

Coral communities of Biscayne Bay, Florida and adjacent offshore areas: diversity, abundance, distribution, and environmental correlates

DIEGO LIRMAN*, BETH ORLANDO, SILVIA MACIÁ, DEREK MANZELLO,
LOUIS KAUFMAN, PATRICK BIBER and TAHZAY JONES

*Marine Biology and Fisheries Division, Rosenstiel School of Marine and Atmospheric Science,
University of Miami, Miami, USA*

ABSTRACT

1. Hardbottom habitats of Biscayne Bay, a shallow lagoon adjacent to the city of Miami, Florida, USA, contain a limited number of coral species that represent a small subset of the species found at nearby offshore hardbottom and reef habitats of the Florida Reef Tract. Although the physical characteristics of this basin make it a marginal environment for coral growth, the presence of dense populations of *Siderastrea radians* and *Porites furcata* indicate that these, as well as other corals that are found at lower densities, are able to tolerate extreme and fluctuating conditions. Three factors, temperature, sedimentation, and salinity, appear to limit coral abundance, diversity, and distribution within Biscayne Bay.

2. Temperatures exhibit high frequencies of extreme high and low values known to cause coral stress and mortality elsewhere. Similarly, sedimentation rates are very high and sediment resuspension caused by currents, storms and boating activities commonly bury corals under sediment layers. Sediment burial was shown experimentally to influence growth and mortality of *S. radians*.

3. The salinity of Biscayne Bay is influenced by freshwater inputs from canal, sheetflow and groundwater sources that create a near-shore environment with low mean salinity and high salinity fluctuation. Coral communities along this western margin have the lowest coral density and species richness. Chronic exposure to low salinity was shown experimentally to cause a decrease in the growth of *S. radians*.

4. The location of Biscayne Bay, downstream of a large restoration effort planned for the Everglades watershed, highlights the need to understand the relationship between the physical environment and the health of benthic communities. The data presented here provide the type of scientific information needed so that management decisions can take into account the potential impacts of human activities on the health of coral populations that are already near their tolerance limits for temperature, salinity, and sedimentation.

Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: hardbottom habitats; coral communities; Biscayne Bay; Florida; salinity; sedimentation; boating; Everglades restoration

*Correspondence to: D. Lirman, Marine Biology and Fisheries Division, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA. E-mail: dlirman@rsmas.miami.edu

INTRODUCTION

Biscayne Bay is a shallow subtropical lagoon adjacent to the city of Miami, Florida. The location of Biscayne Bay along a highly populated, rapidly growing urban centre and just downstream of the proposed Everglades restoration activities makes this important natural resource especially vulnerable to human disturbances and changes in water quality. The purpose of this study is to document the abundance, diversity and distribution of hard corals within Biscayne Bay in relation to environmental factors such as salinity and sedimentation, as a baseline assessment against which the effects of future watershed restoration activities may be discerned. In addition, field surveys supplemented by exposure experiments are used to evaluate the potential impacts of the proposed Everglades restoration activities on the health of coral populations within this coastal ecosystem.

The hydrology of South Florida has been drastically modified in the last 50 years by the construction of the Central and Southern Florida Project. This water management system comprises an extensive network of levees, canals, water control structures and pump stations that have altered the natural timing, quantity and quality of freshwater flow across the landscape and caused significant modifications in the structure and function of upland and coastal habitats (McIvor *et al.*, 1994; Browder and Ogden, 1999). One example of the recent drastic ecological changes attributed to the altered hydrology was the mass mortality of seagrasses within Florida Bay, where over 4000 ha of *Thalassia testudinum* beds were lost starting in 1987 (Zieman *et al.*, 1989, 1999; Robblee *et al.*, 1991; Durako, 1994). Although the exact causes of this demise are still being debated, the reduction in freshwater inputs and modification of salinity fields within coastal lagoons as a consequence of the water management system now in place are often cited as likely triggers (Smith *et al.*, 1989; Fourqurean and Robblee, 1999). Similarly, hypersalinity and reduced water levels have been correlated with a decline in pink shrimp (*Penaeus duorarum*) catches (Browder, 1985; Browder *et al.*, 1999).

In response to these patterns of environmental degradation, the recently approved, multi-billion dollar Comprehensive Everglades Restoration Project (CERP) has been charged with the restoration, preservation and protection of the South Florida regional ecosystem. The multiple components of this plan have been designed to restore historic hydrologic conditions and increase water storage and supply for the natural system as well as for urban and agricultural use. One of the proposed goals of this restoration effort is to increase freshwater inputs into coastal bays from upland sources to recover estuarine conditions along near-shore environments (Davis and Ogden, 1994; Browder and Wanless, 2001).

Considering the potential future changes in freshwater deliveries into Biscayne Bay, which may alter not only salinity patterns but may also introduce increased sediment loads from land-based sources, it is important to document the relationship between these physical factors and coral diversity, abundance and distribution. Thus, the purpose of this assessment is to provide the scientific information required to include hard corals found within the coastal bays of South Florida as relevant endpoints to be considered within the context of the Everglades restoration project. Such information will provide important inputs into the restoration efforts that, by focusing largely on improving conditions for species like wading birds, shrimp and seagrasses, may adversely affect obligate marine species such as hard corals.

METHODS

The abundance, diversity and spatial distribution of hard corals within Biscayne Bay and adjacent offshore areas was documented in 2000 from random sampling locations ($n = 88$ random sites) using a stratified random sampling design modified from methods described by Lirman and Cropper (2002). Hardbottom habitats within the study region were divided into four strata: West Bay, Central Bay, East Bay and Offshore areas (Figure 1). Survey points within strata were determined by selecting cells at random from

