

## ECOLOGICAL STRUCTURE AND DYNAMICS OF NEARSHORE HARD-BOTTOM COMMUNITIES IN THE FLORIDA KEYS

*M. Chiappone and K. M. Sullivan*

### ABSTRACT

An ecological monitoring project was initiated in 1989 on two nearshore hard-bottom communities in the middle Florida Keys to document changes in community structure on nearshore benthic communities. The purpose of this monitoring project was three-fold: 1) to characterize nearshore hard-bottom communities in terms of dominant benthic flora and fauna; 2) to examine the biological variability between two initially similar communities; and 3) to assess the rate of change in benthic community structure over time. Survey methodologies were used to both characterize and monitor changes in the spatial patterning of benthos, and included substratum and lifeform characterization, species presence/absence inventories, and density and area coverage of benthic algae and invertebrates. Nearshore hard-bottom communities were characterized by low relief, low coral cover (<1%), a visual dominance of octocorals, and a seasonal change in algal abundance. Changes observed on nearshore communities included an increase in algal coverage and a mass mortality of milleporid hydrocorals associated with hyperthermal conditions in nearshore waters during the summer of 1991.

Ecological monitoring can assist in directing management action and conservation of marine protected areas throughout Florida and the Caribbean. Monitoring is the collection of information about the state of a system and its changes over time (Dahl, 1981; Spellerberg, 1991). Two features characterize all natural communities: 1) they are dynamic, and 2) they are spatially heterogeneous (Goldsmith, 1991). A goal in monitoring natural communities is the identification and segregation of natural fluctuations in communities or populations from changes induced by anthropogenic impacts (Brown and Howard, 1985). Results from monitoring programs on tropical marine communities indicate that significant changes in benthic community structure may occur in the absence of known anthropogenic disturbances (Bak and Luckhurst, 1980; Davis, 1982; Dustan and Halas, 1987).

The Florida Keys and adjacent Florida Bay represent a mosaic of soft-sediment and hard-bottom communities that exhibit extreme variability in terms of community size, dominant species, and environmental controls on community structure (Jaap, 1984). Historically the southeast Florida coast represented a subtropical ecosystem with estuarine and marine components. Florida Bay was an estuarine lagoon, but has been transformed to a marine lagoon with the alteration of freshwater flow through the Everglades watershed. A wide, shallow shelf area from northern Florida Bay out to the reef tract supports a great diversity of benthic communities. This community mosaic is determined by various climatic and oceanographic forces, which affect both the structuring and patterning of benthic communities from inshore to offshore.

Low-relief, nearshore hard-bottom communities represent one major category of marine benthic communities in south Florida, and are considered the dominant hard-bottom community class in the Florida Keys; seagrass beds are the dominant soft-sediment communities (Marszalek, 1981a). Nearshore hard-bottom communities are common throughout the tropical western Atlantic and often cover large areas in coastal ecosystems. Low-relief hard-bottom communities typically occur shoreward of fringing or barrier reefs in back reef lagoon areas. In south Florida, low-relief hard-bottom communities are characterized by their proximity to shore,

shallow depth ( $<3$  m), and visual dominance of octocorals. These communities have also been referred to as live-bottom communities and alcyonarian-sponge communities (Zischke, 1973; Opresko, 1973; Jaap, 1984).

An ecological monitoring program was initiated in 1989 on two nearshore hard-bottom communities in the middle Florida Keys. Monitoring programs in south Florida have documented changes on offshore reef communities related to dredging (Marszalek, 1981b), thermal stress (Porter et al., 1982), and natural destructive events (e.g., hurricanes) (Shinn, 1976). However, little attempt has been made to provide information on characteristics and changes in nearshore benthic communities. This paper presents changes documented on low-relief hard-bottom communities over a 4-year period.

## MATERIALS AND METHODS

*Survey Sites.*—Two nearshore hard-bottom communities in the middle Florida Keys between Long Key and Lower Matecumbe Key were selected as monitoring sites from 1989 to 1992. The Craig Key site (CKS) is located at  $24^{\circ}49.703'N$ ,  $80^{\circ}45.826'W$  and is approximately 100 m offshore on the Atlantic Ocean side of Craig Key, an island built from fill during the construction of the overseas highway. The Fiesta Key site (FKS) is located  $24^{\circ}50.544'N$ ,  $80^{\circ}47.785'W$  and is approximately 100 m from shore on the Florida Bay side of Fiesta Key, an island also built from fill. Sites were selected based on similar depth ( $<2$  m), low topographic complexity, and location (e.g., both sites are near Channel Five east of Long Key).

Both CKS and FKS are classified as low-relief hard-bottom communities; these communities are nearshore ( $<500$  km), exhibit lower three-dimensional complexity compared to other reef types in the Keys (e.g., patch reefs, bank reefs), and are composed of a sparse assemblage of benthic algae, sponges, octocorals, and stony corals (Jaap, 1984). Existing habitat maps of the Florida Keys indicate that low-relief hard-bottom communities covered the largest area relative to patch reefs and bank reefs (Marszalek, 1981a). The hypothesis of this study was that the nature and rate of change in benthic community structure should be similar for both sites. Both sites are likely to be influenced by similar meso-scale oceanographic events (e.g., cold fronts).

