

Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract

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Abstract

Localized declines in coral condition are commonly linked to land-based sources of stressors that influence gradients of water quality, and the distance to sources of stressors is commonly used as a proxy for predicting the vulnerability and future status of reef resources. In this study, we evaluated explicitly whether proximity to shore and connections to coastal bays, two measures of potential land-based sources of disturbance, influence coral community and population structure, and the abundance, distribution, and condition of corals within patch reefs of the Florida Reef Tract.

In the Florida Keys, long-term monitoring has documented significant differences in water quality along a cross-shelf gradient. Inshore habitats exhibit higher levels of nutrients (DIN and TP), TOC, turbidity, and light attenuation, and these levels decrease with increasing distance from shore and connections to tidal bays. In clear contrast to these patterns of water quality, corals on inshore patch reefs exhibited significantly higher coral cover, higher growth rates, and lower partial mortality rates than those documented in similar offshore habitats. Coral recruitment rates did not differ between inshore and offshore habitats. Corals on patch reefs closest to shore had well-spread population structures numerically dominated by intermediate to large colonies, while offshore populations showed narrower size-distributions that become increasingly positively skewed. Differences in size–structure of coral populations were attributed to faster growth and lower rates of partial mortality at inshore habitats. While the underlying causes for the favorable condition of inshore coral communities are not yet known, we hypothesize that the ability of corals to shift their trophic mode under adverse environmental conditions may be partly responsible for the observed patterns, as shown in other reef systems.

This study, based on data collected from a uniform reef habitat type and coral species with diverse life-history and stress–response patterns from a heavily exploited reef system, showed that proximity to potential sources of stressors may not always prove an adequate proxy for assigning potential risks to reef health, and that hypothesized patterns of coral cover, population size–structure, growth, and mortality are not always directly related to water quality gradients.

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Keywords: Florida Reef Tract; Patch reefs; Coral growth; Coral population structure; Water quality gradients

1. Introduction

A myriad of recent reports have highlighted declining trends in coral abundance and condition worldwide (Gardner et al., 2003; Pandolfi et al., 2003; Wilkinson, 2004). In

numerous cases, declines have been linked to land-based stressors that influence gradients of water quality (e.g., nutrients, sedimentation, salinity) and levels of use and exploitation (e.g., Brown, 1997; Jackson et al., 2001; Fabricius et al., 2005; Pandolfi et al., 2005). In fact, local and regional risk assessment studies that rank the degree of vulnerability of reefs are based primarily on the distance between reef resources and potential land-based sources of disturbance (Bryant et al., 1998; Burke and Maidens,

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2004). While hypotheses that relate reef condition to distance to potential sources of stressors are intuitively straightforward, only a limited number of studies have provided direct tests for these hypothesized patterns (e.g., Fabricius and De'ath, 2004; Fabricius et al., 2005). Moreover, several studies have shown that healthy corals and coral communities are often found in marginal environments (Perry and Larcombe, 2003 and references therein).

In this study, we evaluate whether proximity to shore and connections to coastal bays, two measures of potential land-based sources of disturbance, influence community and population structure, abundance, distribution, and condition of corals within patch-reef habitats of the Florida Reef Tract. Our approach combined: (1) spatial analyses of patch-reef distribution; (2) commonly used indicators of reef condition (e.g., coral cover, colony size); and (3) coral demographic statistics (e.g., growth, mortality, recruitment). The location of Florida reefs near the northernmost limit of reef development and adjacent to a rapidly growing urban center makes this system specially vulnerable to coral stressors commonly associated with development and industrial and agricultural activities (Glynn et al., 1989; Lapointe and Clark, 1992; Lipp et al., 2002; Lapointe et al., 2004; Ward-Paige et al., 2005; Fauth et al., 2006). Similarly, the Florida Reef Tract and adjoining coastal lagoons, Biscayne Bay and Florida Bay, support extensive recreational and commercial harvesting activities that provide a multi-billion dollar income to the local economy but that have resulted in significant over-exploitation of most commercial stocks (Ault et al., 2005).

In addition to these activities, the Florida Reef Tract is located downstream of one of the world's largest water management systems, which has altered the hydrology of the natural landscape, causing significant modifications in the quality and extent of coastal habitats (Davis and Ogden, 1994; Browder and Ogden, 1999). In response to concerns over declining ecosystem health, the Comprehensive Everglades Restoration Project has been developed to restore the integrity of the South Florida natural ecosystem. One of the proposed goals of the restoration efforts is to increase fresh water inputs from upland sources into Florida Bay and Biscayne Bay to recover lost estuarine conditions (Davis and Ogden, 1994; Browder and Wanless, 2001). The proposed increased flow of freshwater from source areas with high human development and intense agricultural activities has raised concerns about future changes in water quality and potential increases in the concentration of nutrients and pollutants within coastal lagoons and adjoining reef habitats.

In Florida, reef development and coral condition have been directly linked to the development of the coastal bays and water exchange between the Florida shelf and these shallow basins. The flooding of Florida Bay and Biscayne Bay (<4000 ka) resulted in the formation of tidal channels where the exchange of terrestrial material, sediments, and organic matter is believed to have resulted in conditions unfavorable for reef development in areas with major tidal

passes (Ginsburg and Shinn, 1964, 1993). More recently, the direct hydrological link between the Florida Reef Tract and these coastal lagoons has been established in circulation studies that have documented net flows across all major tidal channels (Lee et al., 2002; Smith and Pitts, 2002). Moreover, remote sensing studies have documented the flow of nutrient- and phytoplankton-rich water masses from upstream sources in the Gulf of Mexico and Florida Bay across tidal passes in the Lower Florida Keys with associated negative impacts on benthic organisms (Hu et al., 2003, 2004). Thus, the potential for increased flows across tidal channels as well as for increased groundwater flows as a result of the Everglades restoration (Bacchus, 2002) raises concerns for the health of reef communities of the Florida Reef Tract that are already showing significant signs of decline (Porter et al., 2002).

Considering the potential impacts of these disturbances, it is easy to envision a scenario in which human activities create a spatial gradient of influence where disturbance levels are higher for those coral reef communities closer to shore and areas with direct connections to coastal bays. Moreover, this prediction is further sustained by examples from other areas of the world where human development along coastal zones resulted in drastic increases in factors such as sedimentation and nutrient concentrations with adverse impacts on coral condition (reviewed by Wilkinson, 2004). In this study, based on data collected from a uniform reef habitat type (i.e., patch reefs) and coral species with diverse life-history and stress-response patterns from one of the most heavily exploited reef systems in the world, we show that proximity to shore, urban centers, or terrestrial sources of pollution may not always prove an adequate proxy for assigning potential risks to reef health, and that hypothesized spatial patterns of coral cover, population size-structure, growth, and mortality are not always directly related to water quality gradients.

