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REPORT

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Spatial patterns and ecology of benthic communities on a high-latitude South Florida (Broward County, USA) reef system

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Abstract High-latitude reef communities consisting of typical Caribbean fauna of variable composition and density exist on four parallel ridges at varying depths along the Broward County (Florida, USA) coast. Two of these ridges, at 7–13 and 15–30 m in depth, are drowned early Holocene coral reefs of 5 and 7 ky uncorrected radiocarbon age. In this study, community data were collected on each reef using 50-m, line-intercept transects. Using multivariate non-metric statistics, the data show distinct differences in benthic community structure across several spatial gradients. Diversity indices revealed that while all values were low, species diversity (H′) was consistent throughout the county, and species richness (d) and evenness (J′) increased along a north-south gradient. Scleractinian coral (27 species) cover was low (<6%) in all areas, and *Montastrea cavernosa* dominated as the major hermatypic scleractinian. Notably absent was the major Caribbean reef-builder *Acropora palmata*. A rich alcyonacean fauna was present on all studied reefs, and these were typically the most important faunal group determining community structure. Although during the 2-year period 2000–2002 mean water temperatures never fell below 20 °C, scleractinia were small in size.

Keywords High-latitude reefs · Spatial patterns · Broward County, Florida · Benthic coral reef ecology

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Introduction

High-latitude reefs have been described in a variety of locations throughout the world, including: Australia (Hatcher 1985; Spalding et al. 2001), Bermuda (Laborel 1966; Thomas and Logan 1992), Brazil (Castro and Pires 2001), Japan (Kan et al. 1995; Yamano et al. 2001), and South Africa (Riegl et al. 1995). Reefs are found at high latitudes (above 25°N) in Florida, northward of Miami and the Florida Keys (Duane and Meisburger 1969; Goldberg 1973). The best developed part of this reef system, located offshore Broward County, FL, USA (25°58′N to 26°19′N), has been previously described as consisting of three progressively deeper, shore-parallel terraces (Macintyre and Milliman 1970; Lighty 1977; Macintyre 1988). The terrace furthest from shore (herein termed the outer-reef), is best described in terms of its geology and paleoecology by Lighty et al. (1978) who interpreted it as a drowned early Holocene *Acropora palmata* reef that terminated growth about 7 ky ago. Based on their sea-level curve and later carbon dating, the middle and inner reefs reef are estimated to be about 6–7 and 5–6 ky in age, respectively (Lighty et al. 1978). The modern communities consist of typical Caribbean fauna, however community structure on these reefs is highly variable and does not conform to existing reef classification or zonation schemes (e.g. Goreau 1959; Stoddart 1969; Loya 1972; Done 1982). This variability may be the result of the high-latitude location of the reefs (with corresponding high water temperature range), fresh water inputs from runoff, groundwater seepage, sewage effluent and tidal inlet discharge (Goldberg 1973), and high variability of substratum composition and complexity. Hurricanes and major winter storms associated with cold fronts are common in the area and the reefs occur in an area of Florida with high recurrence intervals of hurricanes and tropical storms (Simpson and Lawrence 1971; Muller and Stone 2001).

Although the ecology and some geomorphology of the northernmost portion of the reef system have been described (Goldberg 1973), no comprehensive study has yet examined in detail the community structure of the benthic habitats along these reefs. The aims of this study were to: (1) determine if different ecological communities exist between neighboring reef structures; (2) describe in terms of species diversity, richness, benthic cover, and within-group similarities, the spatial patterns of the ecological communities in this high-latitude setting; (3) correlate spatial patterns of benthic communities with bathymetry obtained from detailed surveys and produce benthic habitat maps; and (4) identify possible factors responsible for influencing community structure.

Materials and methods

Four areas of the shelf offshore the Broward County coastline were selected at approximately even distances from north to south. Each area (herein termed a 'corridor' and numbered 1 to 4 from north to south) was approximately 2.4 km in cross-shelf width, and 1.3 km in along-shelf length, with an area of about 3.1 km^2 (Fig. 1).

For geomorphological analysis and to better understand the environmental setting, we used shaded relief images created from bathymetry data taken with a laser airborne depth sounder (LADS; 4 m horizontal, 0.03 m vertical resolution). LADS bathymetry surveys use aircraft from which short-wave green light is emitted to penetrate the water surface and reflect from the substrate, while longer-wave red light reflects directly off the surface of the water (Lewis 2001). LADS bathymetry has been used successfully to determine the geomorphology of parts of the Great Barrier Reef (Lewis 2001) and provides bathymetry data to a maximum depth of 70 m (Wellington 2001). All bathymetry illustrated in this report is based on this dataset.

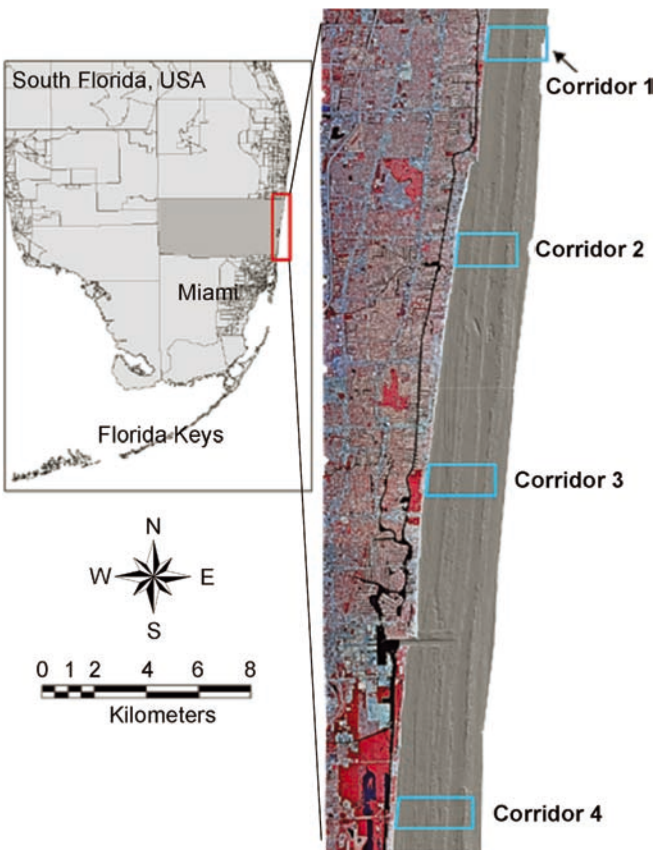


Fig. 1 Composite map of study area, consisting of aerial photographs merged with a sun-shaded Laser Airborne Depth Sounder (LADS) image mosaic, showing the location of the four corridors sampled in this study

Ecological data collection

Two sites were selected on each reef within each corridor, amounting to six sites in corridor 1 (Fig. 2), and eight sites each in corridors 2 through 4. In corridor 3 (Fig. 3), an additional site was added to better document high stony coral cover on the ridge complex. In total, 31 sites were sampled. At each site, six 50-m, point-intercept transects were surveyed by scuba divers, with the exception of eight transects being surveyed at the added site in corridor 3, giving a total of 188 transects for the entire study. Transects were arranged as follows: two adjacent sets of three parallel transects at a 5-m spacing, with a 5-m distance between the adjacent sets. All transects were oriented parallel to the reef edges (Fig. 4).