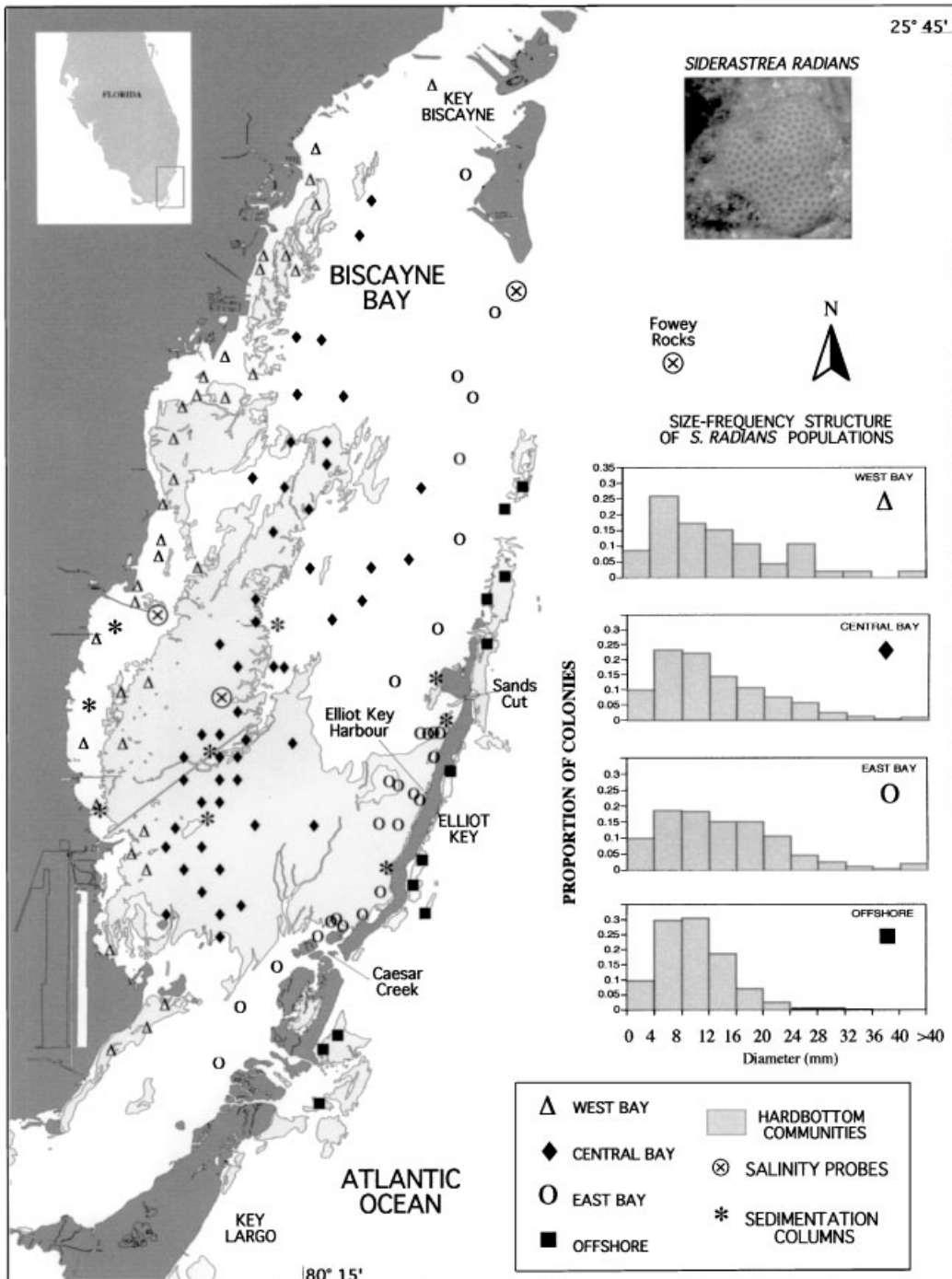
the SEASCAPE model of Biscayne Bay that divides the region into 170 848 square grid elements (Cropper *et al.*, 2001; Lirman and Cropper, 2002). The centre coordinates for the cells chosen for each stratum were determined and a differential GPS unit was used to locate the stations in the field. Benthic habitats in the study area are under the jurisdiction of Biscayne National Park.

At each location, divers surveyed 15 haphazardly located plots using 0.25 m² PVC quadrats. Within each plot, the number of coral colonies visible was determined. The number of coral colonies was assessed once again after the sediments were cleared from each plot. The proportion of colonies completely buried by sediments at the time of the survey was thus obtained. All corals were identified to species and maximum diameter and height for each colony were determined with calipers. Lastly, sediment depth measurements were obtained by pushing a marked metal pole into the sediments until the carbonate platform was reached. To test the hypothesis that settlement and/or survivorship would be higher on topographical high-points within the limestone matrix, sediment depth measurements ($n = 20-40$) were taken adjacent to live colonies of *S. radians*, as well as haphazardly in the surrounding areas. Sediment depths were averaged by site for analysis. To obtain sediment depth contours for the study region, the measurements for each site were interpolated with ArcView's Spatial Analyst Extension using an Inverse Distance Weighted interpolation procedure with a cell size of 100 m².

Representative salinity and temperature values from locations within the three survey strata within Biscayne Bay and one offshore reef location were obtained from field instruments for 1998 and 1999 (Figure 2). Sedimentation rates were determined using sedimentation columns made of PVC (height = 25 cm, diameter = 5 cm, distance from bottom = 40 cm, $n = 5$ columns per site) deployed at nine sites (3 per stratum; Figure 1) and surveyed bi-monthly between January 2000 and January 2001. The total amount of sediments (dry weight) as well as the proportion of fine (silt-clay fraction, $< 63 \mu\text{m}$) and coarse (sand-gravel fraction, $> 63 \mu\text{m}$) was determined for each column and averaged within sites and strata. The sediments collected were first sieved through a 63 μm sieve and the fraction retained in the sieve collected as the gravel-sand fraction. The silt-clay fraction was measured volumetrically from sub-samples of the wash water collected with a 20 ml pipette ($n = 3$). Drying of all fractions was done at 100–110°C to a constant weight.

Although these columns were deployed to determine seasonal and spatial patterns of sedimentation, it was recognized that sediment resuspension events caused by disturbance events concentrated over a short period of time (i.e. hours to days) such as storms or boating activities may also have highly localized impacts that may be overlooked by the seasonal sampling. To document the potential impacts of boating, an important recreational activity within Biscayne Bay, sedimentation columns were placed at Caesar Creek Channel (one of the main boating channels used to access offshore areas) and at Elliot Key Harbor (one of the principal recreational areas used by weekend boaters) (Figure 1). For comparison, additional sedimentation columns ($n = 4$ per site) were placed at increasing distances from the harbour and away from the boating channel. To estimate the impacts of weekend boating activities, these columns were deployed on Thursday, March 28 and recovered on Monday, March 31, 2001. Total sediments were estimated as before and averaged within sites.

To provide an initial test to the hypothesis that both salinity and sedimentation influence growth and survivorship of corals within Biscayne Bay, experiments were carried out where colonies of *S. radians* were exposed to low salinity (20 ppt) and sediment-burial treatments for periods of 24 h at weekly intervals. Small (< 5 mm in diameter), single-polyp colonies collected from hardbottom communities of Biscayne Bay were glued onto ceramic tiles using underwater epoxy. Four colonies were glued to each tile and four tiles ($n = 16$ colonies) were exposed to the experimental conditions. For the low-salinity exposure, each tile was placed inside a 2L bucket. The salinity was adjusted using RO fresh water and buckets were aerated with air stones. For temperature control, buckets were kept in a flow-through water table inside an outdoor greenhouse under natural lighting. A control group of colonies ($n = 16$) was kept under the same conditions in Biscayne Bay water (35 ppt).



