

Changes in coral reef communities among the Florida Keys, 1996–2003

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Abstract Hard coral (Scleractinia and Milleporina) cover data were examined from 37 sites surveyed annually from 1996 to 2003 in the Florida reef tract, USA. Analyses of species numbers and total cover showed that site-to-site differences were generally very much greater than differences among times within sites. There were no significant differences among different geographical areas within the reef tract (Upper, Middle and Lower Keys). Large-scale changes documented included a reduction in species

numbers and total cover on both deep and shallow offshore reefs between 1997 and 1999 followed by no recovery in cover, and only scant evidence of any recovery in species numbers by 2003. These changes coincided with bleaching events in 1997 and 1998, and the passage of Hurricane Georges through the Lower Keys in 1998. The lack of recovery among offshore reefs suggests that they were no longer resilient. Multivariate analyses revealed that some sites showed relatively little temporal variation in community composition, essentially random in direction, while others showed relatively large year-on-year changes. There was little evidence of any major region-wide changes affecting assemblage composition, or of any events that had impacted all of the sampling sites in any single year. Instead, different sites exhibited differing patterns of temporal variation, with certain sites displaying greater variation than others. Changes in community composition at some sites are interpreted in the light of knowledge of events at those sites and the relative sensitivities of species to various stressors, such as changes in cover of *Acropora palmata* and *Millepora complanata* at Sand Key following the bleaching events and hurricane in 1998, and declines in *Montastraea annularis* at Smith Shoal following a harmful algal bloom in 2002. For most sites, however, it is impossible to determine the causes of observed variation.

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Introduction

Coral studies in the Florida Keys began in the 1850s when the US Coast Survey was in search of a solution for the numerous ship losses on reefs in the region. Louis Agassiz (1852)

conducted a reef survey as a preliminary to recommending sites for lighthouse construction. Thirty years later, his son Alexander Agassiz (1882) mapped the reefs and sea floor at Dry Tortugas. From 1905 to 1939 there was a very active research laboratory at Loggerhead Key, Dry Tortugas, where pioneering work on coral growth rate (Vaughan 1915) and temperature tolerance (Mayer 1914) was conducted. Research resumed after World War II with a focus on fish (Springer and McErlean 1962; Stark and Davis 1966). By 1970, coastal development in the Keys reached fever pitch, and dredge and fill projects destroyed vast areas of mangrove forests, negatively impacting the reefs (Solecki et al. 1999).

Monitoring of Florida Keys reefs began in the late 1970s in Biscayne and Dry Tortugas National Parks, and at various other reef locations for short durations through the 1980s. By this time there was extensive loss of *Acropora* spp. due to a cold-water event in 1978 (Davis 1982; Roberts et al. 1982) and white diseases (Jaap et al. 1988). Three large ship groundings in 1989 (Jaap 2000) prompted the creation of the Florida Keys National Marine Sanctuary (FKNMS). Stretching from Miami to the Tortugas Banks, the FKNMS encompasses >960,000 ha of the sea floor from the coast to 91 m depth (Suman 1997) and includes mangroves, sea grasses, sediment and rubble, with ~140,000 ha of hard bottom habitat and coral reefs (Jaap and Hallock 1990; Lidz et al. 2006). The FKNMS Water Quality Protection Plan monitoring program, to evaluate the status and trends of the coral communities throughout the sanctuary, was finalised following technical meetings in 1994. Sampling protocols were approved by the US Environmental Protection Agency (EPA) in 1996 to generate four annual station-level data products: a species list of all stony corals (Scleractinia and Milleporina), a qualitative list of conditions affecting the vitality of the scleractinian corals (bleaching and diseases by coral species), a benthic cover survey based on video imagery, and a *Diadema antillarum* census.

The present study examined benthic cover data from 1996 to 2003. Up to five various events occurred during this period which are known to have, or might be expected to have, had effects on coral assemblages: (1) Seawater temperature recorded by the National Data Center Buoy Station SANF1, at Sand Key, peaked above 32°C on 9–10 August 1997, a temperature sufficiently high to cause expulsion of zooxanthellae (Jaap 1979) and to discolour many species of Milleporina and stony corals (Goreau and Hayes 1994); (2) Another high-temperature event occurred in the late summer of 1998, associated with the most severe worldwide bleaching event on record at the time (Hoegh-Guldberg 1999); (3) Hurricane Georges crossed the Straits of Florida near Key West on 25 September 1998; (4) On 14 October 1999 Hurricane Irene reached hurricane status over the Florida Straits, moving over Key West the next day; (5) In early 2002, a body of dark-coloured water was

reported between Marco Island and Key West (Hu et al. 2003), and high concentrations of Rhizosoloniaceae diatoms and the toxic dinoflagellate *Karenia brevis* (red tide) were found in water samples. This harmful algal bloom, termed the “Black Water event”, extended over Content Keys and Smith Shoal.

In order to examine changes in the benthic cover data, univariate and multivariate approaches were used in this study, focusing special attention on the relative variation in community structure among sites, and groups of sites, through time. Observed changes were related to the known events where possible.

Materials and methods

Field methods

Seafloor habitat maps were used to create hexagonal divisions of the FKNMS (Overton et al. 1990); each hexagon covering 6 km². From hexagons with coral reef and/or hard bottom habitat a random lottery was used to select sampling sites within the Upper (North Key Largo to Conch Reef), Middle (Alligator Reef to Molasses and Content Keys), and Lower (Looe Key to Smith Shoal) Keys (Fig. 1, Table 1). In 1994 and 1995 40 permanent sampling sites were installed. At each site, four sampling stations were each defined by two reference markers (2.5 × 2.5 cm stainless steel tubing) installed in the reef platform 20–22 m apart. For detailed sampling protocols see Porter et al. (2002). Annually, each station was prepared for sampling by installing a plastic chain between the station markers, a 2-m plastic pipe centred on each marker, and a fibreglass tape between the ends of the pipes, delimiting a 20–22 × 2 m area.

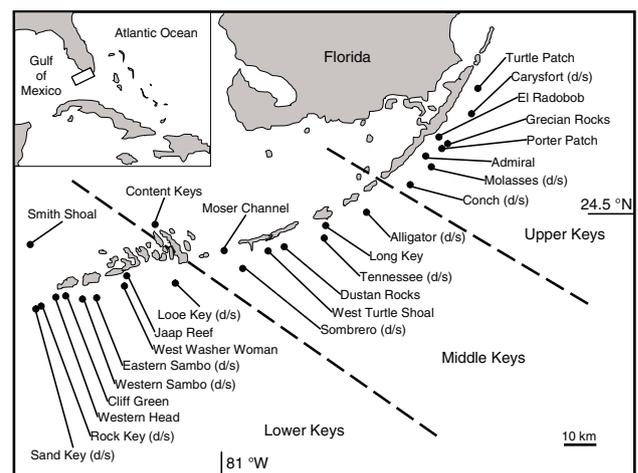


Fig. 1 Location of sampling sites along the Florida reef tract. (d/s) indicates locations where both deep and shallow offshore reefs were sampled

Table 1 Sites, their position in the Keys (L, Lower Keys; M, Middle Keys; U, Upper Keys), Stratum (H, Hard bottom; P, Patch reef; S, Shallow offshore reef; D, Deep offshore reef), number of sampling stations for which data are available 1996–2003, maximum depth in metres, and average percent cover by Scleractinia and *Millepora* spp. over the period 1996–2003