2. Methods

2.1. Site selection

Reefs of the Florida Reef Tract can be divided into two types, bank reefs located along the seaward edge of the shelf and patch reefs located within the inner lagoon between the Florida Keys and the outer bank reefs (Marszalek et al., 1977). Patch reefs of the Florida Keys are high relief features (up to 9 m of vertical relief), dome- or linear-shaped, range in size from a few to up to 700 m, and can appear as single features or as clumped aggregations (Marszalek et al., 1977; Jaap, 1984). By concentrating on a single habitat type, this study avoids introducing confounding factors that may be influenced by depth, zonation, or habitat type.

Coral communities on patch-reef habitats were surveyed using a nested sampling design. The location of patch reefs was obtained from the benthic habitat map of the Florida Keys (FMRI, 1997). This habitat map, developed from aerial surveys, identifies 6000 polygon features as individual or

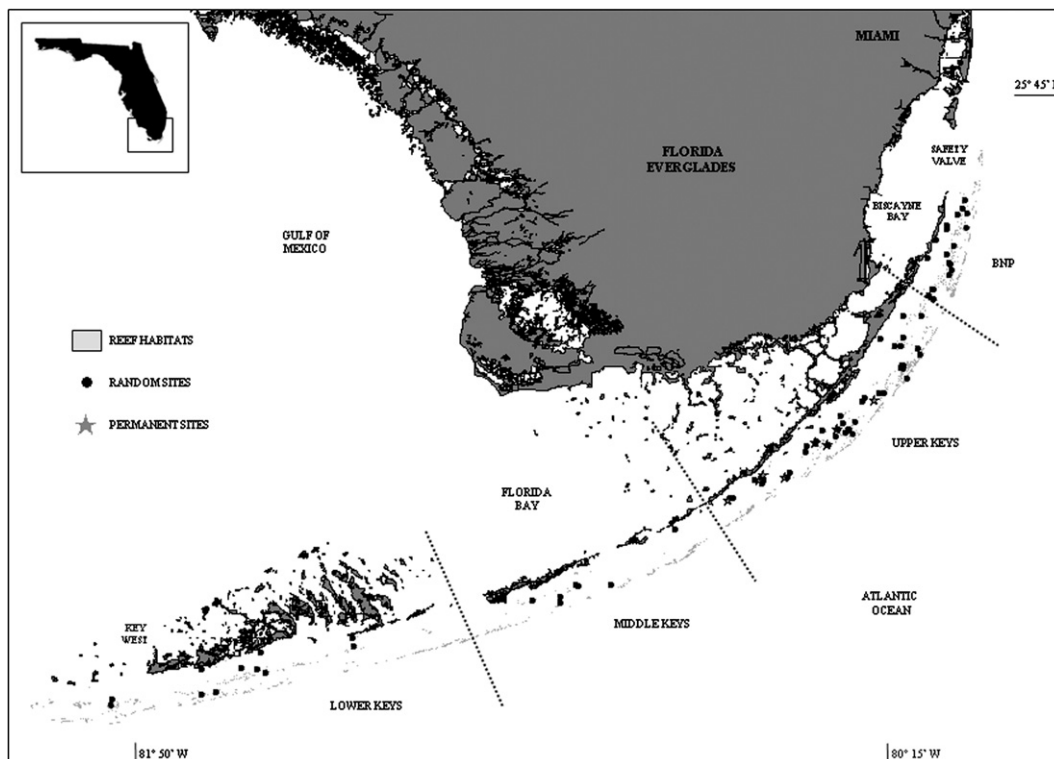


Fig. 1. Map of the study area showing the location of reef habitats of the Florida Reef Tract and the random survey sites (dots) and the permanent sites (stars) where the demographic information was collected.

aggregated patch reefs from Miami to the Dry Tortugas, representing a total area of 46.5 km². The Florida Reef Tract was divided into four regions: (1) Biscayne National Park (BNP); (2) Upper Keys; (3) Middle Keys; and (4) Lower Keys (Fig. 1). The location of survey sites within each region was determined at random from the benthic habitat map. The number of sites within 2-km buffers at increasing distance from shore (i.e., >2, 2–4, 4–6, 6–8, >8 km from shore) were sampled in proportion to their abundance within these buffers, with a minimum of two sites within each buffer. Each patch reef (i.e., a distinct polygon in the GIS coverage) was assigned a number and sites were determined by choosing a set of these numbers at random. The coordinates for each site were obtained from the habitat map and used to locate the sites in the field using a GPS unit.

The distance to shore (distance to closest point on the Florida Keys) and tidal creeks (mid-point of discharge on the ocean side of the Florida Keys) was calculated for each patch reef surveyed in ArcView using the distance tool. The influence of the distance to tidal creeks on coral metrics was evaluated using only the data collected at inshore habitats (<4.5 km from shore) most likely to be impacted by the outflow from coastal bays. All spatial queries were conducted in ArcView (ESRI).

2.2. Water quality in the Florida Keys

An extensive network of water quality stations located within the different habitats and regions of South Florida

have been surveyed quarterly since 1995 (Boyer and Jones, 2002), providing a unique database that can be used to analyze spatial gradients in water quality parameters in relationship to distance to urban centers, shore, and connections to coastal bays (Keller and Itkin, 2002; Kruczynski and McManus, 2002). Using multi-variate techniques, the >150 stations sampled were divided into eight statistically distinct clusters. Stations from three of these statistically defined clusters (clusters 3, 5, and 6) are found within reef habitats of the Florida Reef Tract at increasing distance from shore (Boyer and Briceño, 2006). Cluster 5 (mean distance to shore of sites within this cluster = 1.0 km) and cluster 6 (4.1 km) represent water quality patterns within inshore habitats, while cluster 3 (7.4 km) represents water quality patterns of offshore reef habitats. In this study, the raw data collected at individual sites at quarterly intervals from 1997 to 2005 were accessed from the SERC-FIU Water Quality Monitoring Network (<http://serc.fiu.edu/wqmnetwork/FKNMS-CD/DataDL.htm>) and used to calculate descriptive statistics for water quality parameters from each cluster.

2.3. Coral community composition and coral population structure

Between June 2001 and August 2003, 84 patch reefs (depth = 3–5 m) were surveyed to document the distribution and abundance of corals, and size-structure of coral populations within this habitat type. At each patch-reef

site, divers surveyed haphazardly deployed 10-m² belt transects (1 × 10 m; $n = 6–8$ transects per site) where the length, width, and height of coral colonies were measured. Only the living portions of colonies were measured and corals were measured if >50% of their tissue was found within the transect boundaries. Percent coral cover was estimated by calculating the projected surface area of the all the corals within each transect assuming a circular shape. The total surface area occupied by corals was divided by the total area surveyed (10 m²) to obtain an estimate of percent cover for each transect. While only the living portions of colonies were measured in this study, this method may still result in an overestimation of coral cover by failing to account for the presence of patches devoid of living tissue within colonies.