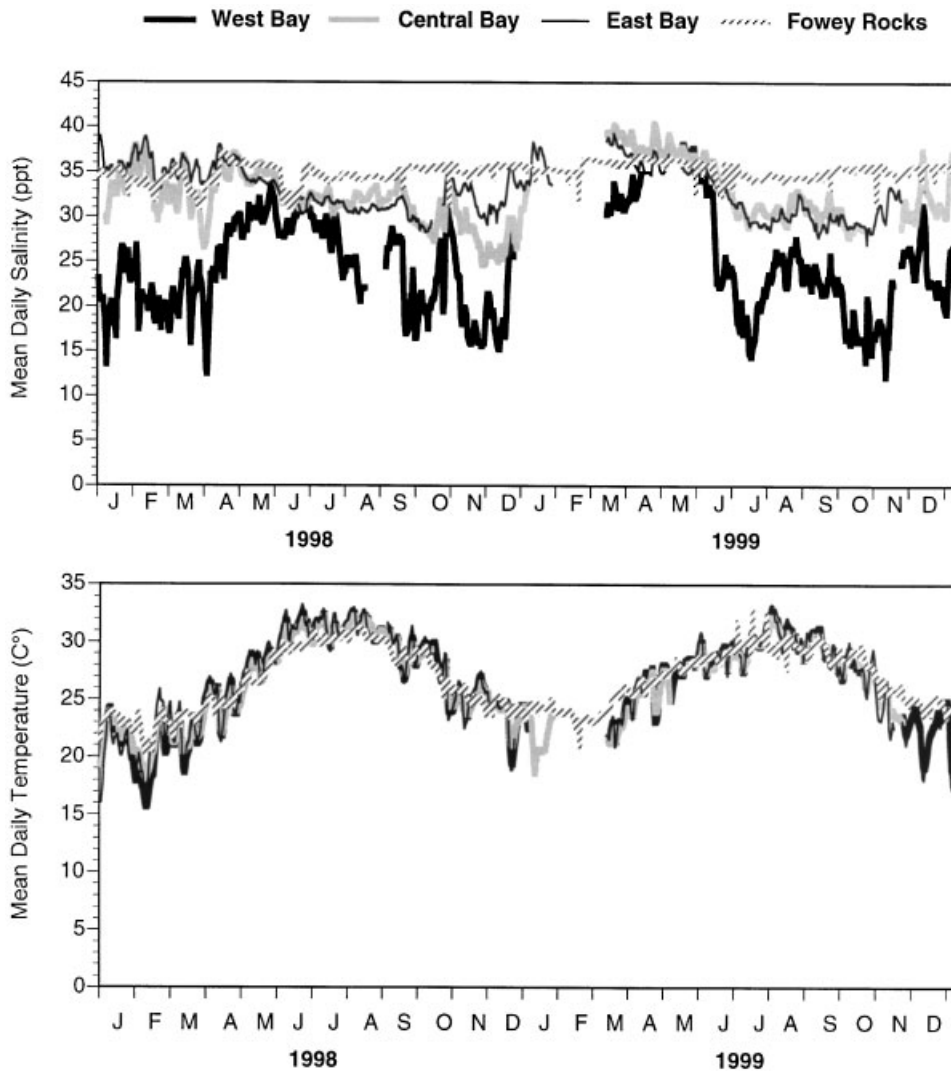


Figure 2. Mean daily salinity and temperature values for sites within Biscayne Bay (West Bay, Central Bay, and East Bay) and the Florida Reef Tract (Fowey Rocks) in 1998 and 1999. For site locations refer to Figure 1.

To test the effects of chronic sediment burial, small *S. radians* colonies were covered by sediments collected from hardbottom habitats of Biscayne Bay for periods of 24 h at weekly intervals. At the beginning of each exposure period, all tiles ($n = 4$ control and 4 exposure) were covered completely by a layer of sediments (3 cm in depth) as commonly encountered in the field. Unlike exposure tiles that

Figure 1. Map of study area showing the location of survey sites, temperature and salinity probes, and sedimentation columns. The photograph showing a *S. radians* colony (diameter = 3.5 cm) was taken at East Bay (depth = 1.5 m). Size-frequency distributions represent the proportion of colonies for each size class averaged for all sites surveyed within the stratum. Distribution of hardbottom habitats was obtained from a digital coverage of benthic habitats of South Florida developed from aerial photographs by the Florida Marine Research Institute.

remained covered for 24 h, control tiles were turned upside-down to remove sediments after the initial burial. The initial diameter of each colony was determined at the onset of the study and again after 1 month using calipers. All colonies were kept in a flow-through mesocosm tank (depth = 1 m) during the experiment.

RESULTS

The salinity patterns measured by field probes within Biscayne Bay differed according to their locations within the strata surveyed (Figure 2). As expected considering the prevailing canal influences in near-shore environments, lower, widely fluctuating salinities were documented at West Bay during both 1998 and 1999. Salinity was below 25 ppt in this area for 188 days in 1998 (minimum daily salinity = 12 ppt) and 156 days in 1999 (minimum daily salinity = 13 ppt). In contrast, salinity was less variable and remained near oceanic values for most of the year at Central Bay and East Bay sites. Salinity did not go below 25 ppt at these sites during either 1998 or 1999. Unlike salinity patterns that differed considerably among strata, water temperature patterns did not exhibit large variation among areas (Figure 2). Water temperature exceeded 30°C 90 days in 1998 (maximum daily temperature = 34°C) and 58 days in 1999 (maximum daily temperature = 34°C) at all three sites. Data collected at nearby Fowey Rocks (25.59°N, 80.10°W; Figure 1) showed that salinity levels on the Florida Reef Tract did not fall below 30 ppt in 1998 or 1999, and that water temperature exceeded 30°C 59 days in 1998 and 24 days in 1999.

Our bi-monthly surveys do not indicate any clear seasonal or spatial patterns in sedimentation rates within the three strata surveyed within Biscayne Bay (Figure 3). Significant effects of both stratum and time of year were detected, as well as a significant interaction between these two main factors (two-way ANOVA, $p < 0.01$). Daily deposition rates were generally higher for both Central and East Bay compared to West Bay (Figure 3). Samples from West Bay had an average of 98.3% silt-clay (SEM = ± 0.6) compared to 97.7% (0.5) for Central Bay and 97.5% (0.5) for East Bay. When sites within strata are compared, no differences in sedimentation rates are observed among sites at West and Central Bay. In contrast, significant differences in sedimentation rates among sites were found at East Bay, where sites located at the central portion of Elliot Key had lower sedimentation rates than sites located closer to Sands Cut and Caesar Creek, the tidal channels connecting Biscayne Bay to offshore areas (Figure 1).

The impact of boating activities on sediment deposition rates was documented at Elliot Key Harbor, where a large number of vessels anchor during weekends. Sedimentation rates here were three times higher than the highest sedimentation values calculated for all nine locations sampled during 2000 (Figure 3). Whereas sedimentation rates at the edge of Caesar Creek Channel, a commonly used boating channel were elevated, the values obtained were within the normal range for the bay (Figure 3). Sedimentation rates decreased significantly (ANOVA, $p < 0.01$) with distance from areas of high boating traffic, highlighting the localized impacts of these activities.