Site	Key	Stratum	Stations	<i>m</i>	%
Content Keys	L	H	3	6.1	1.4
Smith Shoal	L	P	3	8.4	15.4
West Washer Woman	L	P	2	8.1	31.3
Western Head	L	P	3	11.3	26.0
Cliff Green	L	P	2	8.4	18.0
Jaap Reef	L	P	3	2.9	26.9
Sand Key Shallow	L	S	3	6.8	8.9
Looe Key Shallow	L	S	3	8.1	22.5
Eastern Sambo Shallow	L	S	3	2.9	10.6
Western Sambo Shallow	L	S	3	5.5	12.7
Rock Key Shallow	L	S	4	6.1	6.6
Sand Key Deep	L	D	3	11.0	4.3
Looe Key Deep	L	D	3	13.9	7.5
Eastern Sambo Deep	L	D	3	15.5	7.6
Western Sambo Deep	L	D	3	12.9	5.9
Rock Key Deep	L	D	2	13.5	5.0
Moser Channel	M	H	2	4.2	1.0
Long Key	M	H	4	4.5	3.5
West Turtle Shoal	M	P	4	7.4	16.2
Dustan Rocks	M	P	3	6.8	19.2
Sombrero Shallow	M	S	4	6.5	4.7
Alligator Shallow	M	S	3	5.5	1.2
Tennessee Shallow	M	S	3	6.8	3.2
Sombrero Deep	M	D	2	16.8	3.4
Alligator Deep	M	D	2	11.9	1.7
Tennessee Deep	M	D	2	14.5	6.3
El Radabob	U	H	2	2.9	0.1
Turtle	U	P	2	7.4	7.2
Porter Patch	U	P	3	5.5	4.0
Admiral	U	P	4	3.5	27.4
Carysfort Shallow	U	S	3	3.5	6.7
Grecian Rocks	U	S	4	6.8	14.7
Molasses Shallow	U	S	3	8.1	7.0
Conch Shallow	U	S	3	6.8	4.5
Carysfort Deep	U	D	2	16.8	7.6
Molasses Deep	U	D	2	16.1	2.6
Conch Deep	U	D	2	18.1	3.7

Video was recorded along transects centred on the fibre-glass tapes and the central chain using a diver-operated underwater video camera system that included a high-resolution camera (400 lines of resolution), buoyancy compensation chamber, lights and a laser system to keep the camera at a fixed distance from the reef. Analogue video was used until 1998 and digital from 1999. At the time of the

changeover, tests based on multivariate analyses of data collected from the same site at the same time detected no meaningful difference between images recorded by the different cameras. Each image covered an area of approximately 0.16 m². A series of images was selected for analysis that covered each transect with approximately 5% overlap and images were frame-grabbed using a SonyTM still image capture board (DVBK-2000) until 2001 and an Observera RavenviewTM capture board and application software thereafter, organised by year, station and transect, and then stored as JPG image files. Cover was analysed using point count analysis (Curtis 1968; Bohnsack 1979; Carlton and Done 1995; Jaap and McField 2001) using 10 random points per image following preliminary tests which indicated that 50–70 0.16 m² images per sampling unit, and 10 points per image, were sufficient to provide a reasonable estimate of benthic cover. Cover categories recorded included the scleractinian taxa and *Millepora* spp., as well as benthic algae, sponges, octocorals, zooanthids and bare substrate. For quality assurance each year 5% of the stations ($N = 8$) were analysed by at least 3 analysts, and all analysts analysed a randomly selected station. Benthic cover results were compared with a goal of 95% agreement between them, a standard achieved throughout.

In 2001 a statistical assessment of the data concluded that a reduction in sampling effort at some sites was possible, and station reductions began in 2002. The 1996–2003 coral reef monitoring database includes records for 1,360 stations, 4,080 video transects and 200,000 images. For the purposes of this study, data on hard and stony species (scleractinians and *Millepora* spp., 41 species in all) from 37 sites were used, for which cover data is available from 2 to 4 stations for every year from 1996 to 2003 (Fig. 1, Table 1).

Univariate analyses

The 37 sites were categorised (Table 1) according to their positions along the Keys (Upper, Middle or Lower Keys) and the type of coral habitat (Stratum) they represent (hard bottom, patch reef, shallow offshore reef or deep offshore reef, as discussed in Jaap and Hallock 1990). For each station within sites and years, data on the number of species (S) and total cover (%) were analysed. There were 840 distinct combinations of station and time. For each variable a Euclidean distance matrix of differences between every pair of stations was calculated and used to conduct tests of differences between Sites nested within Keys and Strata, and between Years, using permutation-based Analysis of Variance (Anderson 2001; McArdle and Anderson 2001). This procedure is formally equivalent to a standard ANOVA but the flexibility and robustness of the permutation approach ameliorates the necessity for variables to fulfil standard assumptions, such as normality.

Multivariate analyses

Community analyses, based on stony coral taxa, used a non-parametric approach (Clarke 1993; Clarke and Warwick 2001). Total cover varied widely among the 41 taxa (Table 2), so cover values were fourth-root transformed to allow multivariate analyses to draw on species from across the whole assemblage rather than being dominated only by the 2 or 3 species with the highest cover (Clarke and Green 1988). Transformed data were averaged across the multiple stations for each site/time combination and, for some analyses, further averaged across times. Averaging the (transformed) cover values across the stations within sites provided a data matrix of 296 samples by 41 species to input to the multivariate analysis. Bray-Curtis similarities (Clarke et al. 2006) were computed between each pair of samples, and the triangular matrices ordinated by non-metric multi-dimensional scaling (MDS: Kruskal 1964) to display and contrast the different sources of variation in assemblage structure. The significance of differences between Stratum or Keys groups was tested using ANOSIM (Clarke and Green 1988; Clarke 1993). Similarity percentage analysis (SIMPER, Clarke 1993) was used to identify taxa primarily responsible for observed differences in assemblage structure in space or through time.

All univariate and multivariate analyses were implemented in PRIMER 6 (Clarke and Gorley 2006) and PERMANOVA + β 18 software.

Results

Univariate analyses

The largest differences in the two univariate measures, numbers of species and total cover, were among sites (Table 3). In terms of univariate measures, the assemblages of scleractinian corals and *Millepora* spp. did not vary significantly among different parts of the Florida reef tract (Keys, Table 3) but differences in numbers of species and total cover among Strata were significant, as might be expected. There were significant differences among years and the interactions between Strata and years were also significant, implying that patterns of variation in mean values through time were different in different types of Strata.

The purpose of the Analysis of Variance is to understand which sources of variation in mean values are significant. Pairwise tests for differences in mean values between years within Strata (Table 4) are problematic as it is difficult to control, sensibly, for Type I error with so many possible combinations (and therefore tests), even omitting comparisons between Strata. A full Bonferroni correction would limit interpretation only to those tests with $P \leq 0.0005$ or

Table 2 Average percent cover of species in different Strata (H, Hard bottom; P, Patch reefs; S, Shallow offshore reefs; D, Deep offshore reefs) across all years

