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Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA

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Abstract Characterizing the Florida Keys National Marine Sanctuary (FKNMS), USA, has gained much attention over the past several decades because of apparent changes in the benthic community structure over space and time representative of patterns occurring in the Caribbean region. We used a 5-year dataset (1996–2000) of macroalgal and sponge cover and water quality measurements as predictor variables of hard coral community structure in the FKNMS. The 16 water quality variables were summarized into 4 groups by principal component analysis (PCA). Hierarchical agglomerative cluster analysis of the mean and standard deviation (SD) of the principal component scores of water quality variables separated the reef sites into two main groups (and five sub-groups), referred to as reefs of similar influence (RSI). The main groups corresponded with their geographical locations within the Florida Keys: the reefs in the Upper and Middle Keys being homogeneous and collectively, having lower water quality scores relative to reefs in the Lower Keys. Canonical correspondence analysis (CCA) between hard coral cover and key predictor variables (i.e., water quality, macroalgal cover and sponge cover) also separated the reefs in the Lower Keys from reefs in the Upper–Middle Keys, consistent with results of the cluster analysis, which categorized reefs based on RSI. These results suggest that the prevailing gradient of predictor variables may have influenced the structuring of coral reef communities at a spatial scale larger than the individual reef. Furthermore, it is conceivable that these predictor variables exerted influence for a long time rather than being a recent event. Results also revealed a pattern showing reduction in hard coral cover and species richness, and subsequent proliferation of macroalgae and sponges during the study period. Our analyses of the Florida Keys present a pattern that is consistent with the characteristics of a reef that has undergone a "phase-shift," a phenomenon that is widely reported in the Caribbean region.

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Introduction

The community structure of coral reefs in the Caribbean, including the Florida Keys, have remained stable for thousands of years before the region suffered a catastrophic coral mass mortality in the 1980s (Hughes 1994; Aronson et al. 1998). Since the 1980s die off, coral reef deterioration has been characterized by a reduction in coral cover by as much as 40%, a shift in the composition of surviving species (Hughes 1994; Greenstein and Pandolfi 1997; Gardner et al. 2003), and a phase-shift from coral-dominated to macroalgal-dominated communities (Dustan 1977; Dustan and Halas 1987; Porter and Meier 1992; Hughes 1994; McClanahan and Muthiga 1998; Porter et al. 2002; Gardner et al. 2003, 2005).

The magnitude, scale and cause of the deterioration of Caribbean coral reefs remain controversial (Hughes 1994; Ginsburg 1994; Murdoch and Aronson 1999; Bellwood et al. 2004). Hypothesized mechanisms working at small spatio-temporal scales (meters to kilometers and days to years) include hurricanes (Gardner et al. 2003), point-source nutrient loading (Ginsburg and Shinn 1994; Leichter

et al. 2003), impacts of upstream land use patterns (Bellwood et al. 2004), and macroalgal overgrowth (Hughes 1994). Other hypotheses suggest the importance of meso- to large-scale processes (tens to thousands of kilometers and decades to millennia), such as sea urchin mass mortality events (Carpenter 1990), larval transport (Galindo et al. 2006), herbivore reduction due to overfishing (Jackson et al. 2001; Pandolfi et al. 2003), disease outbreaks (Aronson and Precht 2001; Porter et al. 2001) and climate change (Walther et al. 2002; Hughes et al. 2003). It is unclear whether the current state of the Caribbean coral reefs represents a permanent phase-shift or that the community structure would rebound (Petraitis and Dudgeon 2004). Long-term monitoring of coral reefs in the Florida Keys (1981–1991) and US Virgin Islands (1989–2003) have indicated no evidence of recovery in terms of coral cover or reduction of algal abundance over a decadal time scale (Porter and Meier 1992; Rogers and Miller 2006).

The main goal of this study is to find evidence of a possible phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. Specifically, this study is designed to determine the correspondence between hard coral cover, macroalgal and sponge cover and water quality variables using the 1996–2000 data of the FKNMS Water Quality Protection Program (WQPP).

Materials and methods

Study site and data collection

The reef tract of the Florida Keys, which represents the third largest barrier reef in the world and the only living coral reef in North America (Lapointe and Matzie 1996), was designated as a marine sanctuary in 1990, and became known as the FKNMS (Keller and Donahue 2006; Fig. 1). The reef tract of the FKNMS, referred to here as the Florida Keys, is partitioned into three regions based on geographic and environmental criteria: Upper Keys, Middle Keys, and Lower Keys (Ginsburg and Shinn 1994). The WQPP was implemented in 1996 to monitor both benthic biota (under the Coral Reef Evaluation and Monitoring Project or CREMP) and water quality (under the Water Quality Monitoring Project or WQMP) in the Florida Keys until 2002 (Keller and Donahue 2006). The CREMP includes 40 reef sites; benthic biota in two to four permanent stations (22 × 2 m transects) were monitored quarterly on each reef site. Field monitoring consists of station species inventories (SSI) and video transects conducted in four permanent stations (22 × 2 m transect) in each reef site. SSI consists of timed (15 min) counts of stony coral species (*Milleporina* and *Scleractinia*) present in each station to provide data on hard coral species richness. Video recordings were taken 40 cm above the reef at a constant swim speed of about 4 m/min yielding approximately 9,000 video frames per transect. Image analysis used a custom software application PointCount for coral reefs, developed specifically for the CREMP (Wheaton et al. 2001). Percent cover of hard corals, macroalgae (fleshy and filamentous and non-coralline) and sponges was calculated from the images. Water quality monitoring under WQMP was undertaken quarterly from 154 stations. Analyses only included those WQPP stations that overlapped with reef sites monitored by CREMP. Sixteen water quality measurements were included in our analyses: temperature (°C), salinity (PSU), dissolved oxygen (DO, mg l^{-1}), and light attenuation (K_d, m^{-1}) were collected in the field; organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), silicate (Si $(OH)_4$), nitrite (NO_2^-), dissolved nitrate (NO_3^-), ammonium (NH_4^+), soluble reactive phosphate (SRP), chlorophyll a (chl a), dissolved inorganic nitrogen (DIN), total unfiltered concentrations of organic nitrogen (TON) and turbidity (NTU) were determined in the laboratory from the water collected in situ (reported in μg l^{-1}) (see Keller and Donahue 2006 for the complete sampling protocol).