*Survey Methodologies.*—Low-altitude, natural-color aerial photographs of each site were taken each year, and aided in the placement of belt quadrat sampling stations. The purpose of the belt quadrat sampling was to assess the maximum variability in benthic patterning across each community (Sullivan and Chiappone, in press). Two 25-m transect lines, marked in 1-m increments, were placed randomly across each site each year. Transect lines were used as a guide for the placement of 1-m<sup>2</sup> quadrats, which were placed contiguously along the transect lines. Sampling efficiency in terms of the number of quadrats sampled and the length of transect lines was determined using species-area curves.

Lifeform characterization was used to characterize the study sites and document gross changes in benthic community structure. Benthic lifeforms were visually estimated in 1-m<sup>2</sup> quadrats, and included algae, sponges, octocorals, and stony corals. Coverage categories included: (0) for 0%, (1) for 0–1%, (2) for 1–5%, (3) for 5–25%, (4) for 25–50%, (5) for 50–75%, and (6) for  $>75\%$ . This method is not useful in detecting small changes ( $<10\%$ ), but can be used to detect seasonal changes in algal abundance or gross changes ( $>25\%$ ) in benthic community structure.

Belt quadrat surveys were used to collect detailed information on the spatial patterning of benthos. Within each 1-m<sup>2</sup> quadrat, sponges and coral colonies were identified and counted. An individual or colony was defined as any individual growing independently of its neighbors. In cases where a coral colony was clearly separated by the death of intervening portions, each living part was considered to be a separate colony (Loya, 1972). Sponges and stony coral colonies were measured to determine planar area coverage (cm<sup>2</sup>). For each sponge or coral colony, dimensions (e.g., diameter, length, width) were measured and used to estimate area coverage (cm<sup>2</sup>). Sponges were measured to the nearest 0.5 cm and corals to the nearest 0.1 cm. Octocorals were measured for colony heights to the nearest centimeter.

*Data Analysis.*—Information from belt quadrat surveys was used to quantify the density and size distribution of sponges and corals. Coverage (cm<sup>2</sup> m<sup>-2</sup>) was calculated for sponges and stony corals. A one-way analysis of variance (ANOVA) was used to test for significant changes in benthic invertebrate abundance (density and coverage) within sites over time and between study sites (Zar, 1984).

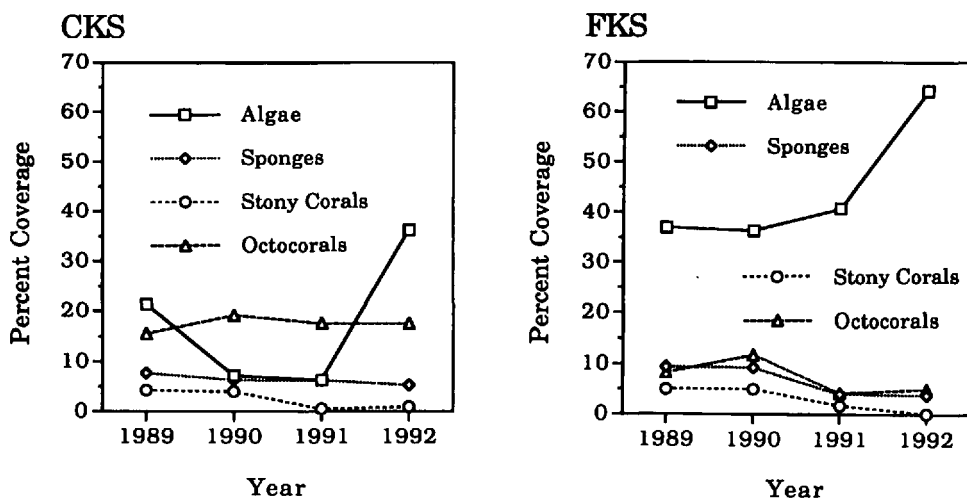


Figure 1. Percent coverage of benthic lifeforms at sites Craig Key (CKS) and Fiesta Key (FKS) at 1989 to 1992. □: algae. ◇: sponges. ○: stony corals. △: octocorals.

## RESULTS

Site CKS was initially characterized by a co-dominance of sponges, corals, and algae (Fig. 1). There has been little change in substrata characteristics since 1989, although coverage of rubble has increased since 1991. The increase in rubble is due to the mortality of *Millepora alcicornis* colonies. Algal coverage at CKR has increased from 21% in 1989 to 36% coverage by 1992. There is a seasonal fluctuation in algal abundance at CKS. During May, 1992, there was a large bloom of *Dasya baillouviana* at CKS, which covered many of the taller (>50 cm) octocoral colonies. By the fall of 1992, the abundance of this species declined and most of the octocorals were no longer covered with the algae.