Species	Form	H	P	S	D
<i>Montastraea annularis</i>	Massive	0.174	8.213	2.991	1.848
<i>Montastraea cavernosa</i>	Massive	0.135	4.207	0.265	0.519
<i>Siderastrea siderea</i>	Massive	0.169	2.461	0.392	0.804
<i>Porites astreoides</i>	Massive	0.261	0.932	1.121	0.237
<i>Colpophyllia natans</i>	Massive	0.004	1.362	0.149	0.206
<i>Millepora palcicornis</i>	Branching	0.082	0.442	0.411	0.617
<i>Acropora palmata</i>	Branching	0.001	<0.001	1.296	
<i>Millepora complanata</i>	Branching		0.007	0.950	0.001
<i>Diploria stigosa</i>	Massive	0.320	0.227	0.078	0.041
<i>Diploria clivosa</i>	Massive	0.439	0.023	0.056	0.004
<i>Acropora cervicornis</i>	Branching		0.033	0.050	0.241
<i>Porites porites</i>	Branching	0.009	0.124	0.043	0.149
<i>Dendrogyra cylindrus</i>	Massive		0.002	0.303	
<i>Agaricia agaricites</i>	Encrusting	0.003	0.061	0.062	0.170
<i>Dichocoenia stokesi</i>	Massive	0.068	0.121	0.031	0.022
<i>Diploria labyrinthiformis</i>	Massive	0.003	0.069	0.091	0.056
<i>Stephanocoenia intersepta</i>	Encrusting	0.037	0.123	0.002	0.036
<i>Oculina diffusa</i>	Branching		0.165		
<i>Meandrina meandrites</i>	Massive		0.055	0.042	0.050
<i>Siderastrea radians</i>	Small	0.060	0.020	0.010	0.007
<i>Solenastrea bournoni</i>	Massive	0.042	0.040	<0.001	0.007
<i>Mycetophyllia danana</i>	Massive		0.027	0.001	0.012
<i>Mycetophyllia aliciae</i>	Massive		0.021	<0.001	0.017
<i>Mycetophyllia lamarckiana</i>	Massive		0.024	0.001	0.003
<i>Eusmilia fastigata</i>	Branching		0.016	0.002	0.010
<i>Mycetophyllia ferox</i>	Massive		0.022	<0.001	0.005
<i>Madracis mirabilis</i>	Branching				0.023
<i>Mussa angulata</i>	Branching		0.020		0.002
<i>Madracis decactis</i>	Branching		0.005	0.002	0.009
<i>Favia fragum</i>	Small	0.002	0.003	0.008	0.001
<i>Agaricia lamarcki</i>	Encrusting		0.006		0.007
<i>Manicina areolata</i>	Massive	0.001			0.002
<i>Isophyllia sinuosa</i>	Massive	0.002	0.001		
<i>Cladocora arbuscula</i>	Branching	0.001	0.001		
<i>Leptoseris cucullata</i>	Encrusting				0.002
<i>Scolymia cubensis</i>	Small		0.001		
<i>Scolymia lacera</i>	Small	0.001	0.001		
<i>Agaricia fragilis</i>	Encrusting		<0.001		0.001
<i>Madracis pharensis</i>	Encrusting				0.001
<i>Solenastrea hyades</i>	Massive	0.001			
<i>Isophyllastraea rigida</i>	Massive		<0.001		

so as being significant in an analysis of all combinations of years and Strata. Limiting the analysis to within-Stratum comparisons limits interpretation to comparisons with

Table 3 Results from permutation-based Analysis of Variance tests for differences in number of species (S) and relative percent cover (Cover) among groups using Type III sums of squares based on 999 permutations of residuals under a reduced model

Source	df	S				Cover			
		SS	MS	F	P	SS	MS	F	P
Key	2	296.66	148.33	1.68	0.228	2506.50	1253.30	1.79	0.204
Stratum	3	2641.00	880.34	9.79	0.001	24588.00	8196.00	11.48	0.002
Year	7	133.77	19.11	6.13	0.001	661.43	94.49	5.28	0.001
Key × Stratum	6	398.04	66.34	0.73	0.598	3724.70	620.78	0.86	0.547
Key × Year	14	42.64	3.05	0.98	0.507	408.25	29.16	1.65	0.085
Stratum × Year	21	134.91	6.42	2.06	0.009	1184.10	56.39	3.25	0.001
Site(Key × Stratum)	25	2379.70	95.19	29.36	0.001	18885.00	755.40	21.98	0.001
Key × Stratum × Year	42	117.26	2.79	0.90	0.646	496.93	11.83	0.69	0.909
Site(Key × Stratum) × Year	175	543.13	3.10	0.96	0.645	2857.80	16.33	0.48	0.999
Residual	544	1763.60	3.24			18695.00	34.37		
Total	839	8201.60				84026.00			

Values of $P < 0.05$ highlighted in bold

$P \leq 0.002$. Using this limit to interpret the values in Table 4, for differences in species numbers, there were no changes on hard bottoms between years, while for patch reefs there were differences between 1999 and 2002, for shallow offshore reefs between 1996 and 2000, 1997 and 2000, 1997 and 2002, and 1998 and 1999, and for deep offshore reefs between 1996 and 2003, 1997 and 1999, and 1998 and 1999. Similarly, for differences in average percentage cover, there were no changes on hard bottoms or patch reefs between years, but on shallow offshore reefs there were differences between 1996 and 1998, 1999, 2000, 2001, 2002 and 2003 and between 1997 and 1999, 2000, 2001, 2002 and 2003, between 1998 and 1999, 2000, 2002 and 2003, and for deep offshore reefs between 1997 and 1998, 1999, 2000, 2001, 2002 and 2003.

Taking a more pragmatic view, that significance levels should be used as a guide to interpretation, rather than as hard limits, the values from Table 4 were reorganised and shown in Table 5 as measures of the strength of support for differences between years, ranging from $P \leq 0.002$ (strong support for differences), through $P \leq 0.01$ (weaker support) to $P \leq 0.05$ (weak support).

Of course, such analyses cannot provide information on the nature of differences, such as whether they represent increases or decreases, or the maintenance of a stable state. To visualise these patterns the appropriate plots, therefore, are of mean values of the univariate measures, averaged within Strata, across years (Fig. 2). Between 1997 and 1999, the number of species observed during surveys on shallow and deep offshore reefs decreased (Fig. 2a). During the same period, the evidence of any decrease in species numbers on the patch reefs was weak, but there was then a significant increase from 1999 to 2002 to pre 1997 species numbers, suggesting that there had been a cycle of

loss followed by recovery. Meanwhile, the evidence of any recovery for offshore reefs was at the best very weak, indeed the deep offshore reefs were still below 1996 species numbers by the end of the sampling period. On hard bottoms, species numbers were always lower than in other Strata, and there was no evidence of a marked decline in numbers in any particular year. Changes in total cover also showed a dramatic decline among both shallow and deep offshore reefs between 1997 and 1999 (Fig. 2b), especially on the shallow reefs where total cover fell by $>50\%$. There was no evidence of recovery throughout the rest of the sampling period. Total cover changed little on patch reefs or hard bottoms throughout the sampling period.

Multivariate analyses

All MDS plots (Figs. 3–5) had stress values ranging between 0.1 and 0.15, within the range that is regarded as giving confidence to the interpretation of these plots (Clarke 1993). A two-dimensional MDS plot displaying the spatial relationship of all 37 sites to each other, for time-averaged data, showed the dominant effect of different Strata in determining the communities (Fig. 3). Hard-bottom assemblages tended not to overlap with those on reefs. No two reefs contained exactly the same assemblages of stony corals (*Millepora* spp. and Scleractinia). There was a general trend in assemblage structure from patch reefs, through deep offshore reefs, to shallow offshore reefs. While some deep offshore reefs, such as Looe Key, Eastern Sambo, Tennessee and Rock Key, were relatively similar in terms of the community of stony corals inhabiting them, others such as Molasses and Alligator differed substantially. Shallow offshore reefs tended to be less similar to each other than deep offshore reefs and generally exhibited the

Table 4 Results of pairwise within-Stratum (H, Hard bottom; P, Patch reef; S, Shallow offshore reef; D, Deep offshore reef) tests for differences between years from permutation-based Analysis of

Variance tests for differences in number of species (S) and relative percent cover (Cover) among groups using Type III sums of squares based on 999 permutations of residuals under a reduced model