Data analyses

Data analyses were conducted at the level of reef site using the 1996−2000 dataset. Average values of percent cover of benthic biota data (hard corals, macroalgae and sponges) and water quality measurements were used for those reef sites with stations at varying depths. In the multivariate analyses, benthic biota data and water quality measurements were arcsine square-root and square-root transformed, respectively, and then data matrices were screened for outliers. Outliers are extreme data values relative to others in a sample and have unduly large effects on the resultant probabilities (McCune and Grace 2002; Quinn and Keough 2006). For example, outliers may distort estimates and *P* values and inflate sums-of-squares, all of which would result in faulty conclusions. In our analyses, we defined outliers as those reefs, coral species or water quality variables with SD (standard deviation) >2 (Quinn and Keough 2006) and/or those with sample points <3 (i.e., rare samples) (McCune and Grace 2002). Outliers were excluded from all data analyses.

Principal component analysis (PCA) was used to extract the underlying patterns of the water quality variables using a correlation matrix based on the average values of the 5-year data. Water quality variables with component loading $\geq \pm 0.5$ were retained in the description of each principal component. The mean and SD of component scores for each reef site were then used as input variables in a hierarchical agglomerative cluster analysis by unweighed pair-group method (UPGMA) linkage rule using Euclidean

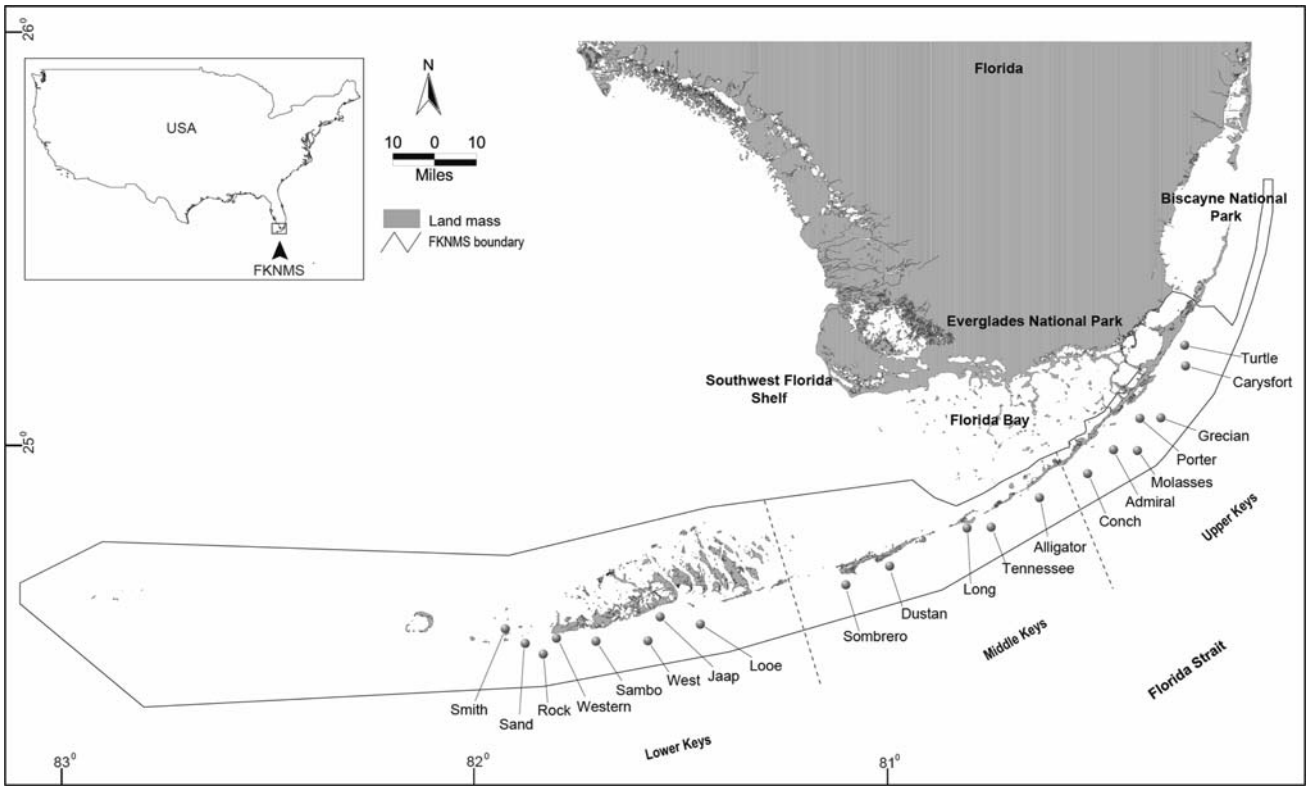

Fig. 1 Map of the Florida Keys showing only the 20 reef sites included in the analyses. Reef abbreviations (enclosed): Western Head (*Western*), West Washer Women (*West*)

distance (ED). Groups of reefs produced by the cluster analysis were linked objectively using the similarity profile (SIMPROF) routine (Clarke and Gorley 2006). Reef clusters were further merged at 0.5 ED to facilitate interpretation and were referred to as reefs of similar influence (RSI). The outcome of this analysis reveals the variation in water quality across reefs in the Florida Keys.

Canonical correspondence analysis (CCA) (ter Braak 1986), the most widely used direct gradient ordination method (Palmer 1993; ter Braak and Verdonschot 1995; McCune 1997; Graffelman 2001; McCune and Grace 2002), was employed to determine the multivariate correlation between hard coral community structure and predictor variables. The minimal set of water quality variables entered in the CCA was identified by the BIOENV routine (Clarke and Ainsworth 1993; Clarke and Gorley 2006). The water quality variables were screened for multicollinearity prior to running the BIOENV routine and only a representative of highly correlated water quality variables (i.e., those with Spearman's $\rho = \geq \pm 0.8$) were used. Pruning of predictor variables to a minimal set that accounts for the largest variation in the hard coral community structure was necessary because the result of CCA becomes less robust as the number of predictor variables increases (McCune and Grace 2002) and to minimize the problem associated with multicollinearity (ter Braak and Looman 1994). In our CCA, the set of water quality variables identified by the BIOENV routine, and macroalgal and sponge cover were used as the predictors of hard coral cover. In addition, the variation in hard coral cover and predictor variables over the 5-year period was examined using a Kruskal–Wallis test. The variation in hard coral, macroalgal and sponge cover, as well as indices of Shannon diversity and species richness of hard corals between 1996 and 2000 were further examined using Mann–Whitney *U* test.