The algal flora at CKS is diverse (23 species), but is dominated by two species, *Laurencia intricata* and *Halimeda opuntia*. Sponges at CKS are represented by

Table 1. Quadrat summary data for Craig Key (CKS) monitoring site. Density of sponges and coral colonies expressed as the mean number per m<sup>2</sup>. Colony sizes for sponges and stony corals expressed in cm<sup>2</sup>. Octocoral colony sizes expressed as mean colony heights (cm). Mean coverage of sponges and stony corals expressed as cm<sup>2</sup> per m<sup>2</sup>. Numbers in parentheses represent 1 standard deviation.

| Taxa         | Year | Density<br>(no. m <sup>-2</sup> ) | Size<br>(cm <sup>2</sup> or cm) | Coverage<br>(cm <sup>2</sup> m <sup>-2</sup> ) |
|--------------|------|-----------------------------------|---------------------------------|------------------------------------------------|
| Sponges      | 1989 | 2.6 (2.7)                         |                                 |                                                |
|              | 1990 | 6.9 (3.1)                         | 57 (265)                        | 392 (715)                                      |
|              | 1991 | 9.2 (4.8)                         | 43 (141)                        | 395 (584)                                      |
|              | 1992 | 13.4 (8.7)                        | 21 (49)                         | 280 (266)                                      |
| Stony corals | 1989 | 2.1 (1.0)                         |                                 |                                                |
|              | 1990 | 7.0 (5.2)                         | 55.8 (192.3)                    | 389 (554)                                      |
|              | 1991 | 5.2 (3.1)                         | 10.0 (30.0)                     | 49 (83)                                        |
|              | 1992 | 4.1 (1.7)                         | 26.8 (103.5)                    | 88 (189)                                       |
| Octocorals   | 1989 | 3.6 (2.4)                         | 36.1 (19.4)                     |                                                |
|              | 1990 | 5.3 (2.5)                         | 45.5 (20.8)                     |                                                |
|              | 1991 | 5.9 (2.8)                         | 45.9 (22.4)                     |                                                |
|              | 1992 | 4.9 (2.5)                         | 47.5 (22.1)                     |                                                |

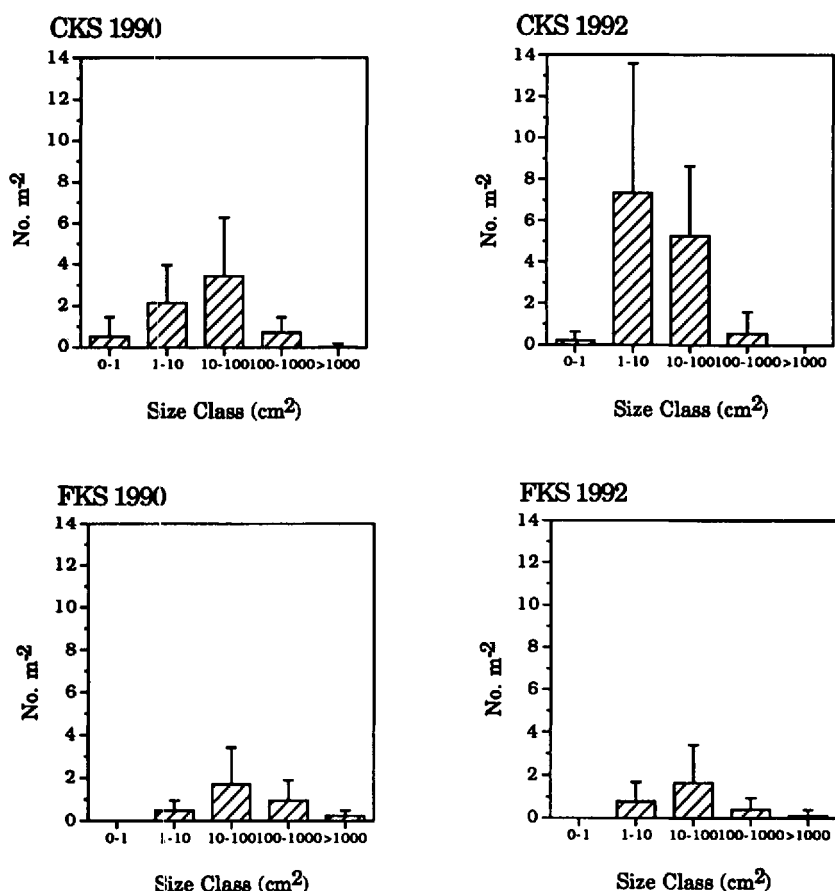


Figure 2. Size-frequency distribution of sponges at CKS and FKS from 1990 to 1992. Sponges have been grouped into logarithmic size classes (cm<sup>2</sup>). Values represent the mean number of sponges of a particular size class per m<sup>2</sup>. Error bars represent 1 standard deviation.

over 12 species and are more abundant than corals. An average of 13 sponges were recorded per m<sup>2</sup> during 1992 (Table 1). The most abundant sponges are *Dysidea etheria*, *Aplysina fulva*, and *Chondrilla nucula*, which accounted for 85% of sponge density in 1992. Sponge sizes are small (<100 cm<sup>2</sup>) with the exception of larger (>100 cm<sup>2</sup>) specimens of *Spheciospongia vesparium*, *Ircinia campana*, and *I. felix*. Over 95% of sponges in 1992 were less than 100 cm<sup>2</sup> in size (Fig. 2). Two patterns of change have been evident in sponge populations at CKS: (1) an increase in the density of sponges and (2) a concurrent decrease in mean sponge size.