A total of 17 hard coral species were found within hardbottom habitats in Biscayne Bay and offshore areas (Table 1). Twelve species were found within Biscayne Bay and 15 within offshore hardbottom habitats. The only species found in all four areas were *S. radians* and *P. furcata*. Coral distribution and abundance were spatially correlated with the distribution of hardbottom habitat; high densities of hard corals were only documented on areas with shallow sediment depth (Figure 4). While most coral species were found exclusively in hardbottom habitats, three species, *P. furcata*, *P. divaricata*, and *Manicina areolata*, were also found at low densities (< 1 colony m^{-2}) at sites dominated by seagrasses. The lowest species richness was found at West Bay where only two species, *S. radians* and *P. furcata*, were found, while the highest species richness was documented at offshore hardbottom communities ($n = 15$ species). Intermediate levels of species richness were documented at Central and East Biscayne Bay where nine and

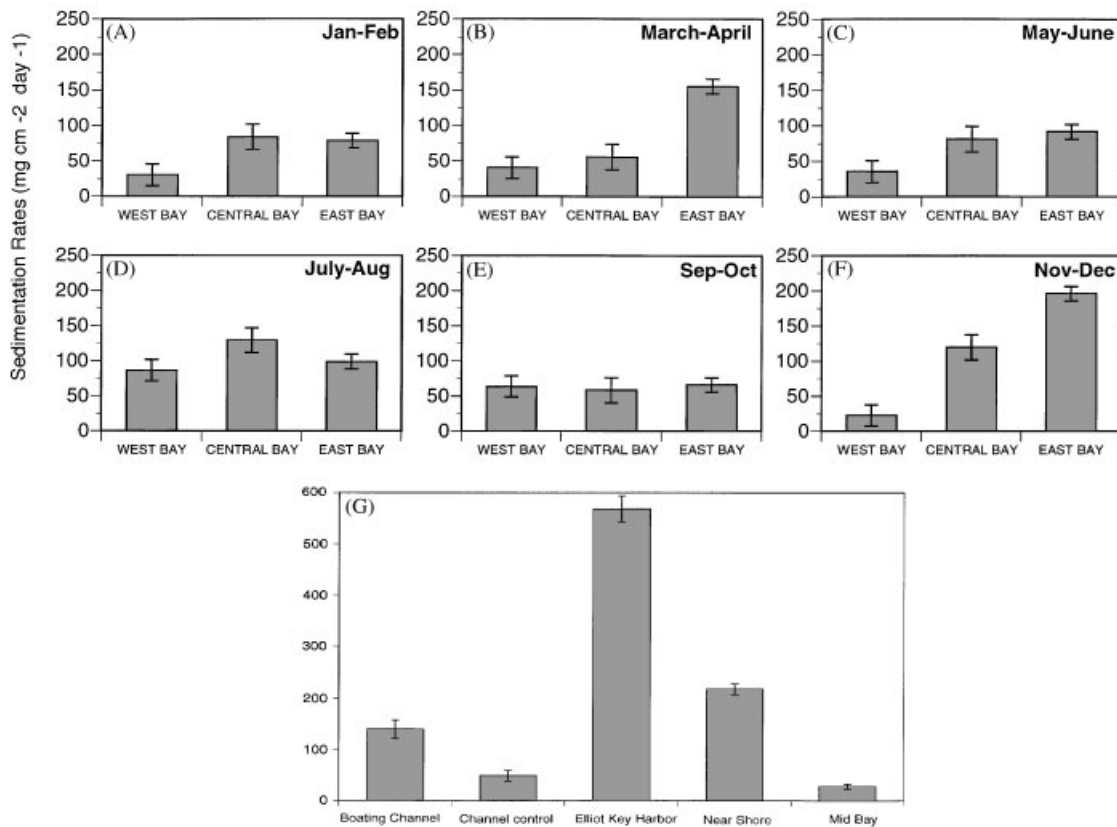


Figure 3. (A)–(F) Mean sedimentation rates ($\text{mg cm}^{-2} \text{ day}^{-1}$) for sites within Biscayne Bay during 2001. Values represent averages from three sites within each stratum. Four PVC sedimentation columns were deployed at each site. (G) Mean sedimentation rates ($\text{mg cm}^{-2} \text{ day}^{-1}$) for locations influenced by boating activities. Values represent averages from four sedimentation columns at each location deployed from March 28 to Monday, March 31, 2001. For site locations refer to Figure 1.

eight species were found, respectively. Colonies of reef-building corals commonly seen in the Florida Reef Tract (e.g. *Montastraea* spp., *Diploria* spp.) were not found within Biscayne Bay and were only observed at offshore sites.

S. radicans is the dominant coral, reaching a maximum density of 68 colonies m^{-2} within Biscayne Bay and 72 colonies m^{-2} within offshore hardbottom habitats (Figures 1 and 4(A)). The highest mean density of this species was documented at offshore sites (23.3 colonies m^{-2}), which had mean densities significantly higher than all other areas (Table 2, ANOVA, $p < 0.05$, Tukey *a posteriori* comparisons). Within Biscayne Bay, the highest mean densities of *S. radicans* were documented at East Bay (3.6 colonies m^{-2}). While offshore sites had the highest density of *S. radicans*, mean colony diameter was smaller here than at all other sites (Table 2). Significant differences in mean diameter were only found between offshore and East Bay (ANOVA, $p < 0.05$, Tukey *a posteriori* comparisons). Branching *Porites* spp. reached a maximum density of 4 colonies m^{-2} in West Bay, 12 colonies m^{-2} in Central Bay, and 24 colonies m^{-2} in East Bay and offshore areas (Figure 4(B)). Maximum densities for all of the other coral species found did not exceed 4 colonies m^{-2} at any location.

The size-frequency distribution of *S. radicans* populations show similar structure among strata (Figure 1). In general, populations are skewed to the right, with smaller colonies dominating numerically. The

Table 1. Distribution of coral species within hardbottom habitats surveyed within Biscayne Bay and offshore areas

Coral species present	West Bay	Central Bay	East Bay	Offshore
<i>Siderastrea radians</i>	●	●	●	●
<i>S. siderea</i>				●
<i>Porites porites</i>			●	●
<i>P. furcata</i>	●	●	●	●
<i>P. divaricata</i>		●		●
<i>P. astreoides</i>			●	●
<i>Manicina areolata</i>		●	●	●
<i>Oculina diffusa</i>		● ^a		
<i>Cladocora arbuscula</i>		● ^a		
<i>Favia fragum</i>			●	●
<i>Dichocoenia stokesii</i>		●		●
<i>Solenastrea hyades</i>		●	●	●
<i>Montastraea cavernosa</i>				● ^a
<i>M. faveolata</i>				● ^a
<i>Diploria clivosa</i>				●
<i>Stephanocoenia michilini</i>				● ^a
<i>Millepora alcicornis</i>		●	●	●

^a corals species present in only one survey site.

