35	8.03	0.9966	3.543
Exuma	HB	Jan 05	hardbar	23	5.683	0.9905	3.106
Exuma	HB	June 06	hardbar	37	8.061	0.9885	3.569
Exuma	FC	July 04	patch reef	39	8.553	0.9833	3.602
Exuma	FC	June 05	patch reef	42	8.723	0.9764	3.649
Exuma	FC	June 06	patch reef	48	9.783	0.988	3.825
Guana	BBC5	Mar 04	patch reef	20	4.963	0.9937	2.977
Guana	BBC5	July 05	patch reef	31	7.015	0.9748	3.347
Guana	BBC5	July 06	patch reef	34	7.575	0.9859	3.477
Guana	JC3	July 05	hardbar	35	7.976	0.9867	3.508
Guana	JC3	July 06	hardbar	21	4.969	0.9886	3.01
Guana	JC1	Mar 04	hardbar	32	7.347	0.9895	3.429
Guana	JC1	July 05	hardbar	33	7.303	0.9818	3.433
Guana	JC1	July 06	hardbar	25	5.862	0.9838	3.167

Table 4. The top 5 species contributing to the differences in benthic macrofauna assemblages over time between the years (A) 2004 and 2005, (B) 2005 and 2006, and (C) 2004 and 2006 determined by SIMPER analysis (performed with PRIMER v5).

A)

Species	**Taxa**	**2004 Av.Abund**	**2005 Av.Abund**	**Contrib%**	**Cum. %**
Porites furcata	hard coral	2.00	0.00	2.32	2.32
Pseudopterogorgia sp.	soft coral	0.60	1.86	2.05	4.37
Montastrea annularis	hard coral	2.00	1.29	2.01	6.38
Millepora alcicornis	hard coral	1.60	0.86	1.89	8.27
Chondrilla nucula	sponge	1.80	2.29	1.87	10.14

B)

Species	**Taxa**	**2005 Av.Abund**	**2006 Av.Abund**	**Contrib%**	**Cum. %**
Holothuria mexicana	echinoderm	2.29	0.00	2.32	2.32
Aplysina fistularis	sponge	0.86	2.83	2.13	4.45
Echinometra lucunter	echinoderm	2.29	0.33	2.08	6.54
Anthosigmella varians	sponge	1.00	2.17	1.87	8.39
Echinometra viridis	echinoderm	0.00	1.83	1.84	10.23

C)

Species	**Taxa**	**2004 Av.Abund**	**2006 Av.Abund**	**Contrib%**	**Cum. %**
Anthosigmella varians	sponge	0.00	2.17	2.53	2.53
Echinometra lucunter	echinoderm	2.20	0.33	2.22	4.75
Echinometra viridis	echinoderm	0.00	1.83	2.13	6.88
Briareum asbestinum	soft coral	1.80	1.00	1.90	8.78
Millepora alcicornis	hard coral	1.60	1.00	1.85	10.63

Table 5. SIMPER analysis (performed with PRIMER v5) based on habitat type (patch reef vs. hardbar sites) showing the top 15 species contributing to the differences in benthic macrofauna assemblages.

Species	Taxa	Patch Av.Abund	Hard Bar Av.Abund	Contrib%	Cum.%
Pterogorgia anceps	soft coral	0.90	2.00	1.99	1.99
Millepora complanata	hard coral	1.80	0.00	1.98	3.97
Montastrea annularis	hard coral	2.10	1.00	1.88	5.85
Condylactis gigantea	anemone	1.00	2.13	1.81	7.65
Erthryopodium caribaeorum	soft coral	1.60	0.88	1.77	9.42
Diploria clivosa	hard coral	0.80	1.63	1.76	11.18
Chondrilla nucula	sponge	1.90	1.35	1.73	12.91
Aplysina fistularis	sponge	1.70	0.63	1.68	14.59
Briareum asbestinum	soft coral	1.80	1.75	1.68	16.27
Anthosigmella varians	sponge	1.50	0.50	1.67	17.94
Porites porites	hard coral	2.80	0.75	1.64	19.59
Millepora alcicornis	hard coral	1.60	0.50	1.63	21.21
Pseudopterogorgia sp.	soft coral	1.50	0.75	1.62	22.83
Holothuria mexicana	echinoderm	1.40	1.00	1.57	24.41
Diploria strigosa	hard coral	1.00	1.88	1.55	25.96