Stratum:	S								Cover							
	H		P		S		D		H		P		S		D	
	t	P	t	P	t	P	t	P	t	P	t	P	t	P	t	P
1996, 1997	0.172	0.885	0.688	0.547	0.090	0.931	0.020	0.990	0.202	0.871	0.452	0.734	0.654	0.558	0.204	0.847
1996, 1998	0.876	0.492	1.342	0.221	2.134	0.064	1.854	0.087	0.467	0.705	0.906	0.406	8.004	0.001	2.529	0.019
1996, 1999	0.363	0.764	2.122	0.073	5.119	<i>0.004</i>	3.977	<i>0.003</i>	0.126	0.927	1.379	0.221	9.519	0.001	3.174	<i>0.007</i>
1996, 2000	1.925	0.213	0.415	0.757	5.114	0.002	2.438	0.040	0.738	0.564	0.659	0.550	8.135	0.001	3.046	0.011
1996, 2001	7.818	<i>0.007</i>	0.294	0.901	3.563	<i>0.007</i>	2.206	0.048	1.095	0.438	0.461	0.733	7.913	0.001	3.129	0.012
1996, 2002	1.353	0.343	1.785	0.109	4.586	<i>0.003</i>	3.371	<i>0.006</i>	0.592	0.637	0.468	0.698	8.031	0.001	2.789	0.021
1996, 2003	0.595	0.630	0.397	0.803	1.812	0.112	4.048	0.002	0.208	0.856	0.979	0.342	9.409	0.001	2.762	0.016
1997, 1998	0.039	0.980	1.840	0.103	1.855	0.104	3.332	<i>0.009</i>	0.155	0.900	0.711	0.511	4.385	<i>0.004</i>	4.993	0.002
1997, 1999	0.609	0.642	2.361	0.043	4.242	<i>0.006</i>	5.591	0.001	0.113	0.926	1.177	0.285	6.174	0.001	5.925	0.001
1997, 2000	0.640	0.596	1.131	0.319	5.271	0.002	3.508	<i>0.004</i>	0.365	0.763	0.557	0.666	5.999	0.002	5.821	0.001
1997, 2001	1.652	0.262	0.435	0.725	3.526	<i>0.009</i>	4.069	<i>0.003</i>	1.015	0.450	0.397	0.776	4.924	0.002	4.635	0.002
1997, 2002	0.270	0.831	0.742	0.525	4.478	0.002	3.663	<i>0.003</i>	0.273	0.834	0.323	0.872	6.423	0.001	5.377	0.001
1997, 2003	0.178	0.874	0.734	0.510	2.365	0.040	4.317	<i>0.004</i>	0.021	0.985	0.937	0.389	5.630	0.001	6.019	0.001
1998, 1999	0.779	0.557	1.514	0.193	6.262	0.001	4.093	0.001	0.374	0.752	1.568	0.149	6.009	0.001	1.749	0.107
1998, 2000	1.203	0.395	0.501	0.696	3.421	<i>0.010</i>	2.201	0.045	0.427	0.713	0.546	0.668	5.603	0.001	1.331	0.210
1998, 2001	5.778	0.020	1.293	0.211	1.874	0.076	1.246	0.245	2.291	0.204	1.101	0.313	4.625	<i>0.003</i>	0.968	0.355
1998, 2002	0.752	0.560	3.015	0.021	2.213	0.058	1.551	0.151	0.280	0.817	0.359	0.853	5.187	0.001	0.851	0.418
1998, 2003	0.333	0.783	2.351	0.050	0.682	0.488	1.494	0.179	0.211	0.866	1.207	0.245	5.430	0.002	0.660	0.545
1999, 2000	3.318	0.084	2.234	0.053	0.518	0.647	0.714	0.499	0.665	0.601	1.279	0.242	0.456	0.681	0.123	0.896
1999, 2001	4.760	0.025	2.877	0.019	1.591	0.146	1.668	0.117	1.369	0.372	4.564	<i>0.003</i>	1.641	0.135	0.952	0.378
1999, 2002	0.915	0.506	5.457	0.002	1.735	0.114	1.111	0.282	0.502	0.674	1.346	0.210	0.307	0.789	1.329	0.189
1999, 2003	0.528	0.680	2.444	0.037	2.376	0.043	2.066	0.050	0.105	0.933	1.488	0.192	1.561	0.157	1.846	0.104
2000, 2001	3.838	0.061	0.743	0.501	1.174	0.262	1.021	0.319	2.673	0.138	2.892	0.017	0.947	0.374	0.463	0.664
2000, 2002	0.220	0.846	2.187	0.053	1.813	0.109	0.512	0.631	0.065	0.956	0.652	0.547	0.018	0.992	0.793	0.450
2000, 2003	0.146	0.916	0.769	0.472	1.735	0.108	0.773	0.444	0.467	0.709	0.981	0.343	0.749	0.499	1.443	0.176
2001, 2002	2.611	0.158	1.564	0.175	0.360	0.723	0.720	0.492	2.155	0.187	1.101	0.290	0.585	0.554	0.201	0.875
2001, 2003	1.311	0.342	0.272	0.914	1.113	0.299	0.182	0.848	1.240	0.404	0.301	0.880	0.066	0.945	0.686	0.514
2002, 2003	0.044	0.974	1.642	0.128	0.874	0.400	0.419	0.674	0.348	0.781	1.316	0.242	0.744	0.492	0.656	0.547

Values of $P \leq 0.002$ highlighted in bold, $P \leq 0.01$ in italics

greatest degree of spatial variability. The major pattern was one of difference between Strata. Analysis of Similarities (ANOSIM) confirmed this observation, as differences among Strata were significant (Global $R = 0.458$, $P < 0.001$, for all pair-wise comparisons $P < 0.003$). There was no evidence of sites grouping together according to their location among the Keys, and no significant differences were found using two-way crossed ANOSIM tests for differences in average assemblage structure between Keys and Strata.

Figure 4 illustrates the temporal variation in assemblage composition from 1996 to 2003 of sites grouped into those of a similar Stratum (shallow offshore reefs, deep offshore reefs, patch reefs) in the Lower, Middle and Upper Keys. This composite figure provides a summary of the

comparative scale and directionality (or non-directionality) of temporal change in relation to spatial site differences within reefs of the same general type in different locations. Within each reef-type \times region combination, there tended to be no overlap of different reefs, even taking into account variation through time at each site. Only deep offshore reefs at Looe Key and Eastern Sambo (Fig. 4b) provided an exception. Therefore, differences through time at each site tended to be smaller than differences between sites.

Second, the changes through time differed from reef to reef. It is the nature of the time trajectories, the detail of how the community on each reef varied through time, that conveys information about the nature and amount of change in the Florida reef tract and reveals the relative effects of man-made and natural changes. It was readily

Table 5 Summary of pairwise within-Stratum tests for differences between years from permutation-based Analysis of Variance tests for differences in number of species (S) and relative percent cover (Cover) among groups using Type III sums of squares based on 999 permutations of residuals under a reduced model

	1997	1998	1999	2000	2001	2002	2003
S							
1996	n	n	S, D	S, (D)	H, S, (D)	S, D	D
1997		n	(P), S, D	S, D	S, D	S, D	(S), D
1998			S, D	S, (D)	(H)	(P)	(P)
1999				n	(H), (P)	P	(P), (S), (D)
2000					n	n	n
2001						n	n
2002							n
Cover							
1996	n	S, (D)	S, D	S, (D)	S, (D)	S, (D)	S, (D)
1997		S, D	S, D	S, D	S, D	S, D	S, D
1998			S	S	S	S	S
1999				n	P	n	n
2000					(P)	n	n
2001						n	n
2002							n

Strata (H, Hard bottom; P, Patch reef; S, Shallow offshore reef; D, Deep offshore reef) are indicated for which mean values differ between pairs of years at varying levels of significance indicated by: bold, $P \leq 0.002$; normal text, $0.002 < P \leq 0.01$; parentheses $0.01 < P \leq 0.05$. *n* indicates pairs of years for which no comparisons had $P \leq 0.05$