Coral size data (i.e., mean diameter) were log-transformed ($\ln[x]$) and coral cover data were arcsin-transformed ($\text{asin}[\sqrt{x}]$) for statistical analyses (Sokal and Rohlf, 1995). Coral cover and mean colony size for each species were calculated for each transect (i.e., the sample unit for these analyses), which were used as replicates ($n = 6–8$ per site) for each site. The influence of region and distance to shore and tidal creeks on coral cover and colony size was tested with ANCOVA with distance as a covariate (Sokal and Rohlf, 1995).

The similarity in coral community composition among patch reefs was evaluated with a Multi-Dimensional Scaling (MDS) analysis. MDS uses a Bray Curtis dissimilarity matrix with root-transformed data of coral abundance to produce an ordination plot in which patch reefs close to each other have similar coral community structures, while those further apart are less similar (Clarke, 1993). The abundance of each species was calculated within each transect and an average abundance was calculated for each patch reef to be used in this analysis. The dissimilarity matrix was further analyzed using a nested Analysis of Similarities (ANOSIM) with region (main factor) and cross-shelf location (i.e., inshore, offshore) as a nested factor. These analyses were conducted using the software package PRIMER (PRIMER-E Ltd.).

The structure of coral populations is presented as the proportion of colonies within size classes. Size of each colony was measured as the average diameter of living tissue (i.e., longest length + widest width/2). Surface area was calculated using the diameter and height measurements assuming a hemispherical colony shape (Fisher et al., in press). Comparisons between size–frequency distributions were made using G -tests (Sokal and Rohlf, 1995). Individual colonies served as the sampling unit for these analyses.

2.4. Coral demography

In 2001, a subset of the patch-reef sites surveyed to document coral population structure were established in the Upper Keys as permanent sites where recruitment and colony-based growth and mortality patterns were documented. Four sites were located at inshore habitats (mean distance to

shore = 2.4 km) and four sites within offshore habitats (mean distance to shore = 7.1 km). Within each site, colonies of *Siderastrea siderea*, *Siderastrea radians*, and *Porites astreoides* were identified within a haphazardly located plot (30 × 5 m), measured, photographed, and marked with metal tags. In addition, eight plots (0.25 m²) were established at each site where the location of all corals was mapped to document rates of coral recruitment. In 2002, the eight permanent sites were relocated and tagged colonies were measured and photographed. Colony growth and partial mortality were both measured as the change in tissue surface area between surveys. Surface areas were measured from digital photographs of each colony using digitizing software (ImageJ). Due to the reportedly high variability in recruitment patterns documented previously for Florida reefs (Miller et al., 2000, Tougas and Porter, 2002) recruitment plots were surveyed in 2002 and again in 2003 to provide an estimate of inter-annual variability. Recruitment rates were compared between inshore and offshore habitats and between years using a two-factor ANOVA with each recruitment quadrat as the sample unit. Differences in partial mortality and growth rates between inshore and offshore sites was tested using ANCOVA with colony size as a covariate and individual colonies as sample units.

3. Results

3.1. Abundance and distribution of patch reefs

The highest abundance of patch reefs was documented in the BNP region (N patches = 3635, area of patch-reef habitats = 9.9 km²), while the lowest was documented in the Middle Keys (N patches = 115, area = 1.8 km²). Within BNP, the lowest abundance of patch reefs ($N = 128$) was documented immediately offshore of the Safety Valve, the area with the widest connection with Biscayne Bay (Fig. 1). The Upper Keys had 1366 patch reefs (area = 11.0 km²) and the Lower Keys had 672 patch reefs (area = 13.7 km²). The region between the Lower Keys and the Dry Tortugas, not sampled in this study, has 616 patch reefs (area = 10.1 km²). The size of individual patch reefs in the GIS coverage ranged from <20 m² to 1.3 km².

Patch reefs also have distinct cross-shelf abundance patterns. Only a small percentage of patch reefs were found within 1 km from shore (0.3% of patch reefs) (Fig. 1). The area with the highest abundance of patch reefs (80%) was located between 4 and 7 km from shore. A limited number of patch reefs were found >7 km from shore as the dominant habitat types in this area were hardbottom and bank-barrier reef habitats. The cumulative abundance of patch reefs with respect to distance to shore showed its largest increase (from 1900 to 3800 patches) between 4 and 5 km from shore, which likely represents the distribution of underlying environmental and/or geological gradients that delineate the likelihood of patch-reef formation and growth within these cross-shelf areas. According to this pattern, two cross-shelf habitats (inshore (<4.5 km

from shore) and offshore (>4.5 km from shore)), were further delineated for the establishment of permanent study sites to study coral demography.

3.2. Water quality in the Florida Keys

A total of 2868 observations were collected from 154 stations at quarterly intervals between 1997 and 2005 (Table 1). Significant differences in water quality along a cross-shelf gradient were documented, with inshore habitats (i.e., clusters 5 and 6) exhibiting significantly elevated nutrients (dissolved inorganic nitrogen (DIN) and total phosphorus (TP)), total organic carbon (TOC), turbidity, and light attenuation, decreasing with increasing distance from shore (Table 1; Boyer and Briceño, 2006). Chl a was higher within clusters 5 and 6 (inshore areas) than in cluster 3 (offshore habitats) and soluble reactive phosphorus (SRP) was highest at cluster 6. The cross-shelf gradient in water quality was consistent throughout the Florida Keys, but especially marked in the Lower Keys where wide connections with Florida Bay are found (Boyer and Jones, 2002). Only 11% of the observations had DIN values that exceeded the threshold of 1 μM DIN proposed by Bell (1992) and Lapointe (1997) for nutrient-related reef degradation, while only 3% of the observations had SRP values that exceeded the proposed threshold value of 0.1 μM SRP.

3.3. Coral community composition and cover

A total of 17,568 colonies were measured in surveys of 84 patch reefs that spanned a distance of 240 km. The species encountered, in order of abundance, were: *S. siderea* (% of total N of colonies = 33%), *P. astreoides* (32%), *S. radians* (16%), *Montastraea faveolata* (7%), and *Montastraea cavernosa* (5%). All other species were present at low abundances (<5%). Two species, *S. siderea* and *P. astreoides*, were found at all sites, while *S. radians*, *M. faveolata*,

and *M. cavernosa* were found at 95% of all sites. *Diploria* spp. were found at 82% of sites and *Dichocoenia stokesii* was found at 80% of sites.