Stony corals are represented by 12 species at CKS. Common species include *Millepora alcicornis*, *Siderastrea radians*, *Porites porites* forma *divaricata*, *Solenastrea bournoni*, *S. hyades*, *Favia fragum*, and *Oculina diffusa*. *S. radians*, *P. porites* forma *divaricata*, and *M. alcicornis* are the most abundant, accounting for 80% of total colony numbers at CKS in 1992. Coral coverage at CKS is low (<1%) (Table 1). Two coral species, *S. bournoni* and *O. diffusa*, account for 90% of coral cover at CKS. There is a large range in colony sizes, although over 90% of the colonies are less than 100 cm<sup>2</sup> in size. The largest coral colonies at CKS

Table 2. Monitoring summary for site CKS. Significant changes ( $P < 0.05$ ; one-way ANOVA and Tukey's Test) in measured attributes are denoted by an asterisk (\*). ns: not significant ( $P > 0.05$ ).

| Taxa         | Attribute | 1989-1990     | 1990-1991        | 1991-1992                   |
|--------------|-----------|---------------|------------------|-----------------------------|
| Sponges      | Density   | Increase(*)   | Increase (*)     | Increase (*)                |
|              | Size      |               | Decrease (*)     | Decrease (*)                |
|              | Coverage  |               | Increase (ns)    | Decrease (*)                |
|              | Result    |               | Fragmentation    | Mortality and fragmentation |
| Stony corals | Density   | Increase (*)  | Decrease (ns)    | Decrease (ns)               |
|              | Size      |               | Decrease (*)     | Increase (*)                |
|              | Coverage  |               | Decrease (*)     | Increase (*)                |
|              | Result    |               | Colony mortality | Loss of small colonies      |
| Octocorals   | Density   | Increase (*)  | Increase (ns)    | Decrease (*)                |
|              | Size      | Increase (*)  | Increase (ns)    | Increase (ns)               |
|              | Result    | Fragmentation | Fragmentation    | Mortality of small colonies |

(>100 cm<sup>2</sup>) are represented by *S. bournoni*, *S. hyades*, and *O. diffusa*. Corals increased in density, but declined in size (Table 2). A mortality of *M. alcicornis* colonies in 1991 accounted for the loss of coral cover and a decrease in colony size (Fig. 2). Recruitment of *S. radians* and *F. fragum* has increased the density of corals.

Octocorals at CKS are represented by 14 species and were more abundant than stony corals in 1992 (Table 1). Octocoral density increased during the study period with mean colony height exhibiting little fluctuation (Fig. 3). Octocoral density is dominated by *Eunicea palmeri*, *Pseudoplexaura flagellosa*, and *Briareum asbestinum*, which accounted for 87% of octocoral colony numbers during 1992.

The Fiesta Key site (FKS) is characterized by a dominance of algae (>50% cover) on a low-relief limestone platform. Lifeform coverage is characterized by a sparse (<10%) coverage of sponges, stony corals, and octocorals (Fig. 1). Algal coverage increased from 37% in 1989 to 64% in 1992; in lieu of the insensitivity of this method to small (<10%) changes, a 30% increase in algae since 1989 is considered to be a significant change at FKS. Similar to CKS, there is a seasonal abundance pattern of algae at FKS. There was an increase in algal coverage during the spring of 1992, which was the result of a bloom of *Laurencia intricata* (M. Chiappone, personal observation). The coverage of this species was significantly reduced by the fall of 1992. During the fall of 1992, more than 50% of the bottom was covered by a single species, *Cladophora prolifera*, which had a sparse coverage in the spring of 1992. The algal flora at FKS is represented by 26 species and was dominated by *Laurencia intricata* before the fall of 1992.

Sponges at FKS are represented by 11 species and are dominated by *Spheciospongia vesparium* and *Tethya diploderma*, which accounted for more than 50% of sponge density in 1992. Sponge coverage at FKS is low (<4%), but higher than at CKS (Table 3). Sponge cover is dominated by a few large specimens of *S. vesparium*. Changes in the sponge fauna at FKS included an increase in density and decrease in sponge size (Tables 3, 4).

Corals at FKS are only represented by three species, *Siderastrea radians*, *Porites porites* forma *divaricata*, and *Solenastrea hyades*. *S. radians* is the dominant coral, accounting for 85% of total colony numbers in 1992, but was recorded in only 50% of the quadrats. All coral colonies at FKS are less than 100 cm<sup>2</sup> in size (Fig. 3). Colony density has remained stable since 1989, although mean colony size decreased as a result of recruitment of small *S. radians* colonies and fragmentation of *P. porites* forma *divaricata* colonies (Table 4).