Along each transect, fauna, flora and bare substratum were recorded at 1-m intervals for six broad categories: scleractinian (stony) corals; alcyonacean (soft) corals; zoanthids, hydroids, and tunicates; macroalgae; sponges; and bare substratum. Within each category, individual reef macrofauna or flora were identified (after Humann 1996) to the lowest taxonomic level possible by field identification (typically to species level for stony corals, sponges, zoanthids, and tunicates) and to genus level for soft corals, hydroids, and macroalgae). If unequivocal field identification was not possible, a descriptive name was applied (i.e. "red algal turf" or "erect yellow sponge").

Statistical analysis of ecological data

Transect data were compiled into a square matrix (species x transects) and fourth-root transformed to counteract the weight of the dominant species without severely diminishing their importance. The transformed species-by-transect matrix was then converted into a triangular transect-by-transect similarity matrix by calculating the Bray-Curtis similarity index between all transect-pairs, based on joint species abundances, and presences and absences. Ecological data were then analyzed for similarity of benthic assemblages using agglomerative hierarchical cluster analysis based on the Bray-Curtis Similarity Index, and a single linkage dendrogram was produced.

Further analysis used non-metric multi-dimensional scaling (MDS, Kruskal and Wish 1978), which constructs a rank similarity-based sample configuration while attempting to comply with all the limitations imposed by the rank similarity matrix (Clarke and Warwick 2001). On the two-dimensional plots generated from MDS analysis, highly similar transects will appear closer together than transects with lower rank similarities, effectively constructing a two-dimensional map of similar transects. If no pattern was evident on the raw MDS plot, transect location information was superimposed to better illustrate if highly similar transects came from the same area.

Several orders of second-level analyses were performed based on the configuration of the MDS plots. If transects taken from the same location (reefs or ridge complexes) were grouped together, a non-metric, one-way, pair-wise analysis of similarity (ANOSIM, Mantel 1967; Clarke and Green 1988) was performed to determine whether significant differences in community composition existed between reefs. If such differences did exist, a non-metric similarity of percentages (SIMPER) analysis (Clarke and Warwick 2001) was applied to determine which species contributed most to the similarity and dissimilarity. Species falling above

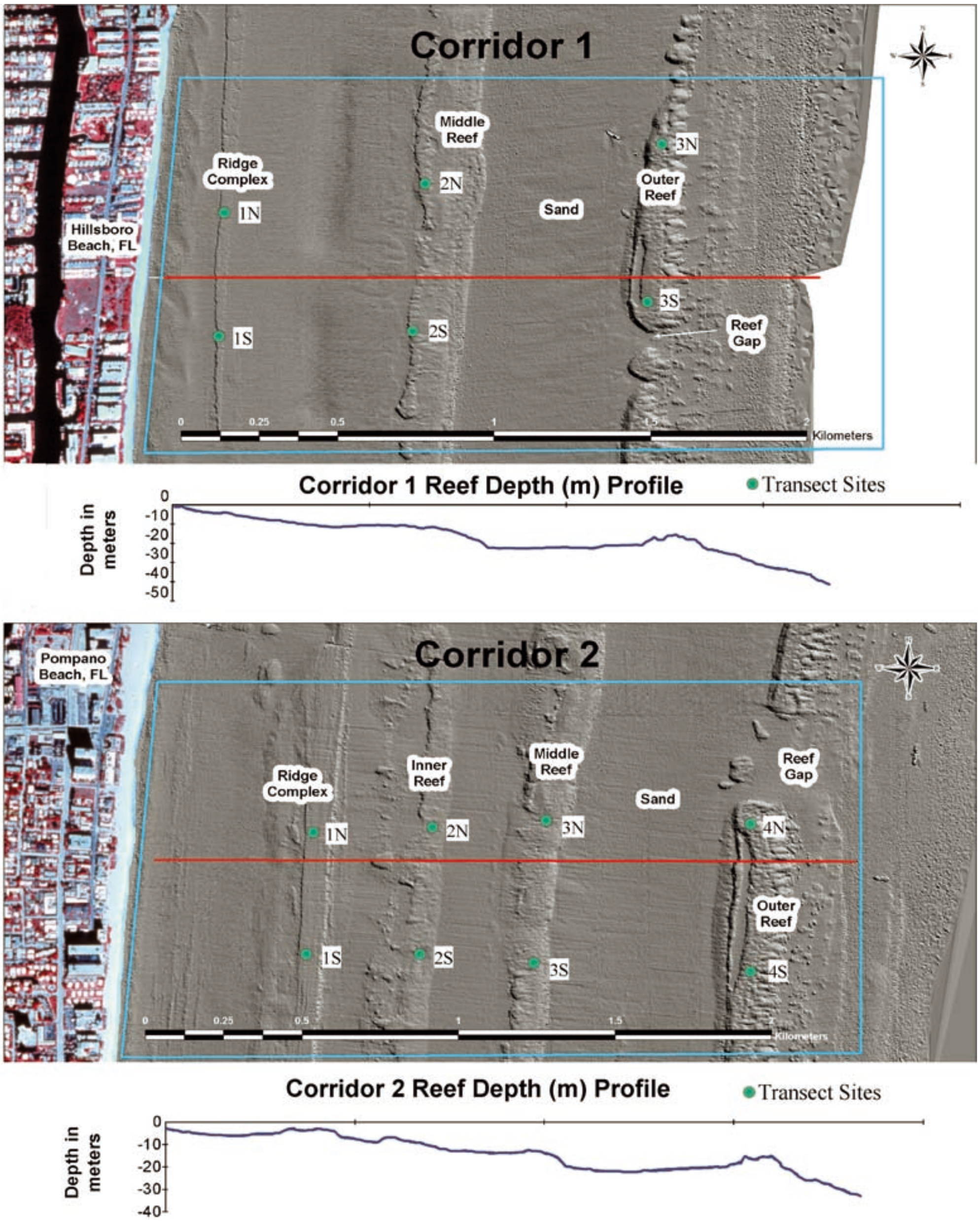


Fig. 2 Sun-shaded LADS bathymetry image showing transect locations and cross-shelf depth profiles in corridors 1 and 2

the 50% similarity threshold were considered to be those most important in determining community structure. Additional calculations determined percent cover and species dominance for each community.