The MDS ordination of coral abundance (stress = 0.2) showed no distinct groupings based on region or cross-shelf location. Moreover, the analysis of similarity (ANOSIM) showed no significant differences ($p > 0.1$) between the factors (i.e., region, distance to shore).

Coral cover decreased significantly with increasing distance from shore (ANCOVA, $p < 0.01$; Table 2). No significant patterns in coral cover were detected based on region, and the negative relationship between coral cover and distance to shore was consistent among the four regions of the Florida Reef Tract (ANCOVA, test for unequal slopes, $p > 0.05$) (Fig. 2A). Moreover, no significant differences in coral cover were found with respect to region and distance to tidal creeks for patch reefs within inshore (<4.5 km from shore) habitats (ANCOVA, $p > 0.1$).

3.4. Coral population structure

Colony size showed significant cross-shelf and regional patterns. For *P. astreoides*, *S. siderea*, *S. radians*, *M. faveolata*, and *M. cavernosa*, the five most abundant species in our surveys, mean colony size decreased significantly with increasing distance to shore (ANCOVA, $p < 0.05$ for all species). Mean colony size was significantly larger in the Key Largo region and smaller in the BNP region for all five species (ANCOVA, $p < 0.05$ for all species; Table 2). The linear relationship between size and distance to shore was consistent among the four regions of the Florida Reef Tract (ANCOVA, test for unequal slopes, $p > 0.05$ for all species) (Fig. 2B shows *P. astreoides* as an example of this pattern). In contrast, no significant patterns were documented when mean colony size was related to distance to tidal creeks for corals on inshore habitats from all four regions (ANCOVA, $p > 0.1$ for all species). A large proportion of colonies within the largest size classes was found in

Table 1
Summary of water quality (WQ) parameters obtained from sampling stations throughout the Florida Reef Tract

Variables	WQ cluster			<i>p</i> Value
	5	6	3	
Mean distance to shore (km)	1.0 (0.6)	4.1 (2.7)	7.4 (2.4)	<0.001
N WQ sites	14	29	37	<0.001
N WQ observations	504	1038	1326	<0.001
Dissolved inorganic nitrogen (DIN, μM)	0.70 (0.49)/(0.06–3.51)	0.61 (0.58)/(0.03–7.36)	0.53 (0.44)/(0–3.66)	<0.001
Soluble reactive phosphorus (SRP, μM)	0.027 (0.03)/(0–0.15)	0.032 (0.03)/(0–0.35)	0.027 (0.03)/(0–0.32)	<0.001
Chl a ($\mu\text{g l}^{-1}$)	0.26 (0.24)/(0–1.79)	0.29 (0.27)/(0–2.02)	0.25 (0.27)/(0–3.12)	<0.001
Turbidity (NTU)	1.22 (2.13)/(0–16.91)	0.75 (0.74)/(0–7.95)	0.39 (0.57)/(0–6.55)	<0.001
Salinity (psu)	36.37 (1.08)/(31.95–38.9)	36.19 (0.85)/(30.48–38.5)	36.13 (0.48)/(32.63–37.8)	<0.001
Temperature ($^{\circ}\text{C}$)	27.15 (3.63)/(15.1–33.4)	26.88 (3.42)/(15.4–32.6)	26.65 (2.98)/(16.3–31.67)	<0.001
Light attenuation (K_d , m^{-1})	0.39 (0.49)/(0.01–3.14)	0.31 (0.43)/(0.01–3.41)	0.23 (0.3)/(0.01–2.75)	<0.001

Data for this table were summarized from quarterly samples taken at the bottom from 1997 to 2005. Clusters 5, 6, and 3 were delineated using multivariate statistical techniques and represent a cross-shelf gradient from inshore to offshore reef habitats. Data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by SFWMD/SERC Cooperative Agreements #C-10244 and #C-13178 as well as EPA Agreement #X994621-94-0. Data are presented as mean (bold type) ($\pm\text{SD}$)/(min – max). Statistical differences in mean values among clusters were tested with a Kruskal–Wallis test.

Table 2

Results from the Analyses of Covariance tests (ANCOVA) used in this study to test the influence of distance to shore and tidal creeks on different coral indicators. Distance to shore and tidal creeks and initial colony size were used as covariates in these tests. The interaction term was used to test for differences between the slopes of the different regression lines. * = $p < 0.05$, ** = $p < 0.01$, ns = not significant ($p > 0.05$). Mf = *Montastraea faveolata*, Mc = *M. cavernosa*, Ss = *Siderastrea siderea*, Sr = *S. radians*, Pa = *Porites astreoides*. The influence of distance to tidal creeks on coral cover and colony size was tested only for corals from patch reefs within inshore habitats (<4.5 km from shore)

Indicator	Factors			Species	Factors			Species
	Distance to shore	Region (BNP, UK, MK, LK)	Interaction		Distance to tidal creeks	Region (BNP, UK, MK, LK)	Interaction	
Coral cover	**	ns	ns	–	ns	ns	ns	–
Colony diameter	**	*	ns	Mf, Mc, Ss, Sr, Pa	ns	ns	ns	Mf, Mc, Ss, Sr, Pa
		Factors						
		Colony size	Inshore/offshore			Interaction		
Growth rates		*	*		*		Ss, Pa	
Partial mortality		*	*		*		Ss, Sr, Pa	