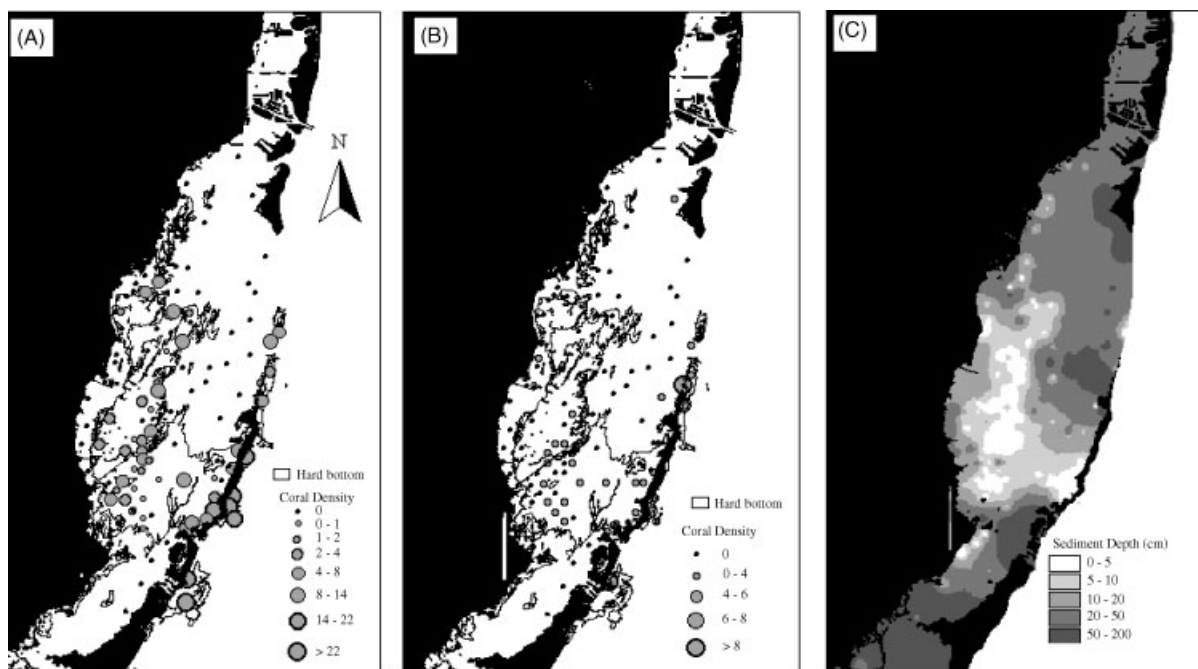


Figure 4. (A) Mean density (colonies m^{-2}) of *S. radians* colonies within hardbottom habitats of Biscayne Bay, (B) Mean density (colonies m^{-2}) of branching *Porites* spp. colonies within hardbottom habitats of Biscayne Bay, (C) Sediment depth contours within Biscayne Bay derived from field surveys. Measurements for each site were interpolated with ArcView's Spatial Analyst Extension using an Inverse Distance Weighted interpolation procedure with a cell size of $100m^2$.

proportion of colonies in the smallest size class (0–4 mm in diameter) is remarkably similar among strata, ranging from 8 to 10%. The largest proportion of colonies are found in the next two size classes (>4–8 and >8–12 mm), with 35–60% of all colonies belonging to these size classes. The narrowest size-distribution is

Table 2. Structural attributes of *Siderastrea radians* populations found in hardbottom habitats of Biscayne Bay and adjacent offshore areas

Hardbottom sites	Coral density (# m ⁻²)	Mean diameter (cm)	Maximum diameter (cm)	Depth (m)	N sites
West Bay	1.9 (0.6)	1.4 (0.3)	4.0	2.2 (0.2)	22
Central Bay	2.6 (.05)	1.1 (0.1)	5.0	2.1 (0.1)	37
East Bay	3.6 (1.0)	1.6 (0.2)	6.5	1.9 (0.2)	17
Offshore	23.2 (4.7)	0.9 (0.1)	3.3	2.2 (0.2)	12

Values represent means (± 1 SEM) calculated for the four main strata surveyed in 2000. Values were averaged by site and stratum.

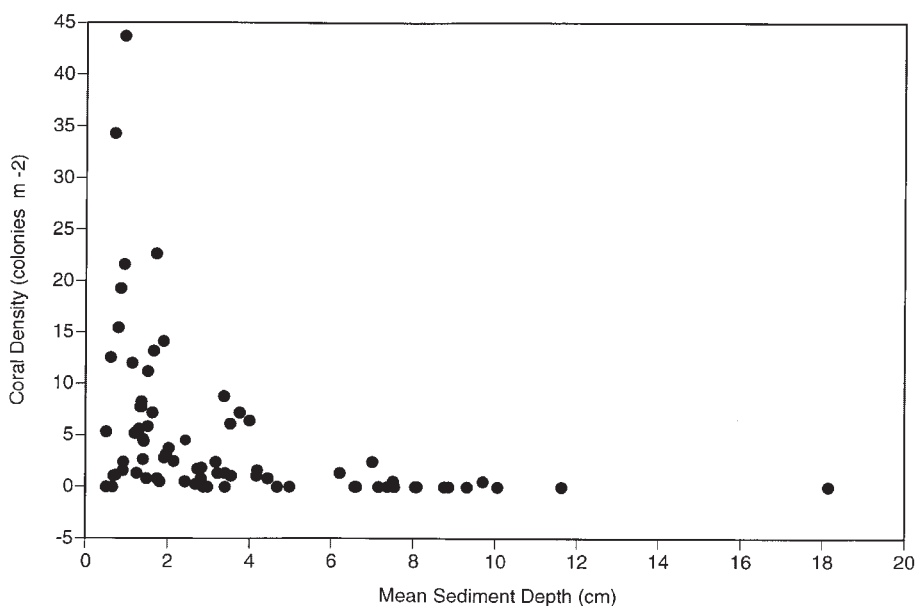


Figure 5. Relationship between sediment depth and coral density within hardbottom habitats of Biscayne Bay and adjacent offshore areas.

found at offshore sites where colonies do not exceed 34 mm in diameter. The largest *S. radians* colony was found at East Bay (65 mm).

Colonies of *S. radians* are commonly covered by sediments within hardbottom communities. An average of 47% (SEM = ± 4.0) of colonies were completely buried under a sediment layer at the time of the surveys. Coral distribution can be influenced locally by sediment depth as live coral colonies are commonly found at high points within the limestone matrix, and sediment depth next to coral colonies (mean = 1.1 cm, SEM = ± 0.1) was significantly lower than mean sediment depth collected haphazardly (mean = 2.6 cm, SEM = ± 0.3) within the same sites (*t*-test, $p < 0.01$). When data were grouped by site, mean coral density decreased exponentially with increasing sediment depth (Figure 5). This relationship suggests a threshold sediment depth of 4–5 cm, with low mean density of *S. radians* recorded at sediment depths larger than this value. To test whether sediment depth may influence the shape of coral colonies, the relationship between sediment depth and the radius-to-height ratio of *S. radians* colonies was evaluated. However, no significant relationship was found between colony shape and sediment depth (linear regression, $r^2 = 0.03$, $p > 0.05$).