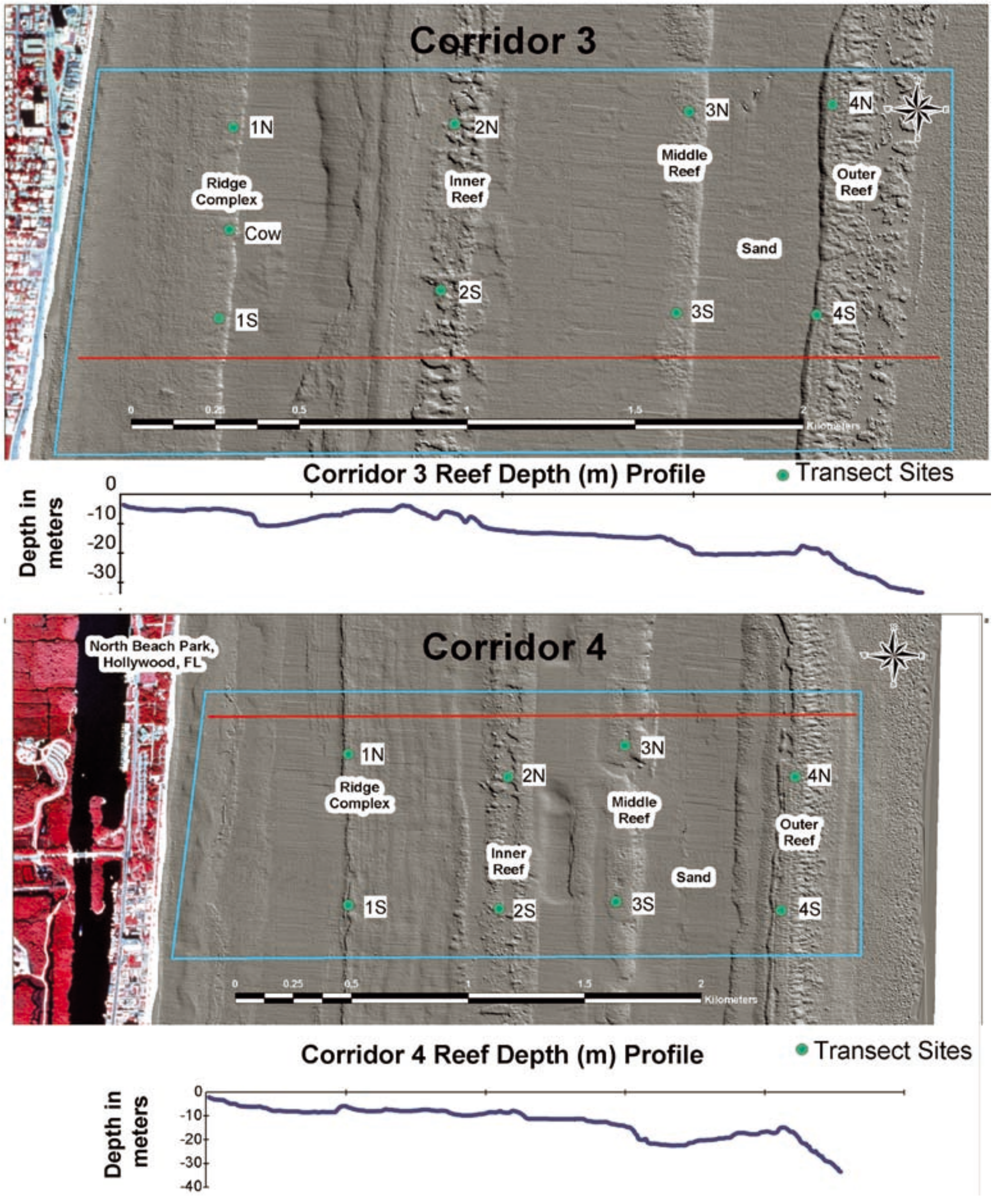
Diversity measures were calculated from the untransformed data for each reef community within each corridor. Indices calculated were: Margalef's species richness index (d), Pielou's evenness coefficient (J′), the Shannon-Wiener diversity coefficient (H′), and Simpson's diversity Index (1- λ) (Clarke and Warwick 2001). In order to overcome sample-size limitations, in particular of the Shannon-Wiener Index and Pielou's evenness measure (Sotaert and Heip 1990), and to reduce sample-size dependent bias, diversity statistics were calculated from the pooled data sets for each reef of each corridor (i.e. all inner-reef pooled, all middle-reef pooled, all outer-reef pooled).

All statistical calculations and graphs were generated using Primer v.5 (Primer-E Ltd. Plymouth, UK).

Results

The structure and distribution of benthic reef communities in this area is complex (Fig. 5). In order to distinguish between the reefs and their associated communities, a descriptive name was given to each feature based on unifying names for continuous features. A distinction is made between the terms reef and ridge complex in this study. Reefs are the three terraces deepest and furthest from shore as described by Lighty (1977). Collectively, these three reefs compose the "*reef* complex." A series of shallow, nearshore ridges lie inshore of the reef complex. They are not always linear

Fig. 3 Sun-shaded LADS bathymetry image showing transect locations and cross-shelf depth profiles in corridors 3 and 4



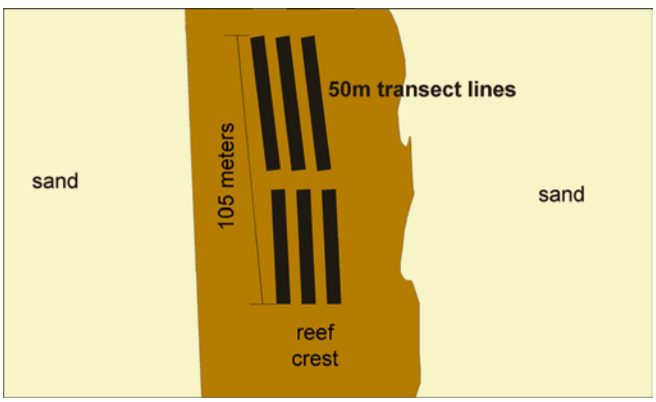


Fig. 4 The spatial arrangement of benthic transects along reef crest axis. Transects were arranged in this manner at every site in the study. Figure not to scale

and their structural relationship to each other and the reef complex is presently unknown. These form the "*ridge* complexes," which are well developed in three distinct areas: north of Hillsboro Inlet, between Hillsboro and Port Everglades Inlets, and south of the Port Everglades Inlet.