The robustness of the result of CCA was determined by Monte–Carlo permutation test (ter Braak 1986). Ordination scores in the CCA biplots were optimized by coral species using the linear combination (LC scores) of predictor variables. LC scores were used because they best represent the relative contribution of each predictor variable to the variation in hard coral cover (McCune and Grace 2002) and have been shown to perform well even in skewed distributions (Palmer 1993). In the ordination biplot, predictor variables are represented as arrows and the length of the arrow indicates the relative importance of each predictor variable (ter Braak 1986). The angle between arrows indicates the degree of correlation between predictor variables; the location of the reef or species relative to the arrow indicates site characteristics or species preferences (Palmer 1993). Since ordination scores were calculated using LC scores, the relative contribution of the predictor

variables in each axis was determined from the intraset correlation output (McCune and Grace 2002). A predictor variable with correlation coefficient of $\geq \pm 0.4$ is considered ecologically relevant (Rakocinski et al. 1996). The main advantage of CCA is that it allowed simultaneous exploration of relationships among different reef sites or coral species with multiple predictor variables.

Cluster analysis and SIMPROF and BIOENV routines were conducted using PRIMER version 6.1.9 (Plymouth Routines Multivariate Ecological Research, PRIMER-E Ltd, Plymouth, UK; Clarke and Gorley 2006) while the CCA was conducted using PC-Ord version 5 (MjM Software, Oregon, USA; McCune and Mefford1999; McCune and Grace 2002). PCA and univariate tests were conducted using SPSS 14 (SPSS Inc., Chicago, USA).

Results

Reefs of similar influence

The 16 water quality variables were reduced into four principal components (PC), explaining 82.3% of the total variation in the data set (Table 1). PC 1 to 4 are referred to as organic component, algal bloom component, inorganic nitrogen component and physical properties component, respectively. Cluster analysis of the mean and SD of the component scores separated the reefs into two main groups and five subgroups; the Upper and Middle Keys reefs form the first main group and the Lower Keys reefs form the second main group (Fig. 2a). The physical property component (PC4: salinity, temperature and DO) and the algal bloom component (PC2: chl a, TP, and turbidity) appeared to be the main components driving Florida Keys-wide variation in water quality, with higher values in the Lower Keys and lower values in the Middle and Upper Keys (Fig. 2b).

Results of running the BIOENV routine revealed that TN, chl a and salinity are the principal set of water quality variables significantly explaining the variation in hard coral community structure ($\rho_w = 0.393$, $P < 0.05$, global BEST permutation test). TN fluctuated significantly across the 5-year monitoring period (Kruskal–Wallis test, $P < 0.01$, Fig. 3a); chl a and salinity remained stable (Kruskal–Wallis test, $P > 0.05$, Fig. 3b, c).

Reef community structure

Macroalgal cover significantly increased from 1996 to 2000 (Kruskal–Wallis test, $P < 0.001$, Fig. 3d), with an almost triple increase from the 1996 (5.7%) to 1998 (16.5%) level. The macroalgal cover in 1996 had significantly increased by 68% in 2000 (9.6%) (Mann–Whitney U test, $P < 0.05$). Although sponge cover had varied significantly across years (Kruskal–Wallis test, $P < 0.01$, Fig. 3e), the difference between 1996 and 2000 was not significant (Mann–Whitney U test, $P > 0.05$).

Forty-two coral species were identified in the Florida Keys. In terms of percent cover, the *Montastraea annularis* complex dominated the hard coral species in the Florida Keys (Fig. 4a). Collectively, hard coral cover showed a decreasing trend

Table 1 Result of the PCA with Varimax rotation for 16 water quality variables

Water quality parameters	Component			
	PC1	PC2	PC3	PC4
Total organic nitrogen (TON)	**0.865**	0.373	0.163	−0.010
Total nitrogen (TN)	**0.860**	0.380	0.194	−0.017
Silicate SI $(OH)_4$	**0.819**	0.335	0.322	0.141
Light attenuation (K_d)	**0.781**	−0.249	0.044	0.053
Total organic carbon (TOC)	**0.752**	0.482	0.326	−0.149
Nitrite (NO_2^-)	**0.572**	0.017	**0.501**	−0.402
Chlorophyll a (Chl a)	0.051	**0.843**	0.050	0.439
Total phosphorus (TP)	0.153	**0.834**	−0.045	0.257
Turbidity	0.361	**0.725**	0.260	−0.082
Nitrate (NO_3^-)	0.232	0.250	**0.887**	0.070
Soluble reactive phosphorus (SRP)	0.038	−0.176	**0.847**	0.113
Dissolved inorganic nitrogen (DIN)	0.384	0.276	**0.829**	−0.176
Temperature	0.208	0.267	0.099	**0.873**
Dissolved oxygen (DO)	0.322	−0.151	0.047	**−0.816**
Salinity	0.477	0.258	0.147	**0.760**
Ammonium (NH_4^+)	0.320	0.236	0.278	−0.475
Percent variance explained (Total = **82.261**)	28.118	18.791	18.141	17.211

Water quality variables with component loadings $\geq \pm 0.5$ (bolded text) were retained to describe each component (PCA PC1 = organic; PC2 = algal bloom; PC3 = inorganic nitrogen; PC4 = physical properties)

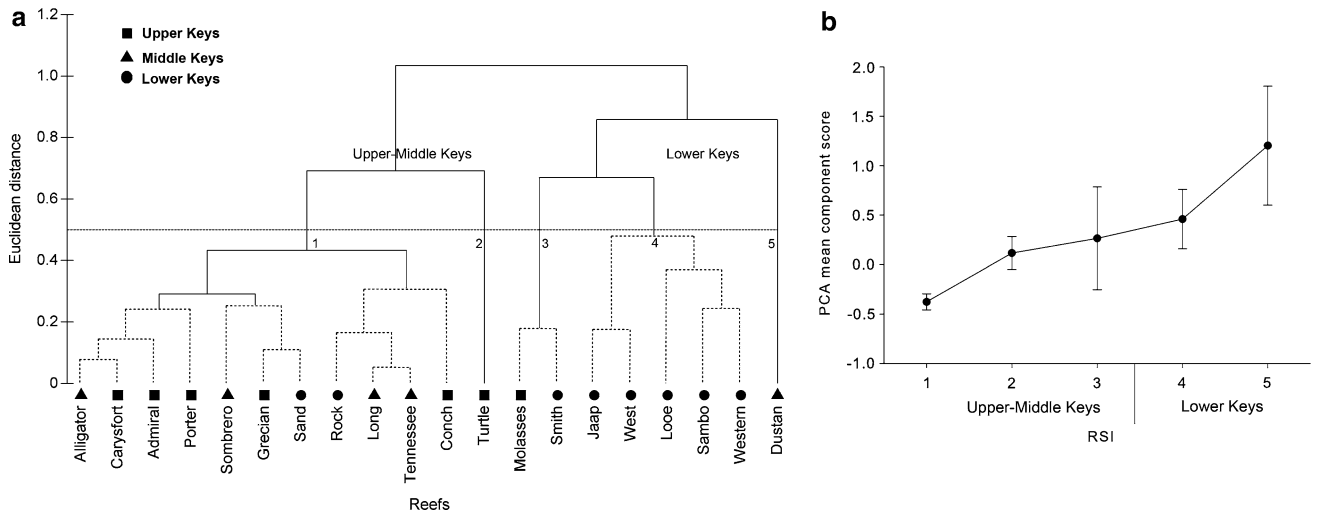

Fig. 2 **a** Dendogram of reef sites based on the cluster analysis of mean and SD of PCA component scores of water quality variables. Objective grouping of clusters (*dashed line*) was based on SIMPROF routine. Clusters were further merged at 0.5 ED resemblance, forming a total of five subgroups (1–5); **b** mean of four PCA component scores of water quality variables across RSI; *error bars* indicate ±standard error of mean. RSI numbers refer to reef clusters in **a**