Chronic exposure to low salinity and sediment burial can influence both growth and survivorship patterns of *S. radians* (Figure 6). After 1 month (four weekly exposures), corals exposed to low salinity (20 ppt) had mean radial growth rates lower than those of controls. However, this difference was not statistically significant (t -test, $p > 0.05$) and no colony mortality was observed within either group. Colonies buried under sediments at weekly intervals had radial extension rates significantly lower than controls (t -test, $p > 0.05$). In this case, 30% of colonies exposed to burial treatments experienced total mortality at the end of 1 month.

DISCUSSION

The hardbottom habitats of Biscayne Bay contain only a small subset of the coral species commonly encountered on nearby reefs of the Florida Reef Tract (Burns, 1985; Miller *et al.*, 2000). Coral communities of Biscayne Bay are dominated by brooding species like *S. radians* and *P. furcata* with traits commonly associated with opportunistic life histories (e.g. high recruitment, small colony size, extended reproductive season) believed to enhance persistence in frequently disturbed environments (Szmant, 1986; Soong, 1991). In contrast, offshore hardbottom habitats contain not only higher densities of the coral species found inside the bay, but also broadcast spawning species such as *Montastraea cavernosa*, *M. faveolata* and *S. siderea*, which are among the main reef-building corals in the region (Chiappone, 1996; Miller *et al.*, 2000). The absence of these reef-building species within hardbottom communities of Biscayne Bay, suggests that environmental conditions within this semi-enclosed basin restrict the recruitment, growth and survivorship of less-tolerant coral species.

Among the factors known to influence coral recruitment, growth, abundance and distribution, temperature, salinity and sedimentation appear to play an important limiting role within Biscayne Bay. Although temperatures within Biscayne Bay and the Florida Reef Tract follow similar seasonal trends, patterns within the bay exhibit higher variability as well as a higher frequency of extreme values that may

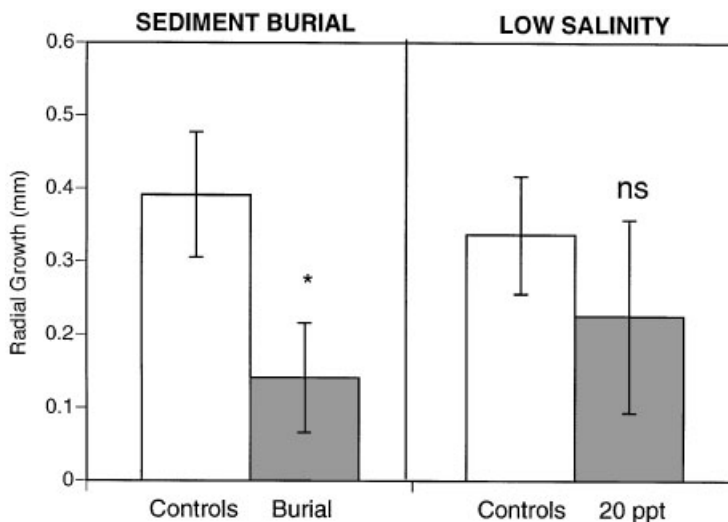


Figure 6. Effects of sediment burial and low salinity exposure on the growth of *S. radians* colonies. Small colonies (<5 mm in diameter, $n = 16$) were exposed to experimental conditions for 24 h at weekly intervals. Radial growth was estimated after 1 month (4 sequential exposures). * = significant difference in growth rates between controls and exposed colonies (t -test, $p < 0.05$). ns = no significant differences.

restrict coral distribution. The narrow thermal tolerance of corals has been well-documented, and temperature values outside this range can result in reduced photosynthesis, coral bleaching and even mortality (e.g. Marcus and Thorhaug, 1981; Glynn and D'Croz, 1990; Kobluk and Lysenko, 1994; Porter *et al.*, 1999). This was evidenced in the coral bleaching event of 1997–1998 where coral communities throughout the world, including Florida, experienced significant mortality due to elevated temperatures (Berkelmans and Oliver, 1999; Warner *et al.*, 1999; Aronson *et al.*, 2000). In 1998, while water temperatures in the Florida Reef Tract were above 30°C for 59 days, this threshold was exceeded during 90 days within Biscayne Bay. Many of the corals absent from Biscayne Bay, especially those with massive morphologies like *S. siderea*, *Diploria* spp. and *Montastraea* spp., were found to be susceptible to temperature-induced bleaching (Goreau, 1992; Lang *et al.*, 1992).

Salinity fields within Biscayne Bay are influenced by precipitation, freshwater inputs from land, canal and groundwater sources, and tidal influx of oceanic water (Alleman, 1995). The spatial and temporal distribution of these influences delineate salinity fields with distinct characteristics. Areas with low, highly variable salinity are found along the western margin due to managed freshwater inflows from canals, groundwater and surface runoff, while higher, more stable salinities are found along the eastern margin where oceanic influences prevail (Wang *et al.*, 1978, 2002; Brook, 1982). Near-shore salinity patterns, characterized by wide fluctuations and low mean salinity values, limit coral distribution and abundance within West Biscayne Bay where the lowest coral density and species richness are found. In fact, only two coral species, *S. radians* and *P. furcata*, are found in this marginal environment, highlighting their tolerance to low and variable salinity. These genera were also found to be resistant to sudden drops in salinity by Vaughan (1916) and Wells (1932) in the first experimental studies of reduced salinity on corals. Although colonies of *S. radians* are able to survive in this fluctuating environment, there can be considerable sublethal effects of reduced salinity that need to be considered. For example, chronic exposure to low salinity can reduce the growth rates of colonies, as shown experimentally in this study. Accordingly, maximum diameter of *S. radians* increases along a salinity-disturbance gradient from West to East in Biscayne Bay. Changes in salinity and salinity values outside tolerance ranges can also impact coral reproductive success as well as photosynthesis and respiration (e.g. Muthiga and Szmant, 1987; Richmond, 1993; Moberg *et al.*, 1997; Nystrom *et al.*, 1997; Porter *et al.*, 1999).

Sediment depth is an important factor determining the location and extent of habitat suitable for coral settlement and survivorship. Wherever mean sediment depth exceeds 10–15 cm, seagrasses are the dominant benthic organisms within Biscayne Bay (Lirman and Cropper, 2002) and only isolated colonies of the branching coral *Porites* spp. or *Manicina areolata* are found among the seagrasses. The inverse relationship between coral density and sediment depth suggests a threshold value of 5 cm in sediment depth for dense coral communities to develop. At a smaller scale, the predominant distribution of live coral colonies on topological high-points within the Pleistocene carbonate matrix suggests a higher survivorship and/or settlement success of corals on locations that, unlike depressions or cavities in the carbonate matrix, minimize exposure to sediment burial. Nevertheless, the fact that 47% of *S. radians* colonies were buried under sediments at the time of survey indicates that corals within this environment must have a high tolerance for sediment interactions. This is true even for stress-tolerant species like *S. radians* that showed both reduced growth and coral mortality under chronic sediment burial. The high density and large mean size of corals within hardbottom habitats at East Biscayne Bay that experience high deposition rates suggests that although corals get commonly covered by sediments in this area, sediments must not remain over the colonies for prolonged periods of time.