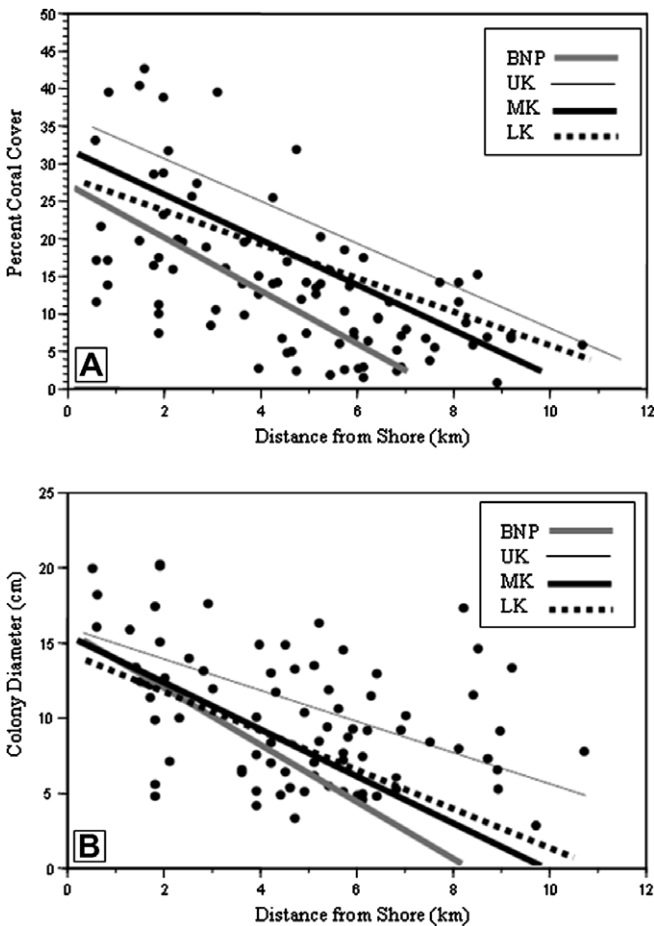


Fig. 2. (A) Average coral cover and (B) mean colony size for *Porites astreoides* within patch reefs of the Florida Reef Tract. Patch reefs were surveyed at increasing distance from shore in four regions (Fig. 1): BNP (Biscayne National Park), UK (Upper Keys), MK (Middle Keys), LK (Lower Keys). At each patch-reef site, divers surveyed haphazardly deployed 10-m² belt transects (1 × 10 m; n = 6–8 transects per site).

the patch reefs closest to shore, and the largest colonies (260 cm in diameter for *M. cavernosa*, 400 cm for *M. faveolata* and *S. siderea*, 125 cm for *P. astreoides*, and 65 cm for *S. radians*) were found in patch reefs in the Upper and

Middle Keys at <2.5 km from creeks with direct connections to Florida Bay.

When corals were grouped into 2-cm size classes (roughly the maximum yearly growth rates measured), a shift in population structure with increasing distance to shore was documented (Fig. 3 shows *P. astreoides* as an

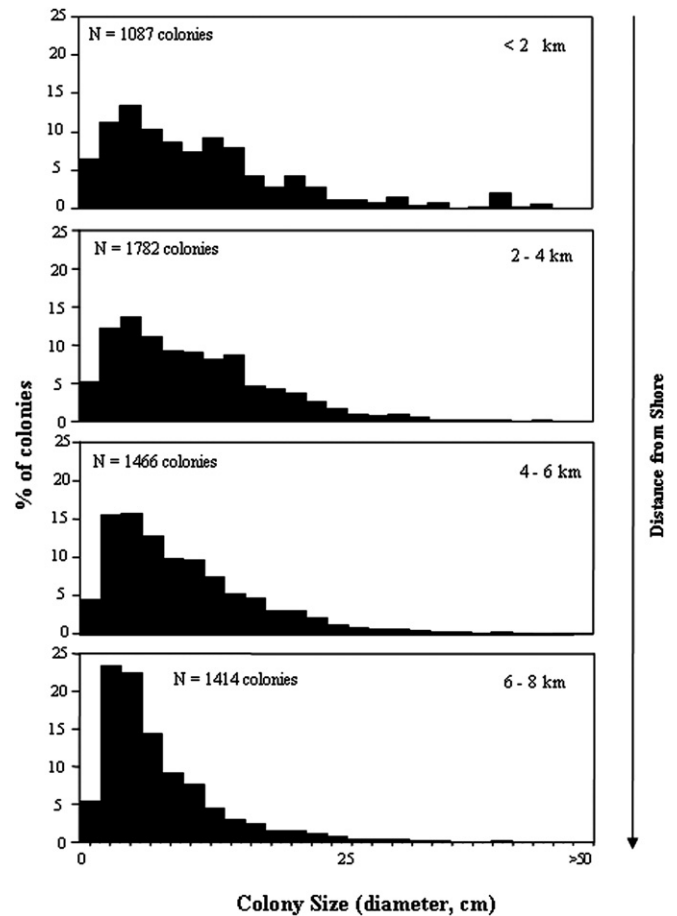


Fig. 3. Size-structure of populations of the stony coral *Porites astreoides* within patch reefs of the Florida Reef Tract at increasing distance from shore.

example of this pattern). Corals on patch reefs closest to shore showed well-spread population structures numerically dominated by intermediate to large colonies, while populations further offshore had progressively narrower size-distributions that become increasingly positively skewed (i.e., numerically dominated by smaller colonies) (Fig. 3). While species-specific patterns were detected, the generalized pattern was consistent among the five coral species analyzed (Fig. 4). Size–frequency distributions of corals on patch reefs at the extremes of their cross-shelf distribution were significantly different for *M. cavernosa*, *S. siderea*, and *P. astreoides* (*G*-tests, $p < 0.05$). In contrast to the cross-shelf gradient documented, no differences in population structure were observed with respect to distance to tidal creek for coral populations within inshore habitats (*G*-test, $p > 0.1$).

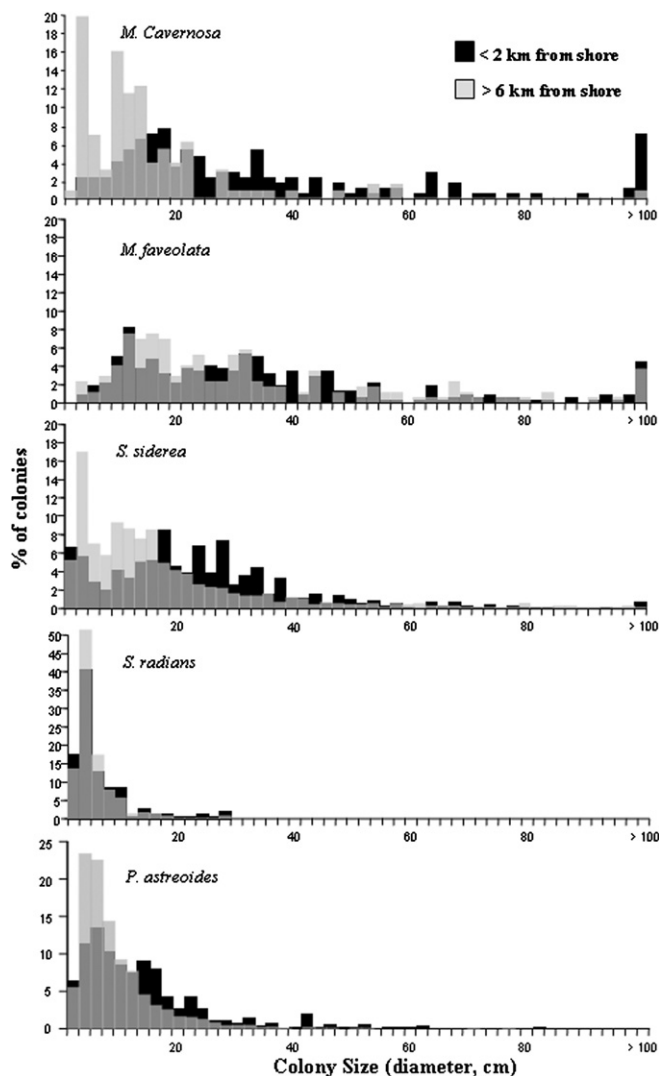


Fig. 4. Size–structure of coral populations within patch reefs of the Florida Reef Tract. Darker shades of grey represent areas of overlap between the two size–frequency distributions in each panel. $N = M. cavernosa$ (371 colonies), *M. faveolata* (485), *S. siderea* (2045), *S. radians* (561), *P. astreoides* (2501).