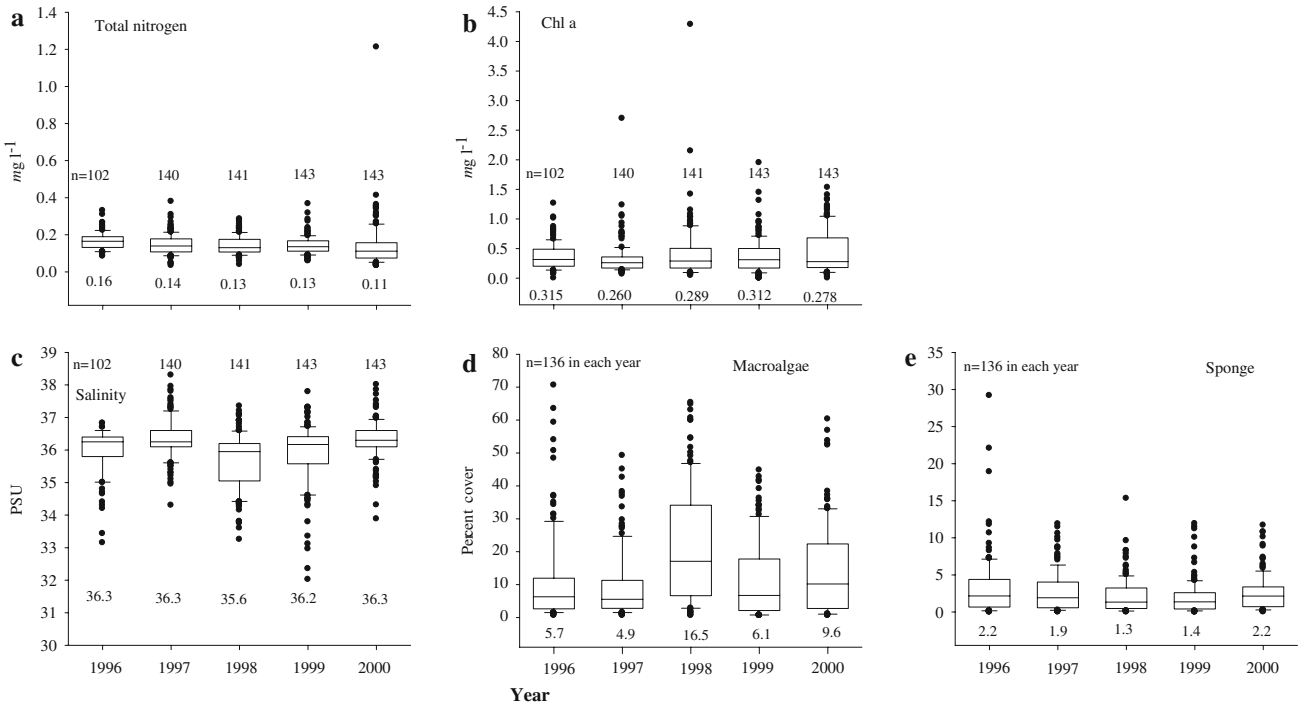

Fig. 3 Box-plots of predictor variables entered in CCA : **a** TN, **b** chl a, **c** salinity, **d** macroalgae, and **e** sponge. The *center line* of the *box* is the median, the bottom and top of the box are the 25th and 75th percentiles and the whiskers below and above of the box are the 10th and 90th percentiles. Points outside the whiskers are the outliers. *Numbers* below the *box* are the median values. These values were calculated from the 20 reefs included in the analyses

across the 5-year monitoring period, with the lowest level occurring in 1999 (Kruskal–Wallis test, $P < 0.01$; Fig. 4b). Hard coral percent cover had significantly decreased by almost 50%, from 8.1% in 1996 to 4.6% in 2000 (Mann–Whitney U test, $P < 0.05$). Differences in species richness and Shannon diversity index over the two periods were not significant (Mann–Whitney U test, $P > 0.05$, Fig. 5a, b).

Correspondence between predictor variables and hard coral community structure

Twenty out of the 25 aggregated reef sites and 35 out of the 42 coral species were included in the CCA after data screening. The CCA revealed two gradients in the coral community structure, with a total variance (inertia) of

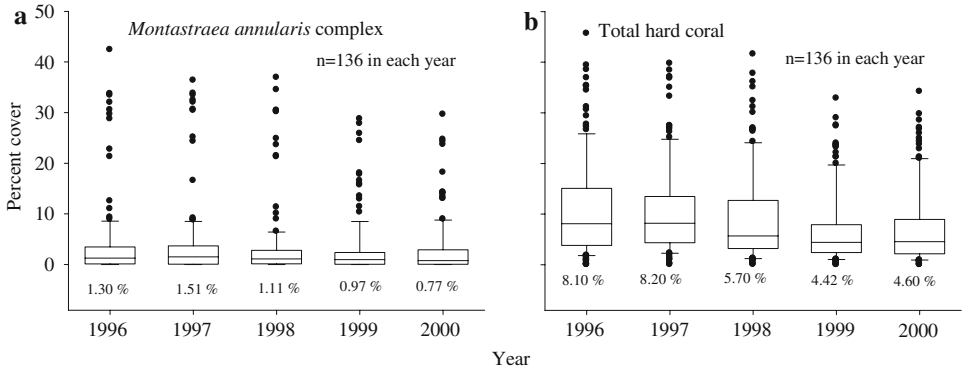

Fig. 4 **a** Percent cover of *Montastraea annularis* complex, the most dominant hard coral species in the Florida Keys, and **b** total hard coral percent cover. These values were calculated from the 20 reefs included in the analyses