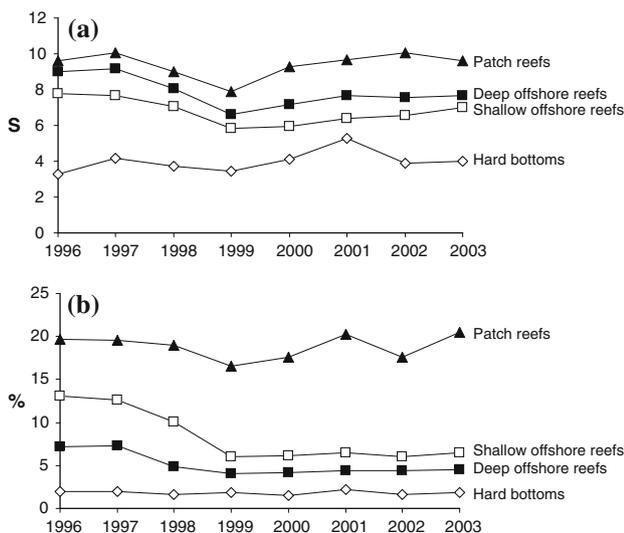


Fig. 2 (a) Mean number of species, and (b) mean total percent cover on hard bottoms (white diamonds), patch reefs (black triangles), shallow offshore reefs (white squares) and deep offshore reefs (black squares) 1996–2003

apparent that the changes on some reefs were greater than changes on others. For example, among shallow offshore reefs in the Lower Keys (Fig. 4a), changes over time at

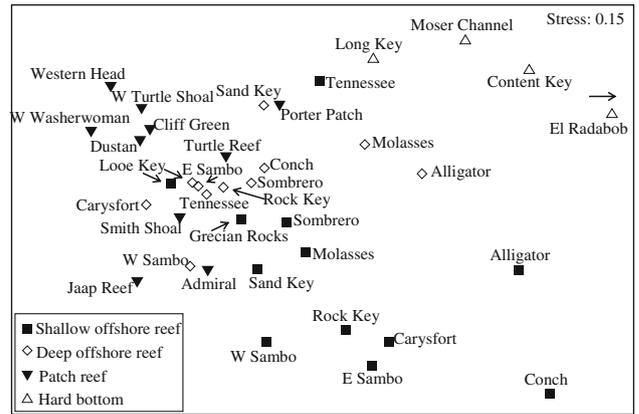


Fig. 3 Ordination by non-metric multidimensional scaling (MDS) of Bray-Curtis similarities between time-averaged fourth-root transformed percentage cover data for corals from each site. Symbols denote the grouping of sites according to their Stratum

Looe Key and Western Sambo were similar in magnitude and direction but less than changes at Sand Key, Rock Key, and Eastern Sambo. Sand Key showed a marked change between 1998 and 1999, which may have been related to the passage of Hurricane Georges or a bleaching event, whereas at Rock Key these events did not induce marked changes. Something happened between 2002 and 2003 that changed assemblages at Rock Key substantially. Changes through time at Eastern Sambo were generally larger than changes at Looe Key and Western Sambo, but there was no evidence of a major shift in community structure in any particular year. Among deep offshore reefs in the same area (Fig. 4b) Eastern Sambo, Looe Key, Rock Key and Western Sambo showed variations through time which were similar in magnitude, though essentially random in direction, while changes at Sand Key tended to be greater. Large changes in community structure at Sand Key occurred between 1996 and 1997, between 1998 and 1999, and between 1999 and 2000 as the community returned to a state similar to that observed in most other years. Among patch reefs in the Lower Keys, small, essentially random, temporal variation was seen at the Western Head, Cliff Green, and West Washer Woman sites (Fig. 4c). In contrast, at Smith Shoal and Jaap Reef relatively large changes were seen in some years, especially between 1999 and 2000 and between 2001 and 2002 at Smith Shoal, and between 1996 and 1997 and between 1998 and 1999 at Jaap Reef. Interestingly, although changes varied among years, assemblages on both these reefs showed diverging linear trends such that differences between the two reefs at the start of sampling, in 1996, were very much less than differences between them in 2003.

Different corals have differing sensitivities as a result of biological properties and habitat preferences. Analysis using SIMPER confirmed that changes in percentage cover

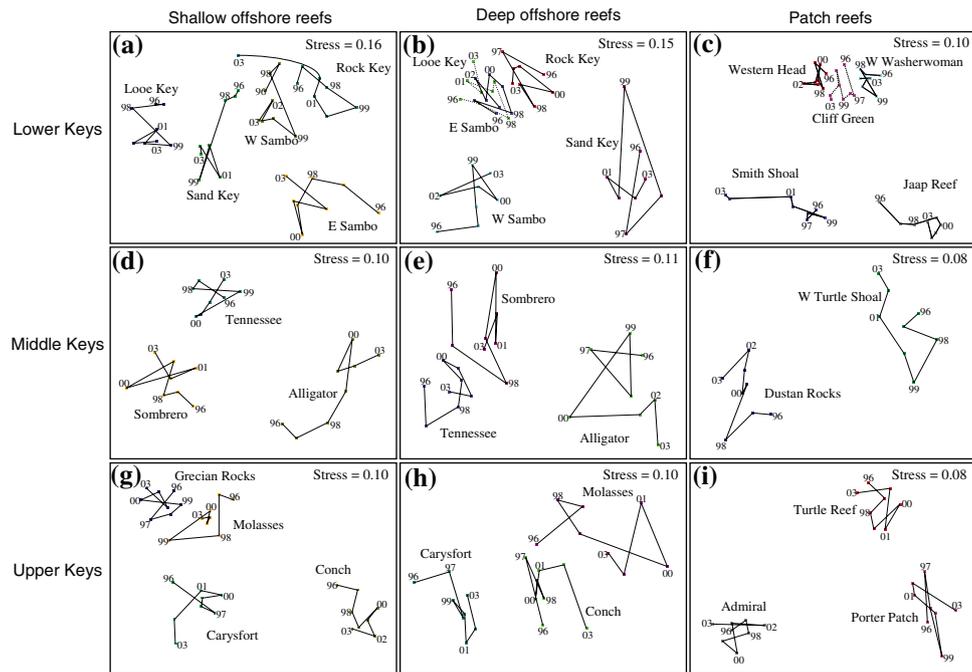


Fig. 4 Ordination by non-metric multidimensional scaling (MDS) of Bray-Curtis similarities between fourth-root transformed percentage cover data for corals from each site within (a) shallow offshore reefs in the Lower Keys, (b) deep offshore reefs in the Lower Keys, (c) patch reefs in the Lower Keys, (d) shallow offshore reefs in the Middle Keys, (e) deep offshore reefs in the Middle Keys, (f) patch reefs in the Middle Keys, (g) shallow offshore reefs in the Upper Keys, (h) deep offshore reefs in the Upper Keys and (i) patch reefs in the Upper Keys. Sites are grouped according to their location along the reef tract (Lower, Middle and Upper Keys). Data from each sampling occasion are the total percent cover across all samples at each site. Lines join consecutive samples from each site to aid in interpreting changes through time (time-trajectories)