3.5. Coral demography

The species that recruited into our plots between 2001 and 2002 were *P. astreoides* (45% of recruits), *S. radians* (18%), *S. siderea* (14%), *Favia fragum* (9%), *P. porites* (9%), and *M. cavernosa* (5%). In 2003, two additional species, *D. stokesii* and *Stephanocoenia* sp., were encountered as recruits. Coral recruitment was higher on offshore reefs (67% of all recruits) compared to inshore reefs (33% of all recruits). Mean recruitment rate between 2001 and 2002 was 1.4 (SE = 1.1) recruits $m^{-2} yr^{-1}$ at inshore sites compared to 3.6 (SE = 1.5) recruits $m^{-2} yr^{-1}$ at offshore sites. This pattern was reversed in 2003 when recruitment rates were 2.8 (SE = 2.9) recruits $m^{-2} yr^{-1}$ at inshore sites compared to 1.5 (SE = 0.6) recruits $m^{-2} yr^{-1}$ at offshore sites. No significant differences in recruitment rates were found between years or habitat type, and no significant interactions were found between habitat and year (two-factor ANOVA, $p > 0.1$).

Growth of *P. astreoides*, *S. siderea*, and *S. radians* was positively related to colony size (Fig. 5A–C). When data were grouped according to reef location, significant differences in growth rates were documented between inshore and offshore habitats for *S. siderea* and *P. astreoides*; both grew significantly faster on inshore reefs (ANCOVA, test for unequal slopes, $p < 0.05$; Table 2). *S. radians* grew faster on inshore patch reefs than on offshore patch reefs, but this difference was not significant.

The incidence of total colony mortality was very low at all sites (0–13 colonies per site). Only 20 colonies of *P. astreoides* (4% of all marked colonies), 41 colonies of *S. radians* (8%), and 32 colonies of *S. siderea* (6%) died between 2001 and 2002. Total mortality was related to colony size; colonies that experienced total mortality were significantly smaller than those colonies that survived between 2001 and 2002 for all three species (*t*-tests, $p < 0.01$).

Partial mortality, estimated as the loss of live tissue area between surveys, was influenced by colony size, with larger colonies experiencing larger tissue losses than smaller colonies. However, when partial mortality was expressed as the percentage of the original live tissue area lost between surveys, smaller colonies lost a larger proportion of their tissue than larger colonies (Fig. 5D–F). Partial mortality rates were significantly higher on offshore reefs than on inshore reefs for all three coral species (ANCOVA using \ln (% relative mortality), test for unequal slopes, $p < 0.05$; Table 2). Finally, *S. radians* was the species that experienced the highest rates of partial mortality (Fig. 5E).

4. Discussion

Established and hypothesized gradients in water quality are commonly used to explain, hindcast, and forecast patterns of abundance, diversity, distribution, and condition of reef organisms (Fabricius and De'ath, 2004; Fabricius et al., 2005). The indicators used in this study of a heavily exploited reef system tested the potential influence of water

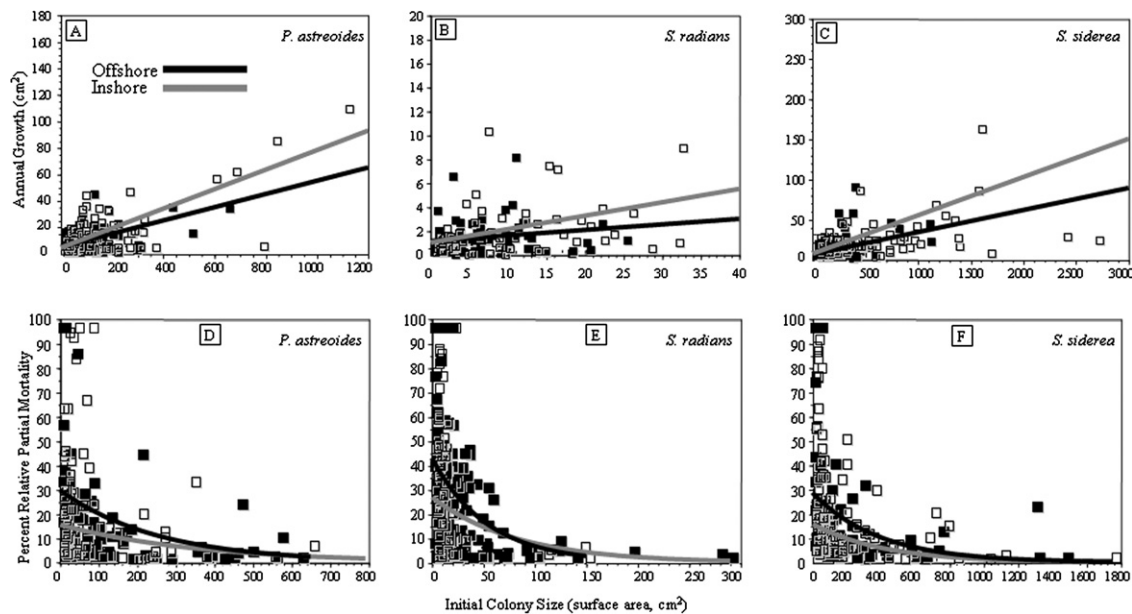


Fig. 5. (A)–(C) Annual growth of coral colonies within inshore (<4 km from shore) and offshore (>4 km from shore) patch-reef habitats between 2001 and 2002. Sample sizes = *P. astreoides* (143 colonies inshore, 100 colonies offshore), *S. radians* (112 inshore, 81 offshore), *S. siderea* (178 inshore, 106 offshore). (D)–(F) Relationship between partial mortality of coral colonies and initial colony size. Partial mortality is expressed as percentage of tissue lost between 2001 and 2002 normalized by initial colony size (surface area). Sample sizes = *P. astreoides* (92 colonies inshore, 77 colonies offshore), *S. radians* (158 inshore, 92 offshore), *S. siderea* (114 inshore, 136 offshore). Open symbols are colonies from inshore sites, solid symbols are from offshore sites.

quality at two temporal scales, patch reef development and present-day coral condition, and the results varied between these two scales (see Table 3 for summary). The development of patch reefs was clearly influenced by cross-shelf gradients and the location of tidal passes and islands of the Florida Keys. The lowest abundance of patch reefs was found closest to shore (<2 km) and in areas with wide connections to coastal bays. These distribution patterns support the hypothesis that the exchange of terrestrial materials through tidal creeks and the flow of “inimical waters” from coastal bays has influenced reef development since the flooding of Florida and Biscayne Bays (<4000 ka) as proposed by Ginsburg and Shinn (1964, 1993). In contrast, spatial patterns in coral indicators do not support the hypothesis that present-day coral reef condition in the Florida Reef Tract is directly related to water quality gradients influenced by land-based sources of disturbance. Moreover, the unexpected favorable condition of coral communities on inshore habitats with higher nutrient and turbidity levels (Boyer and Briceño, 2006) and extreme temperature and salinity values (Hudson, 1981; Walker et al., 1982) challenges the hypothesized relationships between stressors and reef condition.