Comparisons among all corridors

Cluster analysis and the MDS plot superimposed with transect location (Fig. 6A) suggest that three data clusters exist among all corridors. Ridge complex transects formed one cluster, inner-reef and ridge complex transects formed a second cluster, and a third cluster was composed mainly of middle and outer-reef transects. Within the last

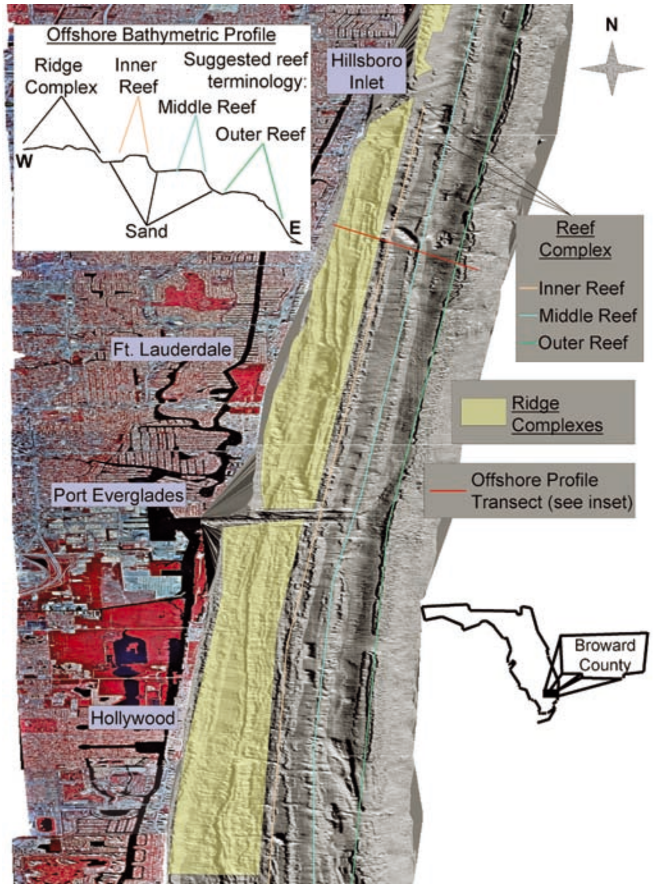


Fig. 5 Overview of the complex reef structure in Broward County, illustrating the relative location of each reef and the terminology defined in this study (also see *inset*; depth profile not to scale). Note: For display purposes, the figure has been stretched horizontally

described cluster, possible subgroups existed with most middle-reef transects falling to the left, and most outer-reef transects falling to the right of the cluster. When corridor location was superimposed onto the MDS plot (Fig. 6B), all ridge complex transects from the first described cluster were formed primarily from the two northernmost corridors, while the group of ridge complex transects from the second cluster all came from the two southernmost corridors. Transects from the last described cluster were equally distributed between all four corridors.

Further MDS analysis of subsets of data from the ridge complexes and each individual reef showed that ridge complex (Fig. 6C) transects from corridors 1, 2, 3, and 4 are distinctly separate from each other. The MDS plot of all inner-reef transects (Fig. 6D) showed that transects from corridors 2, 3, and 4 each formed a single cluster. No apparent clustering pattern, however, was shown on the plot for middle (Fig. 6E) reef transects. The MDS plot of outer-reef transects (Fig. 6F) showed a pattern where transects from corridors 1, 2, and 3, formed one cluster and transects from corridor 4 formed a second cluster.

Diversity measures (Table 1) showed species richness to increase from north to south, with corridor 1 having the lowest value (d = 8.47) and corridor 4 having the highest value (d = 11.12). Diversity (H′) and evenness (J′) were fairly constant among all four corridors, and showed no apparent north-south trend.

Corridor 1

Cluster (Fig. 7A) and MDS (Fig. 7B) analysis showed two distinct groups of transects, with ridge complex transects forming one cluster and middle and outer reefs transects forming a second cluster. The ANOSIM of corridor 1 transects (Table 2) showed no significant difference (R = 0.224, p = 0.8%) between the middle and outer-reef communities, but did show significant differences between the inner and middle-reef communities (R = 0.634, p = 0.1%) and between the inner and outer-reef communities (R = 0.761, p = 0.1%).

A total of 57 species of benthic flora and fauna were recorded in corridor 1. Alcyonaceans were the dominant group on the ridge complex and middle reef, comprising 5% and 21% of the total cover, respectively. On the outer reef, live cover was dominated by alcyonaceans and macroalgae, which accounted for 32% and 20% of total cover, respectively (Fig. 8). Diversity measures in corridor 1 (Table 1) showed that the ridge complex (sites 1 N and 1S) had the lowest species richness (d) and low species diversity (H′ and 1- λ). The middle reef (sites 2N and 2S) had the highest species richness and diversity, and the outer reef (sites 3N and 3S) had high richness but low diversity.

SIMPER analysis showed that on the ridge complex, the sponges *Anthosigmella varians* and *Speciospongia vesparium* made the highest contribution to within-group similarities (19.4% and 19.3%, respectively), along with the scleractinian *Solenastrea bornouni* (9.3%) and the alcyonacean *Pseudoplexaura spp*. (8.9%). On the middle reef, several alcyonaceans were responsible for the within-group similarity, of which *Pseudopterogorgia* sp. (13.3%), *Briareum asbestinum* (10.7%), *Eunicea* sp. (10.5%), and *Pseudopterogorgia americana* (8.0%) were most dominant. A common macroalga, *Dictyota* sp. (7.1%), and the sponge *Holopsamma helwigi* (6.7%) also contributed to the within-group similarity on the middle reef. The outer-reef community had three genera that were primarily responsible for within-group similarity, the green alga *Dicytota* sp. (22.0%), and the alcyonaceans *Pseudoplexaura* sp. (15.2%) and *Eunicea* sp. (15.0%, Table 3).

Corridor 2

Cluster and MDS (Fig. 9) analysis revealed two distinctly clustered groups of benthic transect data. Transects from the ridge complex formed one cluster, while transects from the inner, middle, and outer reefs grouped together