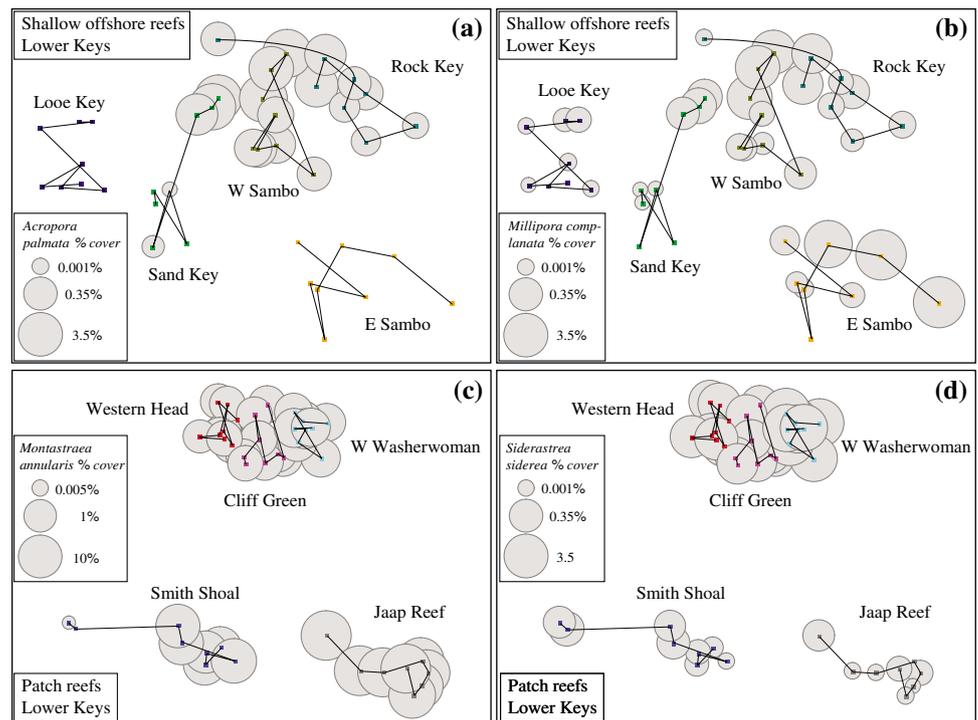
Keys, (h) deep offshore reefs in the Upper Keys and (i) patch reefs in the Upper Keys. Sites are grouped according to their location along the reef tract (Lower, Middle and Upper Keys). Data from each sampling occasion are the total percent cover across all samples at each site. Lines join consecutive samples from each site to aid in interpreting changes through time (time-trajectories)

of 16 species (10 decreasing and 6 increasing) contributed 90% of the dissimilarity between samples from before and after 1998 at Sand Key (Fig. 4a), and 12 species (7 decreasing and 5 increasing) contributed 90% of the dissimilarity between samples from before and after 2002 at Smith Shoal (Fig. 4c). In Fig. 5, a subset of the time trajectories in Fig. 4 (shallow offshore and patch reefs in the Lower Keys) were overlain with symbols representing the total cover of selected species of coral. The most marked change in assemblage structure among these samples was the shift at Sand Key from being similar to assemblages at Western Sambo and Rock Key prior to 1998 to being intermediate in structure between Looe Key and East Sambo in and after 1999. SIMPER analysis showed that only two species contributed almost 50% of the Bray-Curtis dissimilarity between samples from Sand Key before and after 1998, namely *Acropora palmata* and *Millepora complanata*. *A. palmata* is a species that, owing to its growth habit, is sensitive to wave action and tends to inhabit shallow water, making it more vulnerable to hurricane breakage. Among shallow offshore reefs in the Lower Keys (Fig. 5a) *A. palmata* made up a considerable proportion of coral cover at Western Sambo, Rock Key, and Sand Key but not at Looe Key or Eastern Sambo. Between 1998 and 1999 (presumably as a result of

Hurricane Georges and/or a bleaching event) it decreased greatly in coverage at Sand Key, continued to decline in 2000 (perhaps in response to Hurricane Irene), and disappeared entirely by 2001. Although not so obvious, *A. palmata* also declined at the two other sites where it occurred (Rock Key and Western Sambo) between 1998 and 1999 but never disappeared.

M. complanata is another species known to be sensitive to physical disturbance, particularly to heat stress, which leads to bleaching (Jaap 1979). It too disappeared from Sand Key between 1998 and 1999 (Fig. 5b) and only returned, with reduced coverage, in 2000. *M. complanata* tended to be more abundant at Rock Key and Western Sambo than it was at the other three sites and was relatively sparse at Looe Key throughout the sampling period. Against a background of differing average coverage at each site, this species declined on all shallow offshore reefs in the Lower Keys, although at different times and places. Highest percentage cover was found in early years of sampling at all 5 Lower Keys sites, and the greatest declines happened between 1998 and 1999 (as a consequence of bleaching episodes). Highest cover by this species among all 5 sites was observed at East Sambo in 1996 and 1997. Following a minor decline in 1998, the population crashed prior to the 1999 sampling and

Fig. 5 Non-metric multidimensional scaling (MDS) plots, as Fig. 4(a) and (c), overlain with circles scaled in size with the total cover in samples of selected species of stony coral: shallow offshore reefs in the Lower Keys with (a) *Acropora palmata* and (b) *Millepora complanata*; patch reefs in the Lower Keys with (c) *Montastraea annularis* and (d) *Siderastrea siderea*



disappeared entirely in 2000 before recovering to relatively low values from 2001 through 2003. At Western Sambo there was a clear decline in *M. complanata* cover from 1998 through 2001 when cover began to increase somewhat. In contrast, at Rock Key cover began to decline in 1998, showed evidence of recovery between 2001 and 2002, but declined markedly in 2003.

Other species may be sensitive to other stressors. *Montastraea annularis* is a massive coral, less vulnerable to physical damage than *A. palmata* or *M. complanata*. It is generally widespread and abundant on patch reefs in the Lower Keys (Fig. 5c), with higher cover values on Jaap Reef and Smith Shoal than at the other 3 sites. However, it is immediately apparent that the species suffered a major decline between 2001 and 2002 at Smith Shoal. This reef was impacted by the so-called “Black Water Event,” and there may be a causal link between the decline and the black water during this time. A very different pattern of occurrence is shown by *Siderastrea siderea* (Fig. 5d), another coral with a massive growth form. This species was also widespread and accounted for a reasonable amount of cover among patch reefs in the Lower Keys throughout the sampling period, especially on the Western Head, Cliff Green, and West Washerwoman reefs. Cover by this species at Smith Shoal and Jaap Reef was consistently lower than at the other sites. At Jaap Reef, cover declined after 1996, and the species was not observed in 1999, although it subsequently recovered to low values in later years. In contrast, at Smith Shoal the species occurred in low amounts in 1996 and, with the exception of a mild decline

in 1999, has tended to show a steady increase in cover at the site all through the sampling period. Thus differences in cover of this species explain, in part, the contrasting time trajectories at these sites mentioned earlier.

Discussion

Large-scale, repeated, coral reef monitoring programmes are a relatively recent development. As described in the introduction, the FKMS Water Quality Protection Plan monitoring program has operated since 1996. Comparable coral reef monitoring programmes elsewhere in the world include CRAMP, the Hawaii Coral Reef Assessment and Monitoring Program, which was established in 1998 (Jokiel et al. 2004) and the Great Barrier Reef Long Term Monitoring Program (LTMP) which has been operating since 1992 (Ninio et al. 2000). Both use video transects to evaluate changes in coral cover, and for the CRAMP a cost-benefit analysis of different methods (Brown et al. 2004) indicated that, despite a high initial outlay for equipment, digital video yielded the most data of sufficient quality per survey, and that the cost-effectiveness of digital video compared to other methods increased as the number of surveys increased. We accept that there are other ways to assess community structure of corals and the effects of different anthropogenic and natural factors on coral communities. One argument could be that to truly assess community structure one should rely on measurements of colonies measured in situ, and detailed recording of

symptoms of disease (Kramer 2003). In our experience it is often difficult to determine where one colony ends and another begins, for many species, especially when observations are being recorded by divers with varying levels of expertise in varying conditions of water movement and visibility. Using video the diver has only to concentrate on keeping the camera a set distance from the substrate (assisted by lasers), and to take a set time to cover the distance between markers on the seabed, a much easier task which can be achieved consistently. An added advantage is that images are then available for reanalysis, reinterpretation, or for other purposes such as outreach. The causes of routine mortality in corals are poorly understood. Small colonies may be smothered, abraded, eaten or bulldozed, shaded or smothered, and often there is no trace left of a dead coral within a few months of it dying (Hughes and Connell 1999). Generally, individual observations will underestimate underlying levels of damage and turnover. Large corals may be chronically injured, having bare skeleton exposed which may become colonised by fouling organisms or borers. Usually several mechanisms may cause mortality or injury over a short period of time. Periodic censuses months or years apart can only provide a snapshot of these complex sequences of events (Hughes and Connell 1999), and cannot be relied upon as indicating reasons for changes between 1 year and the next.