The relative influence of local and regional sources of disturbance on reef condition has been a recent focus of discussion among reef scientists (Hughes et al., 2003; Pandolfi et al., 2005). Over the past three decades, the rate of decline in coral abundance in Florida has mirrored patterns reported elsewhere (e.g., Miller et al., 2002; Porter et al., 2002; Gardner et al., 2003; Palandro et al., 2003; Pandolfi et al., 2003). The impacts of the demise of the

sea urchin *Diadema antillarum* (Forcucci, 1994), temperature-induced bleaching (Jaap, 1985; Lang et al., 1992), algal competition (Lirman, 2001), hurricanes (Lirman and Fong, 1997), coral diseases (Porter et al., 2001; Richardson and Voss, 2005; Santavy et al., 2005), and overfishing (Ault et al., 2005) have all been documented in Florida, linking the present status of Florida reefs to that of other reef systems in the Caribbean and highlighting the strong influence of regional and global sources of coral disturbance. However, coral reef research in the Florida Reef Tract has concentrated historically on offshore bank reefs where these patterns of coral decline have been documented, and limited attention has been paid to inshore patch-reef habitats that seem to have escaped, to a large extent, the regional declines. No evidence exists to suggest that the impacts of these large-scale stressors may have been restricted to the offshore habitats of the Florida Keys, and the significant cross-shelf patterns in coral condition documented in this study show that local environmental factors can also influence the status and disturbance response of coral populations at small (<10 km) spatial scales.

The magnitude and distribution of coral stressors in the Florida Keys has been a source of controversy and much of the discussion has centered around nutrient sources and availability. Some researchers maintain that coral declines are linked to human-caused eutrophication and nutrient-mediated overgrowth of corals by macroalgae (Lapointe et al., 2002, 2004). Other studies suggest that while inshore waters may indeed have elevated nutrient levels, these decrease to oligotrophic values <1 km from shore, and that no evidence exists to link coral declines with increased

Table 3
Summary of the indicators, hypotheses, tests, and results included in this study

Indicator	Survey methods	Hypothesis	References	Findings
Water quality gradients	Permanent sites	Lower water quality expected inshore due to: (1) higher concentration of nutrients from urban development, wastewater, stormwater, and groundwater discharges; (2) higher TOC and plankton concentrations due to increased nutrient inputs; (3) higher turbidity due to fine-sediment resuspension; (4) wider temperature and salinity fluctuations due to influx of water from shallow coastal bays	Lapointe et al. (2004), Boyer and Briceño (2006), Fabricius (2005)	Significant cross-shelf gradient in water quality with higher nutrients, turbidity, and TOC inshore and in areas with wide connections with coastal bays
Patch reef abundance and distribution	Stratified random surveys	The “inimical water” hypothesis of Ginsburg and Shinn (1964, 1993) suggests that reef development in the Florida Keys is directly influenced by the inflow of lower-quality water from the Gulf of Mexico and the coastal lagoons. Lower abundance of patch reefs was expected close to shore and in areas with wide connections to coastal bays (e.g., across the safety valve area in Biscayne National Park and in the Middle Keys)	Ginsburg and Shinn (1964, 1993), Porter et al. (2002)	Highest abundance of patch reefs was in the BNP region and the lowest abundance in the Middle Keys. Small percentage of patch reefs at <1 km from shore (0.3% of patch reefs). Highest abundance of patch reefs between 4 and 7 km from shore (80% of patch reefs). Largest relative increase in abundance at 4–5 km from shore
Coral community composition	Stratified random surveys	Coral community composition was expected to be influenced by water quality gradients so that inshore patch reefs and those located near tidal passes would be dominated by disturbance-resistant species	Tomascik and Sander (1987b), West and Van Woesik (2001)	No significant patterns in coral community structure with respect to region, distance to shore, or tidal creeks
Coral cover	Stratified random surveys	Coral cover is the most commonly used indicator of reef health and is expected to be higher in areas with better water quality and decrease linearly with proximity to sources of disturbance. Higher cover was expected in areas further away from shore and bay influences (e.g., Upper Keys)	Smith et al. (1981), Fabricius and De'ath (2004)	Highest coral cover close to shore. Coral cover decreases significantly with increasing distance from shore. No significant spatial patterns with respect to distance to tidal creeks. Cross-shelf patterns consistent for all four regions
Coral colony size	Stratified random surveys	Coral size is expected to be influenced by water quality and other disturbance gradients. In the Florida Keys, larger colonies are expected to be found in areas with higher water quality and reduced disturbance regimes such as offshore habitats	Done (1988), Fong and Glynn (1998)	Mean colony size decreases significantly with increasing distance from shore in all regions. Largest colonies in inshore habitats for all species. Mean colony size highest in the Upper Keys region. No patterns with respect to distance to tidal creeks
Population size–structure	Stratified random surveys	Coral population structure is influenced by water quality and disturbance gradients. Coral populations in degraded habitats expected to have a higher proportion of larger colonies as mortality of small colonies increases and recruitment decreases	Bak and Meesters (1999), Meesters et al. (2001), Smith et al. (2005)	Gradual shift in population structure with increasing distance to shore for all species. Corals on patch reefs closest to shore have well-spread population structures numerically dominated by intermediate to large colonies. Offshore populations show narrower size-distributions that become increasingly positively skewed
Coral recruitment	Permanent sites (Upper Keys only)	Coral recruitment was expected to be lower in inshore habitats due to wider temperature and salinity fluctuations, increased nutrients, sedimentation, and turbidity	Tomascik (1991), Birrell et al. (2005)	Coral recruitment higher offshore in 2002, but lower offshore in 2003. No statistically significant cross-shelf differences
Coral mortality	Permanent sites (Upper Keys only)	Coral mortality (total and partial) was expected to be lower in inshore habitats due to wider temperature and salinity fluctuations, increased nutrients, sedimentation, and turbidity	Edinger et al. (2000), Torres (2001)	Partial mortality rates significantly higher on offshore reefs than on inshore reefs for all three coral species. Total mortality negatively related to size (higher for smaller colonies). Low prevalence of total mortality precluded any spatial analyses
Coral growth	Permanent sites (Upper Keys only)	Coral growth was expected to be lower in inshore habitats due to wider temperature and salinity fluctuations, increased nutrients, sedimentation, and turbidity	Nugues and Roberts (2003a,b)	Significantly higher growth rates for <i>S. siderea</i> and <i>P. astreoides</i> in inshore habitats. No difference in growth rates between inshore and offshore habitats for <i>S. radians</i>