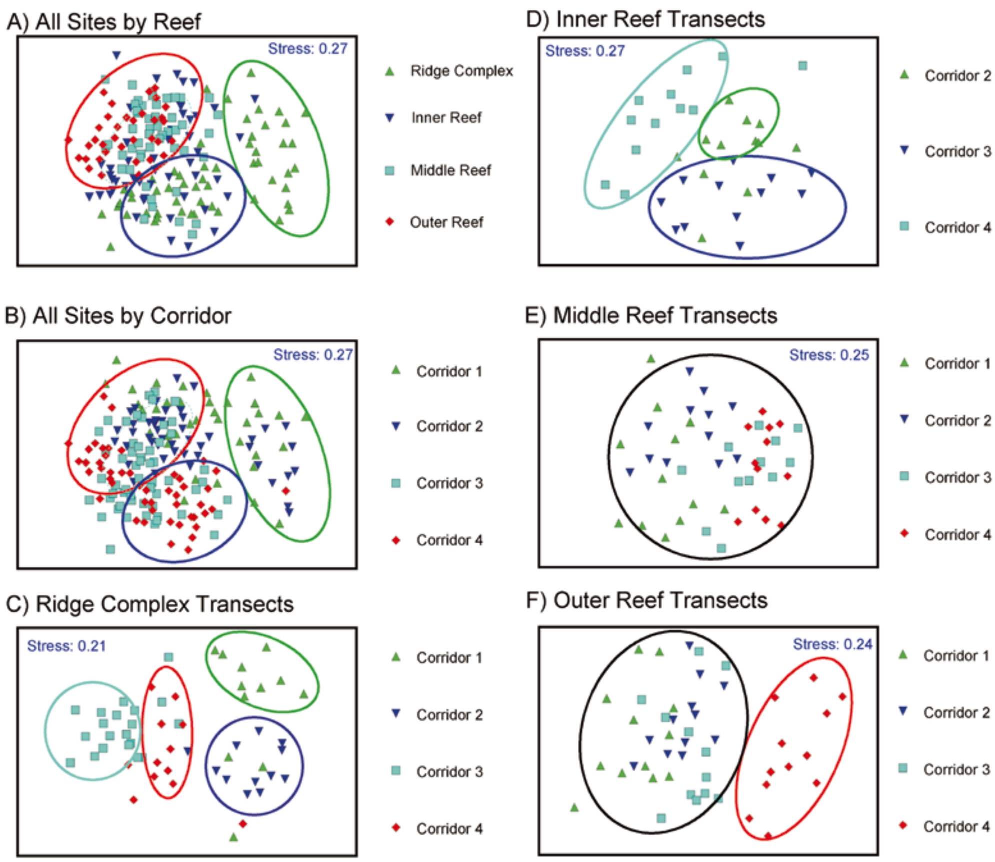


Fig. 6 Two-dimensional MDS plot for all Broward County benthic transect data. MDS plots show: **A** Reef location, **B** corridor location; and all transect coded with corridor location information taken from the: **C** ridge complex, **D** inner reef, **E** middle reef, and **F** outer reef. The *stress value* indicates the ease with which all data points were fitted into two-dimensions. *Ovals* are intended to guide the reader, and were drawn as interpreted by the authors

Table 1 Diversity indices listed for individual sites by corridors, all sites by corridor, and all transects across all corridors. *S* Total number of species (richness); *N* total number of individuals; *d* Margalef's richness index; *J″* Piclou's evenness index; *H″* Shannon-Wiener diversity index; *1-λ* Simpson's diversity index

	Site	S	N	d	J′	H′	1-λ	Site	S	N	d	J′	H′	1-λ
Corridor 1	Site 1N	19	50	4.35	0.99	2.59	0.92	Site 3S	35	203	6.40	0.74	2.63	0.89
Corridor 2		12	38	3.02	0.89	2.23	0.99		24	192	4.37	0.68	2.16	0.79
Corridor 3		22	107	4.49	0.76	2.33	0.85		34	159	6.51	0.69	2.44	0.79
Corridor 4		27	115	5.48	0.86	2.83	0.93		31	144	6.04	0.79	2.71	0.89
Corridor 1	Site 1S	21	49	5.14	0.94	2.85	0.95	Site 4N	N/A	N/A	N/A	N/A	N/A	N/A
Corridor 2		15	73	3.26	0.92	2.49	0.91		25	164	4.71	0.74	2.39	0.86
Corridor 3		22	140	4.25	0.74	2.29	0.85		26	189	4.77	0.65	2.12	0.75
Corridor 4		26	98	5.45	0.85	2.77	0.92		27	120	5.43	0.81	2.67	0.89
Corridor 1	Site 2N	34	131	6.77	0.99	3.16	0.95	Site 4S	N/A	N/A	N/A	N/A	N/A	N/A
Corridor 2		33	124	6.64	0.91	3.18	0.95		34	181	6.35	0.77	2.71	0.89
Corridor 3		27	145	5.22	0.74	2.44	0.86		34	197	6.25	0.65	2.31	0.77
Corridor 4		32	130	6.37	0.65	2.26	0.76		40	130	8.01	0.82	3.01	0.92
Corridor 1	Site 2S	36	133	7.16	0.87	3.12	0.94	Added site	N/A	N/A	N/A	N/A	N/A	N/A
Corridor 2		26	89	5.57	0.89	2.92	0.94		N/A	N/A	N/A	N/A	N/A	N/A
Corridor 3		31	195	5.69	0.59	2.04	0.71		30	168	5.66	0.77	2.61	0.89
Corridor 4		20	162	3.73	0.59	1.76	0.67		N/A	N/A	N/A	N/A	N/A	N/A
Corridor 1	Site 3N	27	190	5.01	0.69	2.27	0.81	All sites	57	746	8.47	0.79	3.17	0.92
Corridor 2		33	136	6.51	0.91	2.84	0.91		69	997	9.85	0.73	3.09	0.91
Corridor 3		34	180	6.35	0.59	2.08	0.68		74	1480	10.00	0.64	2.74	0.84
Corridor 4		36	213	6.53	0.67	2.40	0.79		79	1112	11.12	0.73	3.19	0.92
All corridors								All sites	96	4,335	11.34	0.69	3.17	0.90

to form a larger second cluster. The ANOSIM (Table 2) showed significant differences between the ridge complex community, and the inner (R = 0.877, p = 0.1%), middle (R = 0.902, p = 0.1%), and outer (R = 0.906, p = 0.1%) reef communities. A significant difference (R = 0.484, p = 0.1%) was also observed between the inner- and outer-reef communities. No significant differences were observed between the inner- and middle-reef communities (R = 0.196, 0.9%) or between the middle- and outer-reef communities (R = 0.197, p = 0.3%).

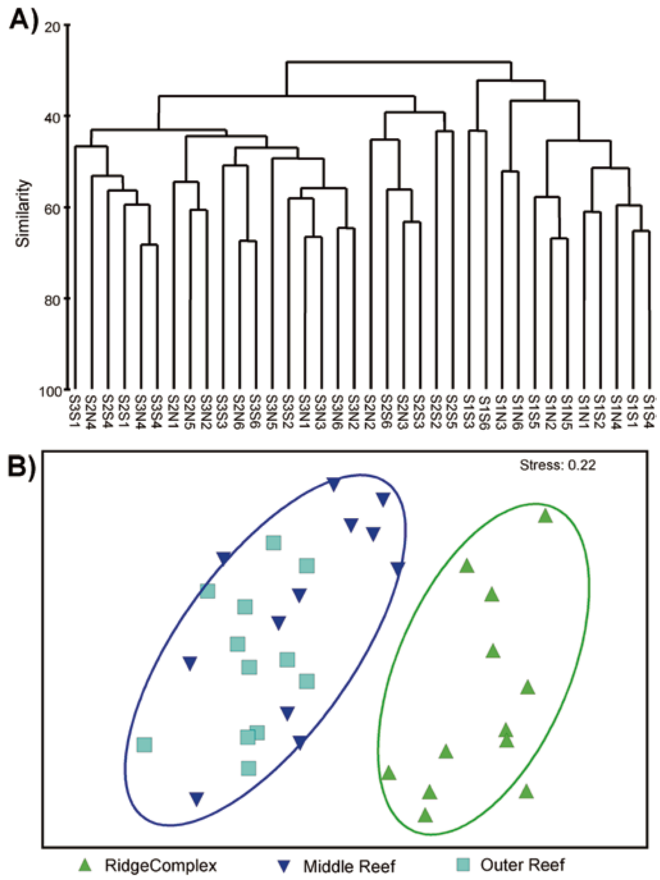


Fig. 7 Dendrogram based on the Bray-Curtis Similarity Index (**A**) and MDS plot combined with reef location (**B**) of corridor 1. Sites are coded by site number, location and transect number, example: Site 3 North Transect 6 = S3N6. *Ovals* are intended to guide the reader, and were drawn as interpreted by the authors

There were 69 species of benthic flora and fauna recorded, with alcyonaceans being dominant on the ridge complex and inner and outer reefs, comprising 11%, 13%, and 29%, respectively, of the total benthic cover. The inner reef was also dominated by sponges (10%), while macroalgae (16%) were also dominant on the outer reef. The middle reef was dominated by macroalgae (24%) and alcyonaceans (20%, Fig. 8). Diversity measures (Table 1) indicated the ridge complex (sites 1N and 1S) to have the lowest species richness (d), and diversity (H′ and 1-λ), while the inner reef (sites 2N and 2S) had the highest species richness and diversity. Middle and outer reef (sites 3N and 3S; 4N and 4S, respectively) had high species richness and low diversity.