The sedimentation rates recorded in this study, especially those measured near boating channels, are generally higher by at least an order of magnitude than those recorded using similar methods in reefs at different locations throughout the world (e.g. Rogers, 1983; McClanahan and Obura, 1997; Gleason, 1998). Sedimentation rates as high as those observed in Biscayne Bay were reported to inhibit coral growth, recruitment, survivorship and distribution in severely stressed reefs in Hawaii (Maragos, 1972), Costa Rica

(Cortes and Risk, 1974) and Guam (Randall and Birkeland, 1978). In a review of the impacts of sedimentation on reefs, Rogers (1990) predicted that habitats exposed to heavy sediment loads ($>10 \text{ mg cm}^{-2} \text{ day}^{-1}$) would have low species diversity, low coral cover and dominance by species resistant to smothering or reduced light levels. Results from our surveys agree with these predictions as hardbottom communities within Biscayne Bay are dominated by the stress-tolerant *S. radians*, and contain a reduced number of coral species and lower coral densities compared to comparable offshore habitats.

Coral populations of Biscayne Bay are located on critical habitat likely to be affected by the future Everglades restoration and can provide important endpoints whereby the impacts of these activities can be measured. Two aspects of the restoration that will influence the extent of the impact of these activities on corals are the quantity of freshwater to be redirected into Biscayne Bay, as well as the method of delivery of these diverted flows. Ample evidence exists to show that there has been a historical reduction in freshwater flows into the coastal lagoons of South Florida and that, as a consequence, bay waters are now more saline and remain at high salinity levels longer than before the construction of the water management system (reviewed by McIvor *et al.*, 1994 and Sklar *et al.*, 2002). This shift in salinity may have expanded the suitable habitat for obligate marine species like hard and soft corals and sponges that can now be found on near-shore hardbottom areas. Thus, a net increase in freshwater flow could be potentially detrimental to corals in Biscayne Bay.

However, water quantity is just one of the variables that need to be considered. The management system has modified historical freshwater deliveries, decreasing the relative contribution of overland and groundwater flows, replacing these by canals that release large amounts of freshwater over short periods of time. These patterns of release lower the salinity in adjacent areas drastically and have caused the rapid mortality of marine species like sponges (Storr, 1976; Knight and Fell, 1987; Montague and Ley, 1993). This pattern of concentrated point releases has created restricted near-shore environments that are unavailable to corals and sponges and are largely dominated by tolerant species like the seagrass *Halodule wrightii* (Cropper *et al.*, 2001; Lirman and Cropper, 2002). To remediate this pattern, the Everglades restoration project will either remove canal structures or build spreader structures to provide a more natural sheetflow into the coastal fringe. Therefore, even if freshwater flows increase, by spreading the delivery over a larger area, salinity impacts on corals and other marine species may be mitigated, allowing these important organisms to continue to occupy hardbottom habitats along the western margin of Biscayne Bay. If, on the other hand, water delivery continues to be predominantly through canal discharge, an increase in the amount of freshwater released into Biscayne Bay will likely expand the areas with low and variable salinity, adversely affecting the health of coral populations.

CONCLUSIONS

The location of Biscayne Bay, near the city of Miami and downstream of a massive watershed restoration effort planned for the Everglades hydroscape, highlights the need to understand the relationship between the physical environment and the health of benthic communities. Although the physical characteristics of Biscayne Bay make this basin a marginal environment for coral growth and prevent reef development, dense populations of stress-tolerant coral species are found here and can provide important endpoints to evaluate the impacts of the proposed Everglades restoration. Coral populations, especially those located in near-shore habitats, will likely experience changes in salinity and sedimentation patterns and thus need to be considered within the restoration framework. The data presented here suggest species-specific tolerance limits to changes in salinity and sedimentation that could be used to predict future impacts and draft mitigation plans.

If the areas of low and fluctuating salinity are expanded by the diversion of additional freshwater into Biscayne Bay, a decrease in coral diversity, abundance, and survivorship can be expected. However, these

negative effects could be mitigated by replacing the present method of delivery through canals with a system that increases overland flows and spreads the impacts of salinity fluctuations over a wider fringe area. The balance between the increased freshwater flows and the method of delivery can be crucial for the conservation of hard corals as well as other obligate marine species like sponges and soft corals that can reach high abundance in hardbottom habitats of Biscayne Bay.

Similarly, the relationship between coral abundance and diversity and sediment depth suggests that the input of additional sediment loads from land sources will likely result in a decrease in coral growth, settlement, abundance and diversity. At present, boating activities along the eastern margin of Biscayne Bay cause an increase in sedimentation rates that, superimposed on already high natural rates of sediment deposition, can be detrimental to corals by reducing light availability and increasing burial rates. To reduce the impacts of boating, restricted use or no wake zones could be established in shallow areas with high coral density.

ACKNOWLEDGEMENTS

Financial support was provided by NOAA Coastal Ocean Program (Award #NA67RJ0149), the Florida Department of Environmental Protection (Award # NRD08) and EPA STAR Program (# R-827453-01-0). Richard Curry, Science Director of Biscayne National Park, provided field support for this project.