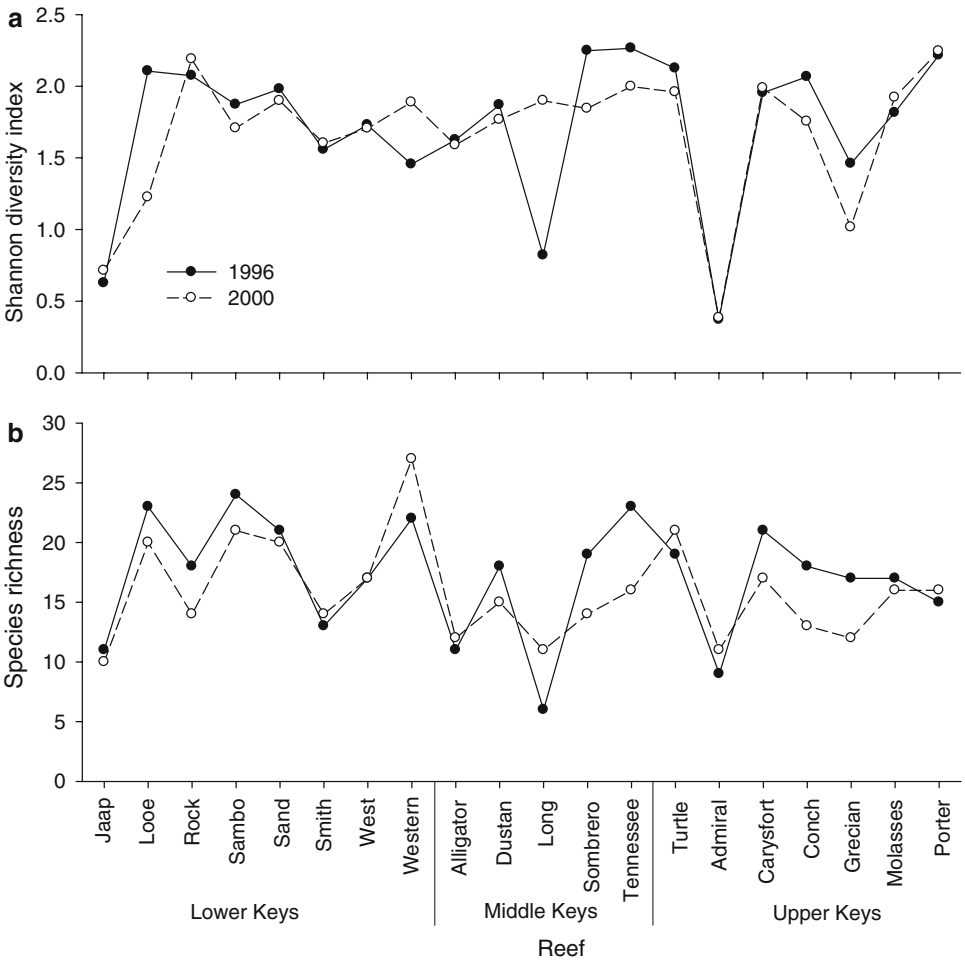

Fig. 5 **a** Shannon's diversity index and **b** species richness of hard corals across reefs between 1996 and 2000

76.52% (Table 2). The Monte–Carlo permutation test revealed that the CCA was robust ($P < 0.01$), indicating a strong correspondence between hard coral community structure and predictor variables. Correlation between hard coral species and the two canonical axes was statistically significant (Monte–Carlo permutation test, $P < 0.01$, Table 2). These canonical axes explained 32% of the variation in coral community structure. Macroalgal and sponge cover accounted for high negative contribution to this variation.

The strength and direction of the relationships between the predictor variables and reef sites and coral species are illustrated in the CCA biplots (Fig. 6a, b). Macroalgae had a negative relationship with chl a ($T = -0.451$), as reflected in their opposing position in the canonical space. Chl a and sponge cover run parallel with salinity because of the positive relationships between the two former predictor variables and salinity (chl a–salinity, $T = 0.64$; sponge–salinity, $T = 0.44$). Reefs in the Upper and Middle Keys aggregated in the upper left corner of the canonical space and toward

Table 2 Results of CCA of 35 coral species in 20 reef sites in relation to the five predictor variables

	Axes		*p* (Monte–Carlo permutation test)
	1	2	
a. Summary statistics of ordination axes			
Eigenvalues (total inertia = 0.765)	0.151	0.094	0.01
Species-predictor correlation (T)	0.611	0.684	0.01
Cumulative % variance explained	19.7	32.0	
b. Axis intraset correlation coefficient of predictor variables (coefficient ≥ ±0.4 are considered ecologically relevant and are in bolded text)			
Macroalgae	**−0.851**	−0.082	
Salinity	**0.778**	−0.056	
Chlorophyll a	**0.713**	0.376	
Sponge	**0.577**	**−0.647**	
Total Nitrogen	0.390	0.310	