SIMPER analysis (Table 4) showed the sponge *Aplysina fistularis* (28.29%), along with the alcyonaceans *P. americana* (16.49%) and *Gorgonia ventalina* (13.30%), to be most responsible for within-group similarity on the ridge complex. On the inner reef, the alcyonaceans *Pseudoplexaura* sp. (12.06%), *B. asbestinum* (10.14%), *Erythropodium caribaeorum* (9.41%), *Pseudopterogogia* sp. (8.76%), and the macroalgae *Halimeda* sp. (10.20%) were most responsible for within-group similarity. Similarity on the middle reef was mostly due to the presence of *Dictyota* sp. (27.24%), *B. asbestinum* (21.67%), and *Eunicea* sp. (12.53%). On the outer reef, *Dictyota* sp. (21.20%), *Pseudopterogorgia* sp. (16.55%), and the sponge *Xestospongia muta* (12.38%) were most responsible for the within-group similarity.

Corridor 3

Cluster analysis and MDS (Fig. 10A) revealed little evidence for sets of clustered data. When transect

Table 2 Results of one-way analysis of similarities (ANOSIM) for all reef communities

Groups	Corridor number	R statistic	Significance level (%)	Significant difference	Possible permutations	Actual permutations	Number ≥ observed
Ridge complex, inner reef	Corridor 1	N/A	N/A	N/A	N/A	N/A	N/A
	Corridor 2	0.877	01	Yes	1352078	999	0
	Corridor 3	0.443	0.1	Yes	225792940	999	0
	Corridor 4	0.310	0.2	No	1352078	999	1
Ridge complex, middle reef	Corridor 1	0.634	0.1	Yes	1352078	999	0
	Corridor 2	0.902	0.1	Yes	1352078	999	0
	Corridor 3	0.763	0.1	Yes	225792840	999	0
	Corridor 4	0.749	0.1	Yes	1352078	999	0
Ridge complex, outer reef	Corridor 1	0.761	0.1	Yes	1352078	999	0
	Corridor 2	0.906	0.1	Yes	1352078	999	0
	Corridor 3	0.645	0.1	Yes	225792840	999	7
	Corridor 4	0.576	0.1	Yes	T352078	999	0
Inner reef, middle reef	Corridor 1	N/A	N/A	N/A	N/A	N/A	N/A
	Corridor 2	0.196	0.9	No	1352078	999	8
	Corridor 3	0.391	0.1	Yes[a]	1352078	999	0
	Corridor 4	0.379	0.1	Yes[a]	1352078	999	0
Inner reef, outer reef	Corridor 1	N/A	N/A	N/A	N/A	N/A	N/A
	Corridoi 2	0.484	0.1	Yes	1352079	999	0
	Corridor 3	0.330	0.1	Yes[a]	1352078	999	0
	Corridor 4	0.514	0.1	Yes	1352078	999	0
Middle reef, outer reef	Corridor 1	0.224	0.8	No	1352078	999	7
	Corridor 2	0.197	0.3	No	1352078	999	2
	Corridor 3	0.130	2.5	No	1352078	999	24
	Corridor 4	0.658	0.1	Yes	1352078	999	0

N/A Not Applicable
[a]Indicates significant difference with low R statistic

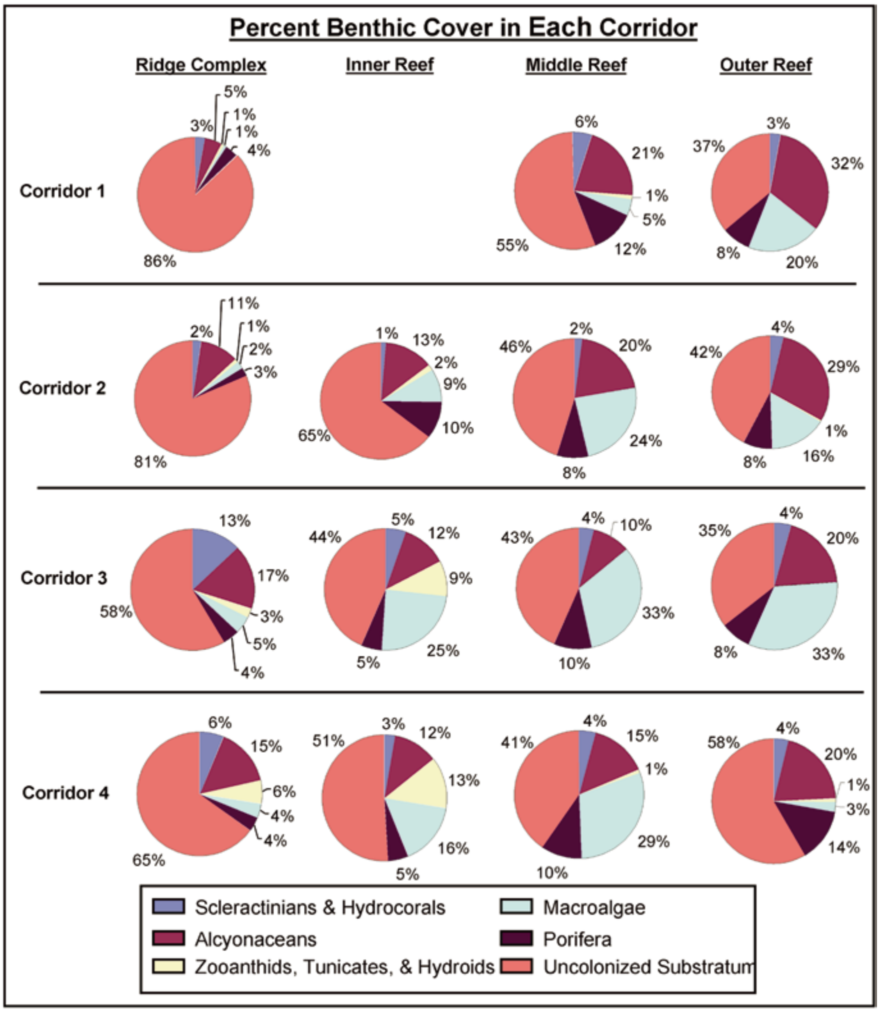


Fig. 8 Benthic cover (%) for each sampling location on each reef in each corridor