REFERENCES

- Alleman RW. 1995. *An Update to the Surface Water Improvement and Management Plan for Biscayne Bay*. South Florida Water Management District: West Palm Beach, FL.
- Aronson RB, Precht WF, Macintyre IG, Murdoch TJT. 2000. Coral bleach-out in Belize. *Nature* **405**: 36.
- Berkelmans R, Oliver JK. 1999. Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* **18**: 55–60.
- Brook IM. 1982. The effect of freshwater canal discharge on the stability of two seagrass benthic communities in Biscayne National Park, Florida. Proceedings of the International Symposium on Coastal Lagoons, Bordeaux, France. *Oceanologica Acta* **1982**: 63–72.
- Browder JA. 1985. Relationship between pink shrimp production in the Tortugas grounds and water flow patterns in the Florida Everglades. *Bulletin of Marine Science* **37**: 839–856.
- Browder JA, Ogden JC. 1999. The natural South Florida system II: predrainage ecology. *Urban Ecosystems* **3**: 245–277.
- Browder JA, Wanless HR. 2001. Science Survey Team Final Report. In: *Biscayne Bay Partnership Initiative. Survey Team Final Reports*. Miami, FL; 65–230.
- Browder JA, Restrepo VR, Rice JK, Robblee MB, Zein-Eldin Z. 1999. Environmental influences on potential recruitment of pink shrimp, *Penaeus duorarum*, from Florida Bay nursery grounds. *Estuaries* **22**: 484–499.
- Burns TP. 1985. Hard-coral distribution and cold-water disturbances in South Florida: variation with depth and location. *Coral Reefs* **4**: 117–124.
- Chiappone M. 1996. *Marine Benthic Communities of the Florida Keys. Site Characterization for the Florida Keys National Marine Sanctuary*, vol. 1. The Preserver: Zenda, WI, 46 pp.
- Cortes J, Risk MJ. 1974. El arrecife coralino del Parque Nacional Cahuita, Costa Rica. *Revista de Biología Tropical* **32**: 109–121.
- Cropper Jr WP, Lirman D, Tosini SC, Diresta D, Luo J, Wang JD. 2001. Sponge population dynamics in Biscayne Bay, Florida. *Estuarine Coastal and Shelf Science* **53**: 13–23.
- Davis SM, Ogden JC. 1994. Toward ecosystem restoration. In: *Everglades. The Ecosystem and its Restoration*, Davis SM, Ogden JC (eds). St. Lucie Press, Delray Beach, FL; 769–797.
- Durako MJ. 1994. Seagrass die-off in Florida Bay (USA): changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. *Marine Ecology Progress Series* **110**: 59–66.
- Fourqurean JW, Robblee MB. 1999. Florida Bay: a brief history of recent ecological changes. *Estuaries* **22**: 345–357.
- Gleason DF. 1998. Sedimentation and distributions of green and brown morphs of the Caribbean coral *Porites astreoides* Lamarck. *Journal of Experimental Marine Biology and Ecology* **230**: 73–89.
- Glynn PW, D'Croz L. 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* **8**: 181–191.
- Goreau TJ. 1992. Bleaching and reef community change in Jamaica: 1951–1991. *American Zoologist* **32**: 683–695.

- Knight PA, Fell PE. 1987. Low salinity induces reversible tissue regression in the estuarine sponge *Micociona prolifera* (Ellis & Solander). *Journal of Experimental Marine Biology and Ecology* **107**: 253–261.
- Kobluk DR, Lysenko MA. 1994. 'Ring' bleaching in southern Caribbean *Agaricia agaricites* during rapid water cooling. *Bulletin of Marine Science* **54**: 142–150.
- Lang JC, Lasker HR, Gladfelter EH, Hallock P, Jaap WC, Losada FJ, Muller RG. 1992. Spatial and temporal variability during periods of 'recovery' after mass bleaching on Western Atlantic coral reefs. *American Zoologist* **32**: 696–706.
- Lirman D, Cropper Jr WP. 2002. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: field, experimental, and modeling studies. *Estuaries*, in Press.
- Maragos JE. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. dissertation, University of Hawaii, Honolulu, 280 pp.
- Marcus J, Thorhaug A. 1981. Pacific versus Atlantic responses of the subtropical hermatypic coral *Porites* spp. to temperature and salinity effects. *Proceedings 4th International Coral Reef Symposium*, Manila. vol. 2, 15–20.
- McClanahan TR, Obura D. 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* **209**: 103–122.
- McIvor CC, Ley JA, Bjork RD. 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: a review. In: *Everglades. The Ecosystem and its Restoration*, Davis SM, Ogden JC (eds). St. Lucie Press, Delray Beach, FL; 117–146.
- Miller MW, Weil E, Szmant AM. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* **19**: 115–123.
- Moberg F, Nystrom M, Kautsky N, Tedengren M, Jarayabhand P. 1997. Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. *Marine Ecology Progress Series* **157**: 53–59.
- Montague CL, Ley JA. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in Northeastern Florida Bay. *Estuaries* **16**: 703–717.
- Muthiga NA, Szmant AM. 1987. The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral *S. siderea*. *Biological Bulletin* **173**: 539–551.
- Nystrom M, Moberg F, Tedengren M. 1997. Natural and anthropogenic disturbance on reef corals in the inner Gulf of Thailand: physiological effects of reduced salinity, copper, and siltation. *Proceedings of the 8th International Coral Reef Symposium*, Panama, vol. 2. 1893–1898.
- Porter JW, Lewis SK, Porter KG. 1999. The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnology and Oceanography* **44**: 941–949.
- Randall RH, Birkeland C. 1978. Guam's reefs and beaches. Part II. Sedimentation studies at Fouha Bay and Ylig Bay. *Technical Report*. vol. 47. *University of Guam Marine Laboratory*. 1–77.
- Richmond RH. 1993. Effects of coastal runoff on coral reproduction. In: *Global Aspects of Coral Reefs. Health, Hazards, and History*, Ginsburg RN (ed.). Miami, 360–364.
- Robblee MB, Barber TR, Carlson PR, Durako MJ, Fourqurean JW, Muehlstein LK, Porter D, Yarbro LA, Zieman RT, Zieman JC. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* **71**: 297–299.
- Rogers CS. 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. *Marine Pollution Bulletin* **14**: 378–382.
- Rogers CS. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**: 185–202.
- Sklar F, McVoy C, VanZee R, Gawlik DE, Tarboton K, Rudnick D, Miao S, Armentano T. 2002. The effects of altered hydrology on the ecology of the Everglades. In: *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. An Ecosystem Sourcebook*, Porter JW, Porter KG (eds). CRC Press, Boca Raton, FL; 39–82.
- Smith III TJ, Hudson JH, Robblee MB, Powell GVN, Isdale PJ. 1989. Freshwater flow from the Everglades to Florida Bay: a historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. *Bulletin of Marine Science* **44**: 274–282.
- Soong K. 1991. Sexual reproductive patterns of shallow-water reef corals in Panama. *Bulletin of Marine Science* **49**: 832–846.
- Storr JF. 1976. Field observations of sponge reactions as related to their ecology. In: *Aspects of Sponge Biology*, Harrison FW, Cowden RR (eds). Academic Press: New York, 277–282.
- Szmant AM. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* **5**: 43–53.
- Vaughan TW. 1916. The results of investigations of the ecology of the Floridian and Bahamian shoal-water corals. *Proceedings of the National Academy of Sciences* **2**: 95–100.

- Wang JD, Daddio E, Horwitz MD. 1978. *Canal discharges into South Biscayne Bay. Report to Metro Dade DERM*, Miami, FL, 76 pp.
- Wang JD, Luo J, Ault J. 2002. Flows, salinity, and some implications on larval transport in South Biscayne Bay, Florida. *Bulletin of Marine Science*, in Press.
- Warner ME, Fitt WK, Schmidt GW. 1999. Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. *Proceedings of the National Academy of Sciences* **96**: 8007–8012.
- Wells JW. 1932. Study of the reef corals of the Tortugas. *Carnegie Institution Washington Yearbook* **31**: 290.
- Zieman JC, Fourqurean JW, Iverson RL. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* **44**: 292–311.
- Zieman JC, Fourqurean JW, Frankovich TA. 1999. Seagrass die-off in Florida Bay: long-term trends in abundance and growth of turtle grass, *Thalassia testudinum*. *Estuaries* **22**: 460–470.