Although it is by now well known that coral reefs are highly variable, being subject to frequent biological and physical disturbances, the temporal and spatial scales of the disturbances are often large and difficult to study (Hughes and Connell 1999). The scientific literature contains a few long-term studies of coral communities (Brown et al. 2002) and most studies which describe temporal trends in coral assemblage structure have had limited spatial resolution (Ninio et al. 2000) and are limited to decadal time-scales. Examples of such studies include those of Brown et al. (2002), examining changes in intertidal assemblages on Phuket Island, studies in Jamaica and sites on Heron Island on the Great Barrier Reef (Connell 1997; Hughes and Connell 1999), and studies of reefs in the US Virgin Islands (Edmunds 2002). The general lack of adequate data to resolve spatial and temporal patterns simultaneously makes it difficult to understand the generality of results obtained from such studies, leaving scientists unable to provide information needed by managers, such as the probable timescales of recovery from disturbance (Ninio et al. 2000). In the absence of genuine replicated time-series data, one approach which may provide useful temporal information is to combine data from a number of relatively small-scale studies. Gardner et al. (2003) used a meta-analytical approach to reveal the scale of coral losses in the Caribbean basin, using data with a geographic coverage from northern South America to Bermuda. Average cover

by hard corals on reefs in the region declined from 50% to 10% within 30 years. The greatest rate of loss was in the 1980s, but losses are continuing to this day. These findings were confirmed by another meta-analytical study (Côté et al. 2005), which also looked in detail at potential sources of bias in meta-analytical methods and, importantly, was able to compare estimates with those derived from a relatively standardised region-wide monitoring programme (the Caribbean Coastal Marine Productivity Program, CARICOMP: UNESCO 1998). This comparison demonstrating that estimated rates of change were similar. Although they concluded that combined analysis of relatively small-scale surveys is a useful method of generating rates of environmental change, they stated that estimates of change in any habitat should ideally be derived from surveys carried out repeatedly in exactly the same locations to control for small-scale environmental heterogeneity (Côté et al. 2005). Another region-wide monitoring programme which is effectively an accumulation of smaller-scale studies, and that includes coral cover among the variables measured, is the Atlantic and Gulf Rapid Reef Assessment (AGRRA) program (Kramer 2003), which showed that significant bleaching and disease-induced mortality associated with the 1998 ENSO (El Niño-Southern Oscillation) event were most apparent in the western Caribbean and Bahamas subregions. This analysis did not include data from Florida, but it seems likely that the event impacted the Florida Keys in a similar way, namely impacting most heavily on the *M. annularis* complex.

Figure 2 shows that following events in 1997–1998 (bleaching events and Hurricane Georges) there was a significant decrease in the number of species and coral cover on both shallow and deep offshore reefs. On patch reefs the apparent decline in species numbers between 1997 and 1999 was followed by a significant recovery by 2002. Meanwhile, deep offshore reefs still had reduced numbers of species 4 years later in 2003, when numbers among shallow offshore reefs were still lower than in 1997. For coral cover, there was no sign of recovery post 1999 in either the deep or shallow offshore reefs. A meta-analytical study (Gardner et al. 2005) focused on the effects of hurricanes on coral cover, and concluded that hurricanes contributed to declines in coral cover on many Caribbean reefs in the 1980s, but that other stressors are now relatively more important in driving overall declines in coral cover in the region. Bythell et al. (2000) found that well documented and severe hurricane impacts caused changes in community structure on reefs on St Croix, in the US Virgin Islands, that were small in scale compared to differences in assemblage structure between reefs within a few hundreds of meters of each other. The worldwide mass bleaching and mortality events of 1997–1998 may not be accounted by localised stressors or natural variability

alone, but the effects of these factors was probably accentuated by an underlying global cause, namely anthropogenic global warming (Reaser et al. 2000). The geographic extent, increasing frequency and regional severity of such mass bleaching events are a consequence of decades of rising sea temperatures and associated strong regional climate events (Hoegh-Guldberg 1999; Reaser et al. 2000). The impacts of climate change may depend critically on the extent to which a reef is already degraded (Hughes and Connell 1999; Hughes et al. 2003), suggesting that the lack of recovery seen among offshore reefs implies that they are already suffering from some underlying stress.

Accepting that coral communities in the western Atlantic have changed dramatically over the recent decades, the magnitude and causes of change remain controversial. Although the effects of individual events may be related to changes on particular reefs, such as the effects of the “black water” event on Smith Shoal and Content Keys (Hu et al. 2003), small-scale patterns observed on individual reefs may be erroneously extrapolated to larger scales (Hughes and Connell 1999; Murdoch and Aronson 1999). Understanding how reef assemblages vary spatially is an essential prerequisite to devising sampling strategies to track the dynamics of coral reefs through time. Murdoch and Aronson (1999) surveyed a number of reefs along the Florida Keys on a single occasion, concluding that variability within sites was low but that variation between reefs was significant, and that estimates from an individual reef could not be taken as characteristic of variation on other nearby reefs, or of reefs within a larger geographical area. This study supports their findings for a larger number of sites and, crucially, by considering changes through time, demonstrates that the temporal variability at each site differs from that at all the rest. Figure 4 shows changes through time in groups of reefs that are selected to be similar in their combination of reef type (shallow offshore, deep offshore, patch) and reef location (Lower, Middle, Upper Keys), yet each site is still clearly unique. Although some sites were undoubtedly impacted by particular events during the sampling period, the changes in composition resulting from these were small in comparison to differences in composition between different reefs. The problems such variability present for detecting the effects of management actions, such as the establishment of no-fishing zones, were discussed by Miller et al. (2002).

There is little evidence in the multivariate analyses of any major region-wide changes affecting the composition of coral communities, or of any events that have impacted all of the sampling sites in any single year. Instead, different sites exhibit differing patterns of temporal variation. The non-parametric multivariate methods employed in this analysis have previously been applied with success to coral

data (Warwick et al. 1990; Clarke et al. 1993; Brown et al. 2002; Kramer 2003; Bythell et al. 2000; Lirman and Fong 2007) where they have proved to be a sensitive and sensible approach to evaluating spatio-temporal changes in community structure. In a statistical analysis of Indonesian coral community responses to an El Niño event, Warwick et al. (1990) demonstrated that although univariate and multivariate approaches clearly detected and illustrated major changes associated with the event itself, the multivariate techniques were more sensitive in monitoring recovery in later years. The analyses presented here reveal, clearly, how entire coral communities in Florida vary with geographical position and habitat type in terms of their composition. They show the relative scales of spatial and temporal variability in community structure within and among sites, and the relative impacts of certain events on the composition of assemblages in specific sites. All of this is important information for the purposes of detecting and assessing the relative magnitude of variation in community structure. What is lacking, in the application of multivariate methods such as these in a monitoring framework, are clear guidelines for determining which changes represent a decrease in environmental quality and which simply represent natural variability. To decide, it is generally necessary to use appropriate multivariate methods to determine where changes have occurred, but then to return to the original data in order to determine what the precise nature of those changes was. This study demonstrates how this may be done. Multivariate analyses were used to determine the relative directions and magnitudes of community change among groups of reefs in the Lower Keys, and the contribution of individual species to those changes, which were then interpreted using information about the relative sensitivities of different species to various stressors, such as changes in cover of *A. palmata* and *M. complanata* at Sand Key following the bleaching events and hurricane in 1998, and declines in *M. annularis* at Smith Shoal following the harmful algal bloom in 2002. Two points to note here are: (1) that this approach is not the same as basing analyses on the cover of a single species, as a multivariate approach will be a more powerful and sensitive approach for the detection of change, and (2) that knowledge about the species involved and their biology are required. The latter is often surprisingly scarce. It is also easy to assume cause and effect erroneously. *A. palmata* is known to be susceptible to storm damage (Lirman and Fong 1997), and this is how the changes observed here are interpreted, but other factors may reduce populations.