location was assigned to the MDS plot (Fig. 10B), the presence of three possible data clusters were shown. On this plot, ridge-complex transects form one cluster, inner-reef transects form a smaller second cluster, and middle- and outer-reef transects form a third cluster. The ANOSIM (Table 2) showed no significant difference ($R = 0.13$) between the middle- and outer-reef communities, but did show significant differences between the ridge-complex and middle-reef communities ($R = 0.763$, $p = 0.1\%$) and between the ridge- complex and outer-reef communities ($R = 0.645$, $p = 0.1\%$). Inner-reef communities were found to be significantly different from middle- ($R = 0.381$, $p = 0.1\%$) and outer-reef ($R = 0.330$, $p = 0.1\%$) communities, however with very low R statistics for both comparisons.

A total of 74 species of benthic flora and fauna were recorded for Corridor 3. On the ridge complex, live cover was dominated by alcyonaceans and scleractinians, which covered 17% and 13% of the bottom, respectively. Live cover on the inner (25%), middle (33%), and outer (33%) reefs was dominated by macroalgae (Fig. 8). The calculation of diversity measures (Table 1) showed the ridge complex (sites 1N, 1S, and cow site) to have the lowest species richness (d), while having the highest diversity (H′ and 1-λ). The inner and middle reefs (sites 2N and 2S; 3N and 3S, respectively) had the highest species richness, and the lowest diversity. The outer reef (sites 4N and 4S) had moderate species richness and low species diversity.

SIMPER analysis (Table 5) revealed that within-group similarity on the ridge complex was most attributable to the scleractinian *Montastrea cavernosa* (28.26%) and the alcyonacean *Pseudoplexaura* sp. (21.89%). *Dicytota* sp. (26.02%) and the encrusting zoanthid *Palythoa caribaeorum* (24.06%) had the highest contribution to within-group similarity on the inner reef. On the middle reef, the highest contributions to within-group similarity were given by *Dictyota* sp. (35.57%), *Halimeda* sp. (10.72%), and *E. caribaeorum* (11.45%). *Dictyota* sp. (29.36%), *Eunicea* sp. (15.31%), and *Pseudopterogorgia* sp. (9.29%) were responsible for similarity on the outer reef.

Corridor 4

Cluster and MDS analysis (Fig. 11A) initially revealed little evidence for existing groups of benthic habitat

Table 3 Species causing similarities within groups and dissimilarities among groups based on Bray-Curtis similarity or dissimilarity indices in corridor 1. Species are listed in ascending order according to percent contributions to respective similarity or dissimilarity. Numbers to the right reflect cumulative percent contribution for each species

Group ridge complex			Groups ridge complex and outer reef		
Average similarity: 16.11			Average dissimilarity: 86.40		
Species	Cont. (%)	Cum. (%)	Species	Cont. (%)	Cum. (%)
Anthosigmella varians	19.40	19.40	*Dictyota* sp.	7.77	7.77
Spheciospongia vesparium.	19.26	38.66	*Eunicea* sp.	5.94	13.71
Solenastrea boronouni	9.78	48.44	*Pseudopterogorgia* sp.	5.49	19.19
Pseudoplexaura sp.	8.94	57.38	*Pseudoplexaura* sp.	5.47	24.66
			Xestospongia muta	4.70	29.36
Group middle reef			*Anthostgmella varians*	4.27	33.63
Average similarity: 34.90			*Spheciospongia vesparium*	4.27	37.90
Pseudopterogorgia sp.	13.25	13.26	*Pseudopterogorgia americana*	3.68	41.58
Briareum asbestinum	10.70	23.96	*Muricea* sp.	3.57	45.15
Eunicea sp.	10.51	34.47	*Briareum asbestinum*	3.57	48.72
Pseudopterogorgia americana	8.04	42.51	*Plexaura flexuosa*	3.21	51.93
Dictyota sp.	7.08	49.59			
Holopsamma helwigi	6.70	56.29	Groups middle reef and outer reef		
			Average dissimilarity: 64.06		
Group outer reef			*Dictoyota* sp.	5.40	5.40
Average similarity: 45.04			*Pseudoplexaura* sp.	4.78	10.18
Dictyota sp.	22.03	22.03	*Briareum asbestinum*	4.03	14.21
Pseudoplexaura sp.	15.19	37.22	*Pseudopterogorgia americana*	4.03	18.24
Eunicea sp.	15.01	52.23	*Eunicea* sp.	3.96	22.20
			Holopsamma helwigi	3.95	26.15
Groups ridge complex and middle reef			*Pseudopterogorgia* sp.	3.68	29.83
Average dissimilarity: 86.02			*Xestospongia muta*	3.60	33.43
Pseudopterogorgia sp.	5.14	5.14	*Plexaura flexuosa*	3.39	36.82
Briareum asbestinum	4.78	9.92	*Palythoa caribaeorum*	3.36	40.18
Eunicea sp.	4.58	14.50	*Erythropodium caribaeorum*	3.20	43.38
Dictyota sp.	4.14	18.64	*Muricea* sp.	3.14	46.52
Pseudopterogorgia americana	4.13	22.77	*Aplysina fulva*	3.05	49.57
Anthosigmella varians	3.90	26.67	*Millepora alcicornis*	2.99	52.56
Pseudoplexaura sp.	3.84	30.51			
Spheciospongia vesparium	3.82	34.33			
Holopsamma helwigi	3.63	37.96			
Palythoa caribaeorum	3.51	41.47			
Solenastrea bornouni	3.07	44.54			
Xestospongia muta	2.98	47.52			
Muricea sp.	2.93	50.45			

data, however when transect location was assigned to sampling sites on the MDS plot (Fig. 11B), it became evident that ridge-complex transects formed one cluster, inner-reef transects formed a second small cluster diagonally across the plot, middle-reef transects formed a third cluster, and outer-reef transects formed a fourth

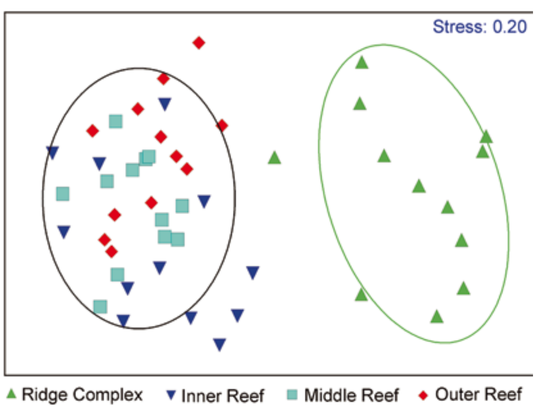


Fig. 9 Two-dimensional MDS plot of corridor 2 ecological data combined with transect location information. *Ovals* are intended to guide the reader, and were drawn as interpreted by the authors

cluster. ANOSIM results (Table 2) showed no significant difference ($R=0.31$, $p=0.2\%$) between ridge-complex and inner-reef communities, but did show significant differences between the ridge complex and middle reef ($R=0.749$, $p=0.1\%$) and between the ridge complex and outer reef ($R=0.576$, $p=0.1\%$). The inner reef was found to be significantly different from at least the outer reef ($R=0.514$, $p=0.1\%$) community; also the inner reef–middle reef comparison yielded a significant difference, but with a very low R statistic ($R=0.379$, $p=0.1\%$). The middle- and outer-reef communities were also found to be significantly different ($R=0.658$, $p=0.1\%$).