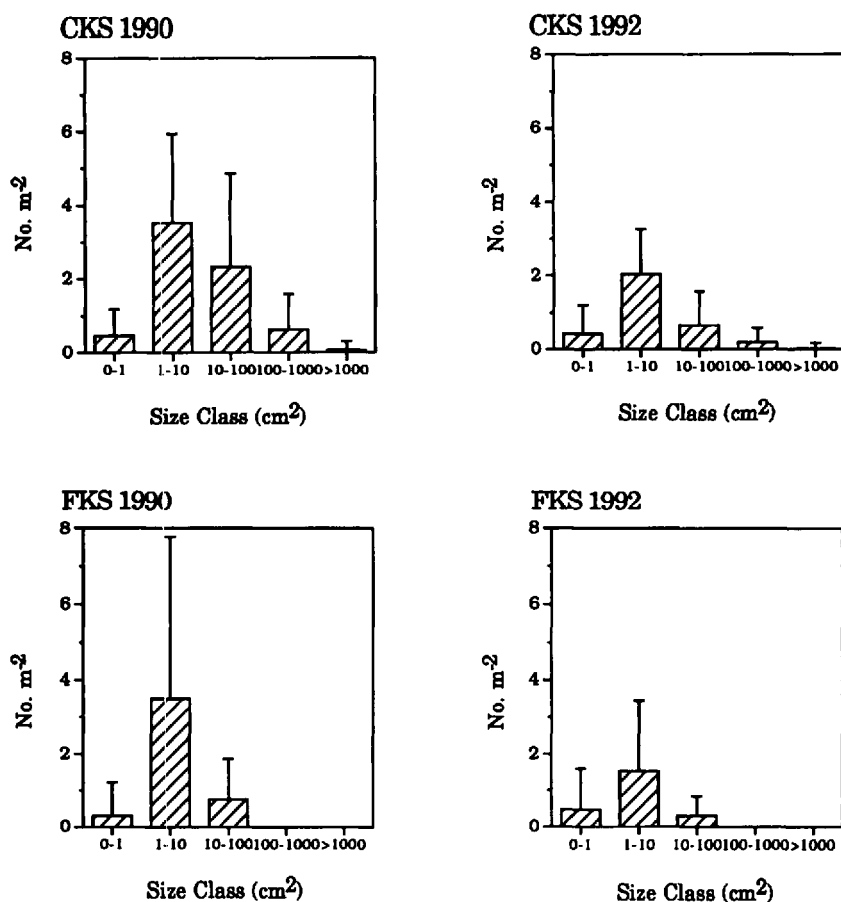


Figure 3. Size-frequency distribution of stony corals at CKS and FKS from 1990 to 1992. Stony corals have been grouped into logarithmic size classes (cm<sup>2</sup>). Values represent the mean number of colonies of a particular size class per m<sup>2</sup>. Error bars represent 1 standard deviation.

Table 3. Quadrat summary data for Fiesta Key (FKS) monitoring site. Density of sponges and coral colonies expressed as the mean number per m<sup>2</sup>. Colony sizes for sponges and stony corals expressed in cm<sup>2</sup>. Octocoral colony sizes expressed as mean colony heights (cm). Mean coverage of sponges and stony corals expressed as cm<sup>2</sup> per m<sup>2</sup>. Numbers in parentheses represent 1 standard deviation.

| Taxa         | Year | Density<br>(no. m <sup>-2</sup> ) | Size<br>(cm <sup>2</sup> or cm) | Coverage<br>(cm <sup>2</sup> m <sup>-2</sup> ) |
|--------------|------|-----------------------------------|---------------------------------|------------------------------------------------|
| Sponges      | 1989 | 1.5 (1.1)                         |                                 |                                                |
|              | 1990 | 3.4 (1.9)                         | 215 (415)                       | 725 (768)                                      |
|              | 1991 | 1.2 (1.2)                         | 179 (277)                       | 292 (312)                                      |
|              | 1992 | 2.9 (1.9)                         | 132 (403)                       | 380 (650)                                      |
| Stony corals | 1989 | 2.5 (3.4)                         |                                 |                                                |
|              | 1990 | 4.6 (4.7)                         | 7.6 (10.9)                      | 35 (38)                                        |
|              | 1991 | 1.3 (1.9)                         | 9.9 (20.9)                      | 13 (28)                                        |
|              | 1992 | 2.3 (2.7)                         | 4.6 (5.1)                       | 11 (13)                                        |
| Octocorals   | 1989 | 1.5 (1.6)                         | 44.5 (14.8)                     |                                                |
|              | 1990 | 2.6 (2.5)                         | 44.2 (14.8)                     |                                                |
|              | 1991 | 0.7 (0.7)                         | 37.0 (10.8)                     |                                                |
|              | 1992 | 1.4 (1.8)                         | 40.3 (16.4)                     |                                                |