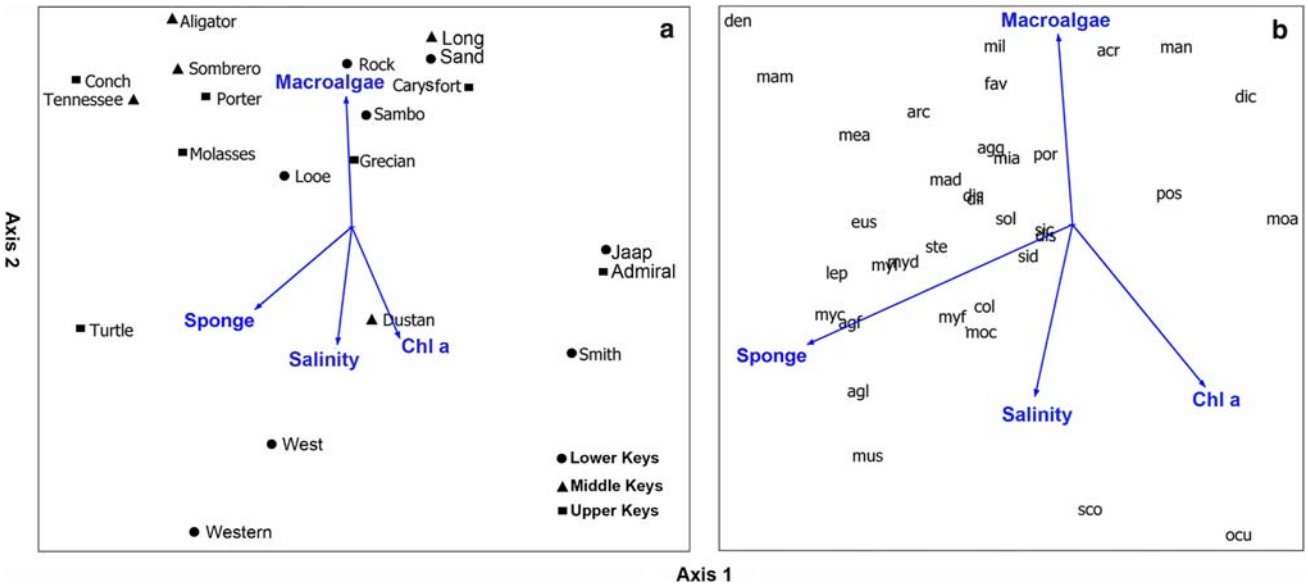

Fig. 6 Biplot of **a** 20 reef sites and **b** 35 coral species in relation to the five predictor variables entered in the CCA. Species abbreviations (enclosed): *Acropora cervicornis* (arc), *Acropora palmata* (acr), *Agaricia agaricites* complex (agg), *Agaricia fragilis* (agf), *Agaricia lamarcki* (agl), *Colpophyllia natans* (col), *Dendrogyra cylindrus* (den), *Dichocoenia stokesi* (dis), *Diploria clivosa* (dic), *Diploria labyrinthiformis* (dil), *Diploria strigosa* (dis), *Eusmilia fastigiata* (eus), *Favia fragum* (fav), *Leptoseris cucullata* (lep), *Madracis decactis* (mad), *Madracis mirabilis* (mam), *Manicina areolata* (man), *Meandrina meandrites* (mea), *Millepora alcicornis* (mia), *Millepora complanata* (mil), *Montastraea annularis* complex (moa), *Montastraea cavernosa* (moc), *Mussa angulosa* (mus), *Mycetophyllia aliciae* (myc), *Mycetophyllia danaana* (myd), *Mycetophyllia feroz* (myf), *Mycetophyllia lamarckiana* (myl), *Oculina diffusa* (ocu), *Porites astreoides* (pos), *Porites porites* (por), *Scolymia cubensis* (sco), *Siderastrea radians* (sic), *Siderastrea siderea* (sid), *Solenastrea bournoni* (sol) and *Stephanocoenia michelinii* (ste)

the macroalgal space; in contrast, reefs in the Lower Keys were spread out (Fig. 6a). Most of the coral species are aggregated toward the sponge space; in contrast, none aggregated near the chl a space (Fig. 6b).

Discussion

The separation of reefs into two main RSI based on water quality measurements corresponded with their geological locations in the Florida Keys (Upper-Middle Keys and Lower Keys). This pattern suggests that the influence of water quality in affecting the structure of the benthic biota in the Florida Keys occurs in two levels. On the one hand, there is similarity in water quality within each locale (e.g., within the Lower Keys) and on the other, there is a difference in water quality between the two regions (e.g., between the Lower Keys and the Upper–Middle Keys). Previous studies offer some bases for the intra and inter-regional variations in water quality in the Florida Keys. The lower physical component scores (i.e., temperature) in the Upper–Middle Keys reefs maybe a reflection of the cold

freshwater flowing from Florida Bay through the island passages in the Middle Keys (Smith and Lee 2003; Keller and Donahue 2006) and to some extent from Biscayne Bay (Jones and Boyer 2002). Water quality measurements in reefs within the Upper–Middle Keys were similar, perhaps because of the mixing of water masses in these areas through wind-forced currents and gravity-driven transport produced by cross-Key sea level differences (Smith and Lee 2003). The strength of these water exchanges exhibit seasonal variations in response to prevailing winds and other oceanographic factors, for example, the Loop current (Keller and Donahue 2006). The higher salinity and algal bloom component scores (i.e., for chl a, TP and turbidity) in the Lower Keys relative to the rest of the FKNMS could be attributed to the onshore movement of high-saline and nutrient-rich deep water into this region (Leichter et al. 2003) brought about by cyclonic gyres spun off of the Florida Current (Szmant and Forrester 1996; Jones and Boyer 2002). Higher nutrient concentration in the Lower Keys could also have an anthropogenic origin, considering that the density of human population in the Lower Keys is higher than the rest of the Florida Keys (Ward-Paige et al. 2005). Alternatively, the lower nutrient concentration in the Upper–Middle Keys relative to the Lower Keys could be attributed to the much higher likelihood of mixing between waters in these regions and the relatively clean Atlantic Ocean waters (Boyer and Jones 2002).

The separation of reefs in the Lower Keys from the Upper–Middle Keys in CCA corroborates the clustering of reefs based on RSI, further illustrating the strong influence of the predictor variables (macroalgae, sponge, chl a, TN and salinity) in the structuring of reef communities at a spatial scale larger than the individual reef. This pattern is consistent with the findings of Ogden et al. (1994) and Murdoch and Aronson (1999) who attributed the inter-reef variations in coral community structure in the Florida Keys to the region-wide differences in environmental characteristics. The influence of environmental gradients in the structuring of reef communities in the Florida Keys may be explained by several possible mechanisms. First, antecedent topography determine the suitability of present substrate for coral settlement and development. For example, Ginsburg and Shinn (1994) reported that the predominance of mobile sand substrates in the Middle Keys and seaward of Biscayne Bay may render these areas unsuitable for coral recruitment, thereby causing reefs in these areas to become impoverished. Second, Florida Bay waters that pass through the Middle Keys may potentially inhibit coral growth, survival and recruitment into this region and adjacent reefs by introducing pulses of waters with extremely variable temperature and salinity as well as with high nutrient and sediment loads (Ginsburg and Shinn 1994; Chiappone and Sullivan 1994; Szmant and Forrester 1996). Third, differential recruitment of corals between regions could help explain the prevailing regional variation in coral community structure in the Florida Keys (Hughes and Tanner 2000). It is well known that the recruitment of corals is affected by several factors, including larval supply, substratum availability, disturbance and regional oceanography (Chiappone and Sullivan 1996). Recently, Moulding (2005) demonstrated that the density and diversity of recruits varies between regions, being significantly lower in the Upper Keys than in the Lower Keys. Finally, it is possible that the Upper Keys is exposed to severe environmental stresses and selective pressures due to the fact that this region is closer to the northern limit of the Florida reef tract (Moulding 2005).