The Florida Keys are susceptible to multiple natural disturbances such as hurricanes, winter cold fronts, bleaching episodes, and algal blooms. These natural disturbances occur frequently and at a magnitude that affects coral reef development (Connell 1978; Connell et al. 1997)

and tend, as here, to be the focus of interpretations of observed changes. With global warming, storms are expected to increase in frequency and intensity, bleaching events are likely to increase, and rainfall is expected to increase (Angeles et al. 2007). Against this variability the effects of other large-scale changes may be relatively difficult to detect and disentangle, even with a large and well designed monitoring programme such as the FKNMS programme, and especially if the effects on coral communities are diffuse or indirect. Such changes are known to have occurred, and are predicted in the future, although there appears to be little agreement about the relative importance and scale of impact of different stressors in the Florida Keys.

Increased rainfall leads to more runoff, potentially moving nutrients, toxic substances, microbes and metals from terrestrial and aquatic systems into the marine system. Increases in nutrients can destroy reefs by allowing benthic algae to grow over the reefs and smother the corals (Smith et al. 1981), decrease water transparency by promoting plankton blooms, increase competition from other benthic plants and animals (Tomascik and Sander 1985; Hallock and Schlager 1986; Cuet and Naim 1992) and the combination of runoff and microbes may foster the development of disease (Patterson et al. 2002). Porter et al. (1999) stated that changes in land use and water management practices in southern Florida altered the quality and quantity of freshwater inflows to Florida Bay, so that by the 1980s there was an extensive hypersaline phase in the bay, but based on isotopic analysis of a coral core from the bay, Sanders et al. (1996) concluded that there was no increase in salinity in Florida Bay over a 160 year period, and that changes in water quality in Florida Bay, towards eutrophication, were initiated by restrictions in water exchange caused by the construction of the railway from Miami to Key West, completed in 1912. A study of nitrogen isotopes in macroalgae (Lapointe et al. 2004) suggested that regional-scale agricultural runoff from the Everglades, and sewage discharges from the Florida Keys, are both significant nitrogen sources supporting eutrophication and algal blooms in coral reef communities in the Lower Florida Keys, but Lirman and Fong (2007) showed that proximity to potential sources of stressors, measured as distance to the shore or tidal passes, was a poor predictor of coral reef condition in the Florida Keys. Despite cross-shelf gradients in nutrients, organic carbon, turbidity and light attenuation, patch reefs closer to shore were in better condition with higher coral cover than those further offshore (Lirman and Fong 2007). Gibson et al. (2008) produced system-wide nutrient budgets which showed that the amount of nitrogen actually introduced to the reef tract from Florida Bay is small relative to offshore inputs, and Szmant (2002) concluded that although over-enrichment may be a cause of localised

declines in coral reef condition, the levels of nutrient enrichment documented at anthropogenically enriched sites cannot affect the physiology of corals in a harmful way, or be a major cause of shifts in the balance between corals and macroalgae. The automatic assumption that a high biomass of algae (or low cover of corals) may be attributed solely to high nutrient loads ignores the numerous other factors which may disturb the balance between corals and algae (Hughes and Connell 1999). Prior to 1983 abundant *D. antillarum* populations controlled macroalgal populations by grazing, but after a disease epidemic in 1983 *Diadema* ceased to be an important herbivore and macroalgae became abundant on western Atlantic reefs, competing with and smothering corals (Tuya et al. 2005). The Porter et al. (1999) study is important, however, as it demonstrates the interactive effects of different stressors on corals are not predictable from knowledge of the effects of stressors operating independently. Although an experimental study demonstrated that increasing nutrient loads could increase the severity of a coral disease (yellow band disease in *Montastraea* spp.) it took a five-fold increase in nutrient concentrations to approximately double the amount of host tissue lost (Bruno et al. 2003).

Data from the 1970s, although limited to a few reefs, shows that coral cover was 30 to 40% on offshore reefs off Key Largo: Carysfort, Grecian Rocks, Key Largo Dry Rocks, Elbow, French, and Molasses (Jaap et al. 1988), much higher than during the present study period 1996–2003 (Table 1). The principal difference between then and 1996–2003 was the superior abundance of *Acropora cervicornis* and *A. palmata*. In 1981, a white disease infected these corals and virtually all populations suffered losses (Porter et al. 2001). Between 1984 and 1991 monitoring at 6 coral reef locations along the Florida Keys showed substantial declines in species richness and coral cover during a period without catastrophic storms and, importantly, no recruitment of any massive frame-building coral species (Porter and Meier 1992). Sources of mortality implicated were disease and bleaching. Although diseases are frequently described as causes of mortality among corals, there is considerable doubt about whether these are true diseases caused by novel pathogens or simply the physical manifestations of opportunistic infections, by normally benign and non-pathogenic bacteria, which take hold in corals weakened by physiological stress (such as elevated temperatures). Thus environmental changes cause physiological stress that subsequently leads to coral mortality or morbidity by many mechanisms, one of which is overwhelming infections by opportunistic pathogens (Lesser et al. 2007), and the increase in such events may be a manifestation of the effects of underlying long-term trends in environmental conditions. Whatever the underlying cause, white diseases continued to contribute to

declines of *Acropora* spp. throughout the Caribbean and western Atlantic (Aronson and Precht 2001; Porter et al. 2001), causing losses so severe (Precht et al. 2004) that both *A. cervicornis* and *A. palmata* were listed as threatened species in May 2006 (Federal Register 2006).

In addition to increases in storms, nutrients and diseases it is also possible that the effects of other anthropogenic changes, such as ocean acidification (Orr et al. 2005), may also become apparent in coming years. There is evidence that growth rates of juvenile corals in the Caribbean have declined. This could be a sublethal effect of increasing temperatures and/or declining aragonite saturation, one consequence of which is the potential slowing of recovery by coral reefs from disturbances (Edmunds 2007).

With so many potential sources of deleterious change for corals in Florida the maintenance of a comprehensive monitoring programme is essential if the relative effects and magnitudes of impacts are to be detected and mitigated. Pandolfi et al. (2003) used a range of data to reconstruct ecological histories of reefs, demonstrating that declines in a range of ecological guilds follow similar trajectories worldwide, but that the timings of declines were related to the regional development of human cultures. Such analyses showed that substantial degradation of coral ecosystems, particularly the removal of large animals with consequent shifts in the trophic structure of communities, took place long before outbreaks of coral disease and bleaching. Extending these methods to include coral reefs in Florida showed that they are among the most degraded in the world (Pandolfi et al. 2005). It appears that Florida coral reefs are at high risk of being irreversibly changed over the next 10 to 20 years (Wilkinson 2004), and this negative outlook can only be mitigated by strong public and political intervention and oversight.

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