Table 4. Monitoring summary for site FKS. Significant changes ( $P < 0.05$ ; one-way ANOVA and Tukey's Test) in measured attributes are denoted by an asterisk (\*). ns: not significant ( $P > 0.05$ ).

| Taxa         | Attribute | 1989-1990     | 1990-1991        | 1991-1992                   |
|--------------|-----------|---------------|------------------|-----------------------------|
| Sponges      | Density   | Increase (*)  | Decrease (*)     | Increase (*)                |
|              | Size      |               | Decrease (*)     | Decrease (*)                |
|              | Coverage  |               | Decrease (*)     | Increase (*)                |
|              | Result    |               | Mortality        | Fragmentation               |
| Stony corals | Density   | Increase (*)  | Decrease (*)     | Increase (ns)               |
|              | Size      |               | Increase (ns)    | Decrease (*)                |
|              | Coverage  |               | Decrease (*)     | Decrease (ns)               |
|              | Result    |               | Colony mortality | Fragmentation and mortality |
| Octocorals   | Density   | Increase (*)  | Decrease (*)     | Increase (ns)               |
|              | Size      | Decrease (ns) | Decrease (*)     | Increase (ns)               |
|              | Result    | Fragmentation | Mortality        | Fragmentation               |

Octocorals at FKS are only represented by three species, *Pterogorgia anceps*, *Pseudopterogorgia americana*, and *Briareum asbestinum*. *P. anceps* is dominant and accounted for 85% of octocoral colonies in 1992, but was recorded in only 50% of the sampled quadrats. Since 1989, octocoral density has fluctuated as a result of fragmentation of *B. asbestinum* colonies with a concurrent decrease in mean colony height (Table 4, Fig. 4).

## DISCUSSION

A challenge in monitoring tropical estuarine and marine ecosystems is the segregation of natural changes in community structure from changes induced by anthropogenic impacts (Hatcher et al., 1989). The dynamics and causal mechanisms of change in natural systems are not well understood (Davis, 1982). Human impacts may often mimic or act synergistically with natural disturbances, making the assessment of human impacts even more difficult (Jaap, 1984). Acute physical disturbances of anthropogenic origin may be identified by the localization and

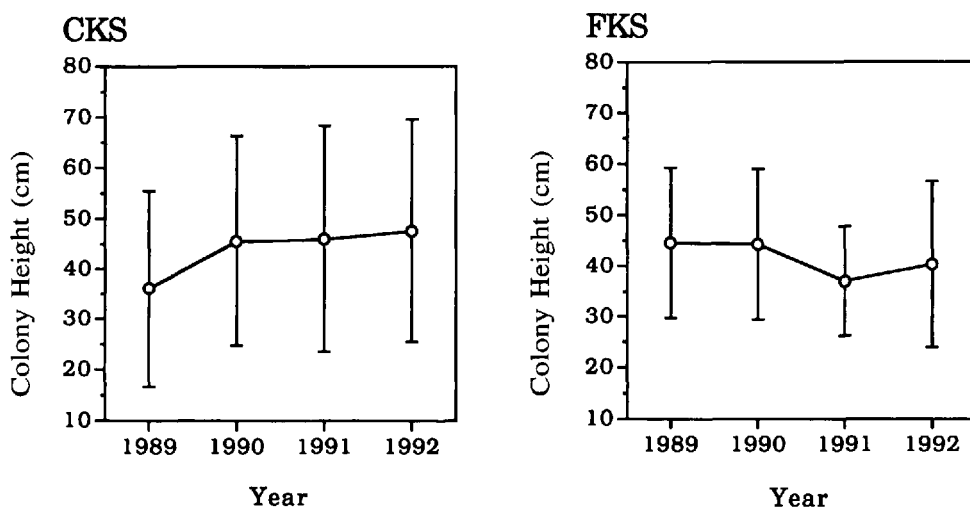


Figure 4. Octocoral colony sizes from CKS and FKS from 1989 to 1992. Values represent the mean height (cm) of colonies. Error bars represent 1 standard deviation.

severity of the impact (e.g., vessel groundings, anchor damage). Assessment of localized physical impacts from known causes requires: 1) historical or baseline information of fauna and community structure and 2) assessment of the extent and area of visible physical damage. The documentation of damage or change in community structure is obvious though the long-term consequences of such damage is unclear. In contrast, changes induced by low-level chronic stresses, including changes in water quality and circulation, require not only baseline information on community structure, but also information on the patterns of change in the benthos over time. The resilience of the benthic community in part defines its function within a larger ecosystem. Monitoring at the species-level may provide essential data on how low-level chronic impacts affect the rate and nature of change in benthic communities over a time scale of years.