Coral reef degradation in the Florida Keys was characterized by marked reduction in coral cover, and subsequent proliferation of macroalgae from 1996 to 2000. In the Florida Keys, the concurrent dominance of macroalgae relative to hard corals over time were documented previously by several authors, including Dustan (1977), Dustan and Halas (1987), Porter and Meier (1992), Murdoch and Aronson (1999), and Porter et al. (2002) (Table 3). Such dramatic changes in coral reef community structure are widely reported in the Caribbean region (Done 1992; Hughes 1994; McClanahan and Muthiga 1998; Gardner et al. 2003, 2005). This phenomenon is often considered an indicator of a coral reef community that is undergoing a phase-shift (McCook 1999; McManus and Polsenberg 2004; Rogers and Miller 2006). In the Florida Keys, the phase-shift from coral-dominated to macroalgal-dominated reef communities may be attributed to the diminished resilience of corals against perturbations (Jackson 2001; Aronson and Precht 2006), hypothesized to be caused by top-down mechanisms such as herbivore reduction (Hughes 1994; Jackson et al. 2001) and bottom-up processes such as nutrient enrichment (Lapointe 1999; Leichter et al. 2003) (Fig. 7 for a diagrammatic presentation of how we perceive these interacting factors that result in a phase-shift).

More recent evidence elucidates the potential mechanisms underlying macroalgal-coral interactions that may lead to a localized phase-shift in the Florida Keys. Miller and Hay (1998) demonstrated that *Dictyota* spp. and *Halimeda opuntia*, the two most abundant macroalgal species in the Florida Keys, inhibited the growth of *Porites porites*. Jompa and McCook (2003a, b) have also shown that some algae (*Anotrichium tenue, Corallophila huysmansii*) can directly cause coral tissue death. Furthermore, Kuffner et al. (2006) have provided empirical evidence that macroalgae (e.g., *Dictyota*) can directly inhibit the settlement of coral recruits (e.g., *Porites astreoides*). The decline in coral diversity and cover has also been associated with an increase in coral disease prevalence (Porter et al. 2001). Increased physical contact between corals and macroalgae

Table 3 Studies in the Caribbean region (Western Atlantic, including Florida and the Bahamas) documenting changes in benthic community structure in the region

Sites	Period	Mean % cover						Proposed direct and indirect agents of change	Source
		Coral		Macroalgae		Sponge			
		Initial	After	Initial	After	Initial	After		
Caribbean region	1970 s–2000 s	50	10	Increasing		Increasing		White band disease; hurricanes; indirectly attributed to increased abundance of macroalgae following mass mortality of the herbivorous *D. antillarum*(DA) in 1983	Gardner et al. (2003) and López-Victoria and Zea (2005)
Florida Keys	1996–2000	8.1	4.6	5.7	9.6 (16.5 in 1998)	2.2	2.2	Disease; bleaching; anomalous extreme salinity and temperature events; eutrophication and sedimentation; low herbivory due to overfishing and mass mortality of DA; high cover of macroalgae and probably sponges	This study; also see Porter et al. (2002)
Florida Keys (Carysfort Reef)	1975–1982							Boat grounding and anchor damage; hurricanes; sedimentation; coral diseases; eutrophication	Dustan and Halas (1987)
	Mean percent cover (all species)	31.6	32.2						
	Acropora palmata (mean colony size in cm)	63	33						
	Agaricia agaricites cm (mean colony size in cm)	4	6						
Florida Keys (Carysfort and Looe Reefs)	1984–1991	28.4	6.6					Disease; bleaching	Porter and Meier (1992) and Connell (1997)
Gulf of Mexico (Flower Gardens Reef)	1980–1990	55.2	8.7					Disease; bleaching	Connell (1997)
St. John, US Virgin Islands (Yawzi Point)	1988–2003	43.4	12.3	Reported macroalgae competing with corals for space				Hurricane; high sea surface temperature (SST); coral disease; macroalgae	Edmunds and Elahi (2007)
St John, US Virgin Islands	1999–2000 (coral) Before- after Hurricane Hugo in 1989 (macroalgae)	18	14	7.3	33.5			Hurricane; diseases; low herbivory due to overfishing and DA mass mortality; failure of settlement	Rogers and Miller (2006)
Panama (Punta de San Blas)	1983–1990	43–45	12–26	<2	10–32			Bleaching; DA mass mortality; sedimentation and eutrophication	Shulman and Robertson (1996)
Jamaica	1977–1980 vs. 1990–1993	52	3	4	92			Overfishing of herbvivores; hurricane; disease; DA mass mortality	Hughes (1994)
Jamaica (Dairy Bull)	1995–2004	<1	11	90	45–6			Long-lived colonies of *Montastraea annularis* provided structural refugia	Idjadi et al. (2006)
Belize (Glovers Reef lagoon)	1970–71 vs. 1996–1997	80	20	20	80			Diseases; low herbivory due to overfishing and DA mass mortality	McClanahan and Muthiga (1998)
Belize (Channel Cay)	1997–2001 (mainly *Agaricia tenuifolia*)	~43	~0	<10 (no change)		~15	43	Bleaching due to high SST	Aronson et al. (2000, 2002)
Costa Rica (Cahuita)	1980–1993	40.4	29.2					Natural disturbances; human impacts	Connell (1997)

A majority of these studies indicate a decrease in coral cover (or a change in species composition), followed by subsequent increase in macroalgal and sponge cover over time

This list in not meant to be exhaustive. For worldwide summary of the impacts of different array of disturbances, see Connell (1997) and Goreau et al. (2000)