nutrient levels originating from land-based sources (Szmant and Forrester, 1996; Szmant, 2002). The long-term water quality monitoring program of the Florida Keys has documented significant spatial patterns in water quality, with inshore areas exhibiting elevated nutrients (dissolved inorganic nitrogen (DIN) and total phosphorus (TP)), total organic carbon (TOC), turbidity, and light attenuation compared to offshore habitats (Boyer and Briceño, 2006). However, water quality parameters in the Florida Keys are generally not as degraded as in other heavily exploited reef systems in proximity to urban centers (Szmant, 2002; Fabricius, 2005). Finally, while significant cross-shelf patterns have been established, researchers have noted that even statistically significant differences in water quality parameters may not necessarily result in significant biological effects (Boyer and Jones, 2002), underscoring the need to distinguish between disturbance and effects patterns, and raising the question of whether solely documenting physical gradients is an adequate method of predicting stress levels of biological communities.

Documentation of healthy coral communities in habitats with reduced water quality has refocused attention on the capability of corals to shift their trophic mode under adverse environmental conditions, thereby broadening their niche boundaries (Anthony, 2000; Anthony and Fabricius, 2000). For example, Fabricius (2005) reports in a recent review of the effects of runoff that the intake of moderate levels of POM can enhance growth in some coral species and compensate for the negative impacts caused by increased DIN, light reduction, and sedimentation. Increased coral feeding in response to changing environmental conditions has also been suggested as a mechanism to resist as well as recover from stress (e.g., Palardy et al., 2005; Grottoli et al., 2006). Finally, Edinger et al. (2000) showed that a decrease in coral extension rates with increasing distance from nutrient sources can be attributed to the potential for corals to supplement their energy supplies by feeding on particulate or dissolved organic matter and the potential for a nutrient-induced enhancement in photosynthesis (Edinger et al., 2000). Higher growth rates (and lower skeletal density) were also documented for corals at inshore habitats of the GBR by Isdale (1983) and Lough and Barnes (1992). It is presently not known whether the trophic environment may be partly responsible for the patterns documented in Florida, where corals on inshore patch reefs exhibit high coral cover, high growth rates, and low partial mortality rates, even when the condition of corals in other habitats has declined both locally and globally. Clearly, further studies are needed to determine the potential role of heterotrophic energy sources on coral growth and survivorship in marginal environments.

In the Florida Reef Tract, corals on patch reefs closest to shore have well-spread population structures numerically dominated by intermediate to large colonies while offshore populations show narrower size-distributions that become increasingly positively skewed. The consistency in the observed patterns among regions and coral species with

different life-history characteristics (e.g., brooders, broadcasters, small maximum size, large maximum size, encrusting morphology, mounding morphology) suggests strong environmental control of demographic processes as previously suggested by Meesters et al. (2001). While one or two years of demographic information is clearly not adequate to fully explain the observed patterns in population structure, preliminary conclusions can still be drawn from these initial surveys. First, it is unlikely that differences in recruitment were the cause of the preponderance of large colonies at inshore habitats. Although low and highly variable, recruitment rates did not show any significant statistical patterns between these areas. This result contrasts with the prediction that dominance by large colonies is caused by lower recruitment rates in degraded reef habitats (Bak and Meesters, 1999). The second conclusion to be drawn is that differences in size-structure of coral populations are most likely due to a combination of faster growth and lower rates of partial mortality at inshore habitats. The positive balance between faster growth rates and lower partial mortality allows colonies within inshore habitats to reach a size refuge from total tissue mortality faster and also attain larger sizes than colonies on offshore habitats. Higher mortality and slower growth rates recorded offshore would prevent colonies from reaching larger sizes, narrowing the size-range of colonies and positively skewing offshore populations.

Inshore patch-reef habitats rank among the healthiest reef communities in the Florida Reef Tract, and it is clear that their persistence may play a role in the long-term survivorship of the Florida reef system. One of the salient features of patch-reef habitats in Florida is the high abundance of large colonies of *Montastraea* spp. that often exceed 2 m in diameter and are increasingly rare in other reef habitats. Aggregations of these colonies, previously described as clusters by Ginsburg et al. (2001), provide essential habitat for reef fishes, hard substrate for other benthic organisms, and potential sources of larvae to replenish depleted offshore habitats. Moreover, the location of patch reefs between the bank reefs and adjacent coastal lagoons underscore the potential role of these habitats as “pit stops” in the ontogenetic migration of several commercially important fish and invertebrate species that spawn in offshore areas and which larvae migrate into nursery habitats in Biscayne Bay and Florida Bay (Ault et al., 2005).

In conclusion, this study has shown that although water quality gradients, by proxy, are often considered one of the main determinants of coral condition, direct relationships between proximity to sources of stressors and coral condition need to be fully documented and not merely assumed. This has important implications for the protection of reef resources and the establishment of Marine Protected Areas, suggesting that nearshore habitats can support keystone reef resources and may be highly resilient to disturbance. However, the negative impacts of further reductions in water quality on coral abundance, spatial

distribution, and condition cannot be dismissed, as the decline in numerous other reef systems in direct response to environmental degradation and human activities has been fully documented. Even if coral communities on patch-reef habitats presently exhibit high coral cover and maintain high growth rates, the potential future impacts of human activities and natural stressors on these communities located at the northernmost limit for reef development and downstream of a major population center cannot be dismissed.

Acknowledgements

Funding for this project was provided by NOAA's National Undersea Research Center at the University of North Carolina Wilmington (Award NA03OAR00088) and NOAA's Coastal Ocean Program South Florida Program (Award NA17RJ1226). This research was conducted under permits FKNMS-2005-007 (Florida Keys National Marine Sanctuary) and BISC-2005-SCI-0013 (Biscayne National Park). Excellent field support was provided by Capt. M. Birns and O. Rutten (NURC), and A. Hazra, R. Carter, D. Manzello, and J. Herlan (University of Miami). Our gratitude goes to C. Sheppard and an anonymous reviewer for their helpful suggestions that improved our manuscript.

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