This study documented patterns of change of nearshore hard-bottom communities in the Florida Keys. The selection of paired study sites aided in assessing the biological variability of two initially similar communities. FKS experienced reductions in species numbers and abundance; CKS exhibited increases in abundance of sessile benthic invertebrates. The notable exception to this is the large loss of coral coverage at CKS from 1990 to 1991. The decrease in coral coverage at CKS was caused by the mortality of *Millepora alcicornis* colonies; dramatic change can be associated with a documented Keys-wide phenomena: hyperthermal conditions reported during the summer of 1991. The loss of area coverage at CKS was species-specific (*Millepora alcicornis*), and during the resurvey of 1991, most colonies of this species were still bleached. The area coverage of this coral changed drastically, but the species re-appeared on the site within a year.

Temperature and sedimentation are likely to be the two most important natural controls on community structure of nearshore hard-bottom communities in the Florida Keys. Results from monitoring nearshore hard-bottom sites in the middle Keys indicate several characteristics in community structure. First, the lack of hermatypic coral species has resulted in low topographic complexity in nearshore areas. Coral populations were composed of small colonies that are resistant to environmental fluctuations in temperature and sedimentation. A diverse fauna of algae is represented that exhibits a seasonal fluctuation in abundance. Understanding the heterogeneity and complexity of natural changes allows for the evaluation of: 1) the rate of change and 2) the nature of change in benthos to determine the extent of influence from anthropogenic changes in water circulation or quality.

Disruptions in nutrient levels resulting from development, storm water runoff, and surface discharge have been implicated in the degradation of nearshore water quality in the Florida Keys, although it remains uncertain whether nutrients from various sources have had significant effects on the outer reef tract (Lapointe et al., 1990; Szmant, 1991). The exact causal mechanism of nutrient loading is not well understood, particularly for non-point sources of nutrients (e.g., injection wells) (Johannes, 1980; Lewis, 1987), and it remains difficult to model the behavior of nutrients in tropical aquatic systems (Andrews and Muller, 1983; Johannes et al., 1983; Furnas, 1992). Offshore reef areas in southern Florida are generally well-flushed due to the proximity of the Gulf Stream. It has been suggested that sewage effluent has had a less severe impact on the Florida Keys compared to other marine ecosystems with enclosed lagoons or embayments (Banner, 1974; Smith et al., 1981; Marszalek, 1987).

In contrast, nearshore hard-bottom communities are more acutely impacted by dredge-and-fill development along the island chain. These communities are important in the Florida Keys ecosystem as refuge for juvenile stages of important fishery target species (*Panulirus argus*), and potentially as preliminary indicators

of eutrophication (Marx and Herrnkind, 1985). Inshore-to-offshore recruitment of invertebrate and fish larvae will be affected by the condition of nearshore benthic communities. Data on nearshore benthic community structure should likely guide water column sampling, particularly as related to the effects of nutrient enhancement or changes in circulation from anthropogenic sources.

Sampling regimes that address the scale and dynamics of nutrients in the water column will be difficult to design and implement. Benthic sampling may provide less ambiguous and costly information on changes induced by natural versus anthropogenic disturbances. The ability of scientists to guide and influence management and restoration efforts in the Everglades watershed and Florida Bay depends on the extent to which historical communities can be compared and contrasted to the current system ecology. The question initially to be resolved is what changes can be documented in the course of 70 years of intensive alteration of water flow and development. Although causal mechanisms are critical to restoration planning and monitoring, the more immediate questions are what has changed and on what time scale? This study suggests that the rapid (years) change in: 1) occurrence of species, 2) size-frequency distribution of individuals, 3) size-selective mortality of individuals, and 4) loss of co-dominance of benthic flora and fauna on near-shore hard-bottom communities can be used to begin assessment of low-level stresses on benthic communities. A long-term goal of marine benthic ecology should be the development of methods that allow for the evaluation of community resilience in responding to climatic variability and the formulation of hypotheses on the potential anthropogenic changes induced by coastal development.

#### ACKNOWLEDGMENTS

The order of authorship is alphabetical; both authors contributed equally to the manuscript. The authors wish to acknowledge the field assistance of Mr. R. Sluka, Mr. J. Levy, Ms. N. Black and Ms. Y. Paroz. Support was provided by The Nature Conservancy Florida Keys Initiative and the University of Miami Marine Science Program. A special thanks is due to the staff of the Keys Marine Lab on Long Key, Florida, for field assistance and boat support. Sea and Sky Foundation provided low-altitude aerial photographs. This manuscript was significantly improved by comments from two anonymous reviewers and Dr. R. Fujita of the Environmental Defense Fund.