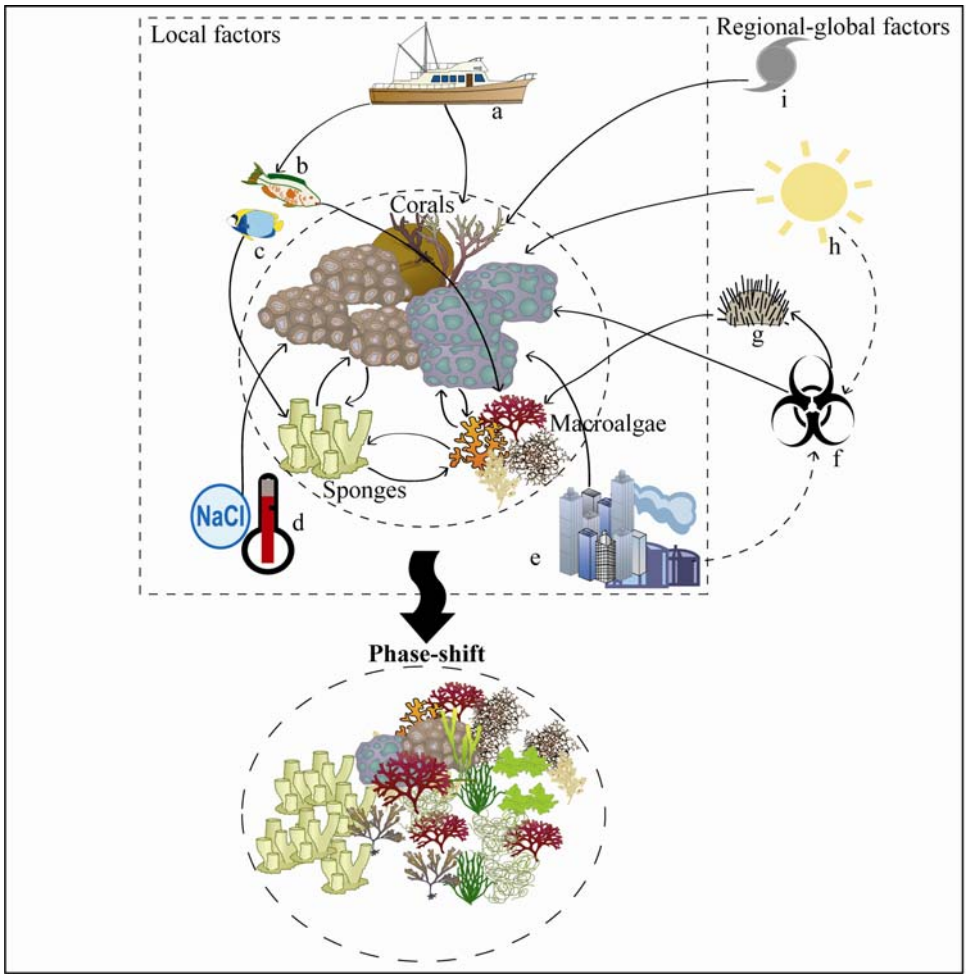

Fig. 7 Diagram showing an array of factors that potentially contributed to the phase-shift in Florida Keys coral reefs from coral-dominated to algal/sponge-dominated community. Only dominant pathways are presented in the diagram. *Solid* and *dashed lines* indicate negative and positive interactions, respectively, and the *arrowhead* of the *line* indicates the trajectory of the interaction. Inside the *dashed circle* are the dominant benthic organisms (corals, macroalgae and sponges). Inside the dashed square are array of local factors that potentially contributed to the phase-shift in the Florida Keys coral reefs: **a** fishing indirectly impact corals through anchor damage and extraction of **b** herbivores and **c** spongivores fishes; **d** extreme seasonal changes of temperature and salinity; and **e** eutrophication, sedimentation and other human disturbances. Regional-global factors include **f** increase severity and incidence of marine diseases, which is partly attributed to the mass mortality of **g** *Diadema antillarum* in 1983–1984 and regional-wide coral bleaching events; **h** global climate change, which has been associated with increased severity and frequency of anomalous high SST causing regional-wide bleaching events; and **i** and historical and natural disturbances such as hurricanes. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Science, USA. For a comprehensive review of phase-shift in coral reefs, see Done (1992); McCook (1999); McManus et al. (2000); McManus and Polsenberg (2004); and Aronson et al. (2006)

due to macroalgal bloom has been hypothesized to provoke coral diseases (Green and Bruckner 2000). This observation was empirically supported by the findings of Nugues et al. (2004) that the increasing physical contact between *Halimeda opuntia* triggered a virulent disease known as white plague type II in *Montastraea faveolata.* The combination of these mechanisms may have contributed to the negative relationship between coral and macroalgal cover in the Florida Keys over the 5-year study period, as demonstrated by the CCA.

Sponge cover was also negatively correlated with hard coral cover in the Florida Keys. There was a subtle increase in sponge cover from 1996 to 2000; this agrees with earlier reports of Aronson et al. (2002) and López-Victoria and Zea (2005) in the Caribbean region. *Cliona delitrix*, *C. lampa*, and *C. caribboea*, known to be aggressive bioeroders, were among the dominant species of sponges in the Florida Keys (Keller and Donahue 2006). Ward-Paige et al. (2005) reported that the Lower Keys had the highest sponge abundance and size, and they attributed this to sewage contamination based on higher δ^{15} N levels in the sponge tissues. Reduction in abundance of spongivorous fishes as postulated by Hill (1998) could also play a role in the increase of sponge cover in the Florida Keys. Spongivory

was previously demonstrated by Pawlik (1998) to be an important agent in controlling the population of at least some sponges. Sponge proliferation could affect corals through several mechanisms: allelopathy (Engel and Pawlik 2005; Pawlik et al. 2007), physical smothering and cellular digestion (Hill 1998) as well as direct space competition (Lopez-Victoria et al. 2006). These mechanisms would lead to increased bioerosion, resulting in a net loss of carbonate, thus compromising the integrity of the coral skeletal structure. However, the positive and negative relationships between hard coral and sponge in the first and second CCA axis, respectively, indicate that sponge-coral relationships are species-specific. This pattern is consistent with the findings of Aerts (1998) who reported that the outcome of coral-sponge interactions depends on the species of both corals and sponges and the frequency of previous encounters between coral and aggressive sponge species.

The positive relationships of both sponge and chl a with salinity is indicative of their wide tolerance to salinity fluctuations. Moreover, the negative relationship between macroalgae and chl a is probably caused by chl a shading in the water column, thereby reducing macroalgal productivity. The chl a concentration in the FKNMS was around 0.4 mg^{-1}, a value that can be considered eutrophic in reef communities (Lapointe et al. 2004). In the biplot, there were no coral species that aggregated in the chl a space, consistent with the findings of van Woesik et al. (1999) and Tomascik and Sander (1985), who demonstrated the negative correlation between chl a concentration and coral cover, growth and diversity. However, it is difficult to separate the effects of chl a on the structuring of coral communities because it is collinear with a variety of other water quality variables.

In summary, results of our analyses revealed a strong correspondence between key predictor variables (e.g., macroalgae, sponge and chl a) and characteristics of the hard coral community structure in the Florida Keys. Water quality variables divide the reef tract of the Florida Keys into two major groups: the Upper–Middle Keys reefs, characterized by lower values of water quality variables and the Lower Keys, characterized by higher values of water quality variables. The negative relationship between hard coral cover and macroalgal/sponge cover suggests a phase-shift in the coral reef structure in the Florida Keys from coral-dominated to macroalgae and sponge-dominated communities. However, the correlative nature of our analyses precludes the identification of precise causal mechanisms that underlie the structuring of the hard coral community in the Florida Keys. It is also probable that the concurrent increase of macroalgal and sponge cover in the Florida Keys reflects an alternative state as a result, rather than the cause of coral demise. We recognize that other factors such as resource availability, herbivory intensity, supply-side factors (e.g., source of propagules), frequency of occurrence of physical disturbance, and historical processes may influence the community structure of corals in the Florida Keys. Future investigations that focus on mechanistic processes need to address whether these factors act alone or interactively, either through mitigative or exacerbative pathways.

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