#### LITERATURE CITED

- Andrews, J. C. and H. Muller. 1983. Space-time variability of nutrients in a lagoonal patch reef. *Limnol. Oceanogr.* 28: 215-227.
- Bak, R. P. M. and B. E. Luckhurst. 1980. Constancy and change in coral reef habitats along depth gradients at Curaçao. *Oecologia (Berlin)* 47: 145-155.
- Banner, A. H. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. Pages 685-702 in Great Barrier Reef Committee, eds. *Proceedings of the Second International Coral Reef Symposium*, Vol. 2. Brisbane, Australia.
- Brown, B. E. and L. S. Howard. 1985. Assessing the effects of "stress" on reef corals. *Adv. Mar. Biol.* 22: 1-63.
- Dahl, A. L. 1981. Monitoring coral reefs for urban impact. *Bull. Mar. Sci.* 31: 544-551.
- Davis, G. E. 1982. A century of natural change in coral distribution at Dry Tortugas: a comparison of reef maps from 1881 to 1976. *Bull. Mar. Sci.* 32: 608-623.
- Dustan, P. and J. C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* 6: 91-106.
- Furnas, M. J. 1992. The behavior of nutrients in tropical aquatic ecosystems. Pages 30-65 in D. W. Connell and D. W. Hawker, eds. *Pollution in tropical aquatic systems*. CRC Press, Boca Raton, Florida.
- Goldsmith, F. B. 1991. *Monitoring for conservation and ecology*. Chapman and Hall, New York.
- Hatcher, B. G., R. E. Johannes and A. I. Robertson. 1989. Reviews of research relevant to the conservation of shallow tropical marine ecosystems. *Oceanogr. Mar. Biol. Ann. Rev.* 27: 337-414.

- Jaap, W. C. 1984. The Ecology of South Florida Coral Reefs: A Community Profile. U.S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-82/08, Washington, D.C. 138 pp.
- Johannes, R. E. 1980. The ecological significance of the submarine discharge of groundwater. *Mar. Ecol. Prog. Ser.* 3: 365-373.
- , W. J. Wiebe and C. J. Crossland. 1983. Three patterns of nutrient flux in a coral reef community. *Mar. Ecol. Prog. Ser.* 12: 131-136.
- Lapointe, B. E., J. D. O'Connell and G. S. Garrett. 1990. Effects of on-site disposal systems on nutrient relations of groundwaters and nearshore surface waters of the Florida Keys. *Biogeochemistry* 10: 289-307.
- Lewis, J. B. 1987. Measurements of groundwater seepage flux onto a coral reef: spatial and temporal variation. *Limnol. Oceanogr.* 32: 1165-1169.
- Loya, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar. Biol.* 13: 100-123.
- Marszalek, D. S. 1981a. Florida reef tract marine habitat and ecosystem (map series). Published in cooperation with the Florida Department of Natural Resources, U.S. Department of the Interior Bureau of Land Management and the Rosenstiel School Marine and Atmospheric Science, University of Miami, Miami, Florida.
- . 1981b. Impact of dredging on a subtropical reef community, southeast Florida, U.S.A. Pages 147-153 in E. D. Gomez, C. E. Birkeland, R. W. Buddemeir, R. E. Johannes, J. A. Marsh, Jr. and R. T. Tsuda, eds. *Proceedings of the Fourth International Coral Reef Symposium*, Vol. 1. Manila, Philippines.
- . 1987. Sewage and eutrophication. Pages 77-90 in B. Salvat, ed. *Human impacts on coral reef: facts and recommendations*. Antenne Museum E.P.H.E., French Polynesia.
- Marx, J. M. and W. F. Herrnkind. 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile lobsters, *Panulirus argus*. *Bull. Mar. Sci.* 36: 423-431.
- Opreko, D. M. 1973. Abundance and distribution of shallow-water gorgonians in the area of Miami, Florida. *Bull. Mar. Sci.* 23: 535-557.
- Porter, J. W., J. F. Battey and G. J. Smith. 1982. Perturbation and change in coral reef communities. *Proc. Nat. Acad. Sci. U.S.A.* 79: 1678-1681.
- Shinn, E. A. 1976. Coral reef recovery in Florida and the Persian Gulf. *Envir. Geol.* 1: 241-254.
- Smith, S. V., W. J. Kimmerer, E. A. Laws, R. E. Brock and T. W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci.* 35: 279-402.
- Spellerberg, I. F. 1991. *Monitoring ecological change*. Cambridge University Press, New York.
- Sullivan, K. M. and M. Chiappone. 1993. Hierarchical methodologies and sampling design for conservation monitoring of tropical marine hard-bottom communities. *J. Aquat. Con.* 3: 169-187.
- Szmant, A. M. 1991. Inshore-offshore patterns of nutrient and chlorophyll concentration along the Florida Reef Tract. Pages 42-62 in *Sustained ecological research related to management of the Florida Keys Seascape. SEAKEYS Phase I. Final Report to the John D. and Catherine T. MacArthur Foundation World Environment and Resources Program from the Florida Institute of Oceanography*, St. Petersburg, Florida.
- Zar, J. H. 1984. *Biostatistical analyses*, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.
- Zischke, J. A. 1973. An ecological guide to the shallow-water marine communities of Pigeon Key, Florida. St. Olaf College, Northfield, Minn. 47 pp.

DATE ACCEPTED: October 14, 1993.

ADDRESS: The Nature Conservancy, Florida and Caribbean Marine Conservation Science Center, University of Miami, P.O. Box 249118, Coral Gables, Florida 33124.