A total of 79 species of benthic flora and fauna were recorded in Corridor 4. On the ridge complex, alcyonaceans were the dominant taxonomic group, covering 15% of the substrate. Live cover on the inner reef was almost equally dominated by zoanthids (13%), alcyonaceans (12%), and macroalgae (16%). The middle reef was dominated by macroalgae (29%), and the outer reef by alcyonaceans (20%) and sponges (14%, Fig. 8). The ridge complex (sites 1N, 1S) had low species richness (d), while having high diversity (H′ and 1-λ, Table 1). The inner and middle reefs sites (2N

Table 4 Species causing similarities within groups and dissimilarities among groups based on Bray-Curtis similarity or dissimilarity indices in corridor 2. Species are listed in ascending order according to percent contributions to respective similarity or dissimilarity. Numbers to the right reflect cumulative percent contribution for each species

Group ridge complex			Groups ridge complex and outer reef		
Average similarity: 26.64			Average dissimilarity: 83.97		
Species	Cont. (%)	Cum. (%)	Species	Cont. (%)	Cum. (%)
Aplysina fistularis	28.29	28.29	*Dictyota* sp.	8.91	8.91
Pseudopterogorgia americana	16.49	44.78	*Pseudopterogorgia sp,*	6.59	15.50
Gorgonia ventalina	13.30	58.08	*Xestospongia muta*	6.58	22.08
			Briareum asbestinum	5.83	27.91
Group inner reef			*Eunicea* sp.	5.75	33.67
Average similarity: 36.80			*Pseudoplexaura* sp.	5.08	38.75
Pseudoplexaura sp.	12.06	12.06	*Aplysina fistularis*	4.45	43.20
Halimeda sp.	10.20	22.26	*Erythropodium caribaeorum*	4.36	47.56
Briareum asbestinum	10.14	32.40	*Plexaura flexuosa*	4.50	51.71
Erythropodium carabaeorum	9.41	41.82			
Pseudopterogorgia sp.	8.76	50.57	Groups inner reef and middle reef		
			Average dissimilarity: 62.87		
Group middle reef			*Halimeda* sp.	4.42	11.10
Average similarity:46.27			*Dictoyota* sp.	6.67	6.67
Dictyota sp.	27.24	27.24	*Halimeda* sp.	4.42	11.10
Briareum asbestimun.	21.67	48.91	*Pseudoplexaura* sp.	4.39	15.48
Eunicea sp.	12.53	61.44	*Pseudopterogorgia* sp.	4.16	19.65
			Eurythropodium caribaeorum	4.12	23.77
Group outer reef			*Briareum asbestinum*	4.06	27.83
Average similarity: 52.05			*Eunicea* sp.	4.01	31.84
Dictyota sp.	21.20	21.20	*Xestospongia muta*	3.95	35.79
Pseudopterogorgia sp.	16.55	37.75	*Iotrochoia birotulata*	3.76	39.55
Xestospongia muta	12.38	50.13	*Aplysina fulva*	3.73	43.28
			Jania adherens	3.73	47.01
Groups ridge complex and inner reef			*Pseudopterogorgia americana*	3.09	40.10
Average dissimilarity: 85.94					
Halimeda sp.	5.39	5.39	Groups inner reef and outer reef		
Briareum asbestimun	5.06	10.45	Average dissimilarity: 63.91		
Dictyota. sp.	5.04	15.49	*Dictyota* sp.	5.68	5.68
Aplysina fistularis	4.85	20.34	*Halimeda* sp.	4.80	10.49
Pseudopterogorgia sp.	4.79	25.13	*Eunicea* sp.	4.67	15.16
Erythropodium varabaeorum	4.73	29.85	*Xestospongia muta*	4.66	19.82
Eunicea sp.	4.35	34.20	*Plexaura flexuosa*	4.21	24.03
Pseudoplexaura sp.	4.20	38.41	*Pseudopterogorgia* sp.	4.17	28.19
Pseudopterogoria americana	4.09	42.50	*Pseudoplexaura* sp.	3.96	32.16
Iotrochota birotulata	4.00	46.49	*Erythropodium caribaeorum*	3.84	36.00
Aplysina fulva	3.82	50.31	*Iotrochota birotulata*	3.54	39.54
			Aplysina fulva	3.40	42.94
Groups ridge complex and middle reef			*Briareum asbestinum*	3.24	46.18
Average dissimilarity: 86.96			*Montastrea cavernosa*	2.96	49.15
Dictyota sp.	9.82	9.82	*Pseudopterogorgla americana*	2.88	52.03
Briareum asbestinum	8.21	18.04			
Eunicea sp.	5.15	23.19	Groups middle reef and outer reef		
Pseudopterogorgia sp.	5.13	28.33	Average dissimilarity: 53.33		
Pseudoplexaura sp.	4.72	33.05	*Pseudoplexaura* sp.	5.47	5.47
Aplysina fistularis	4.60	37.64	*Xestospongia muta*	4.85	10.32
Halimeda sp.	4.32	41.97	*halimeda* sp.	4.82	15.14
Xestospongia muta	3.77	45.74	*Plexaura flexuosa*	4.81	19.96
Pseudopterogorgia americana	3.75	49.49	*Erythropodium carabaeorum*	4.80	24.76
Gorgonia ventalina	3.27	52.76	*Eunicea* sp.	3.84	26.80
			Pseudopterogorgia sp.	3.75	32.35
			Aplysina fulva	3.65	36.00
			Montastrea cavernosa	3.47	39.48
			Jania adherens	3.44	42.92
			Aplysina cauliformis	2.68	45.60
			Briareum asbestinum	2.65	48.25

and 2S, 3N and 3S, respectively) had high species richness, but the lowest species diversity. The outer reef (sites 4N and 4S) had moderate species richness and high species diversity.

SIMPER analysis (Table 6) showed the encrusting zooanthid *Palythoa caribaeorum* to contribute most to within-group similarities on both the ridge complex (28.74%) and inner reef (32.55%). The ridge complex was dominated by the alcyonaceans *Eunicea* sp. (14.91%) and *Erythropodium caribaeorum* (10.58%), which also had a high contribution to within-group similarity on the inner reef (22.27%). On the middle reef,

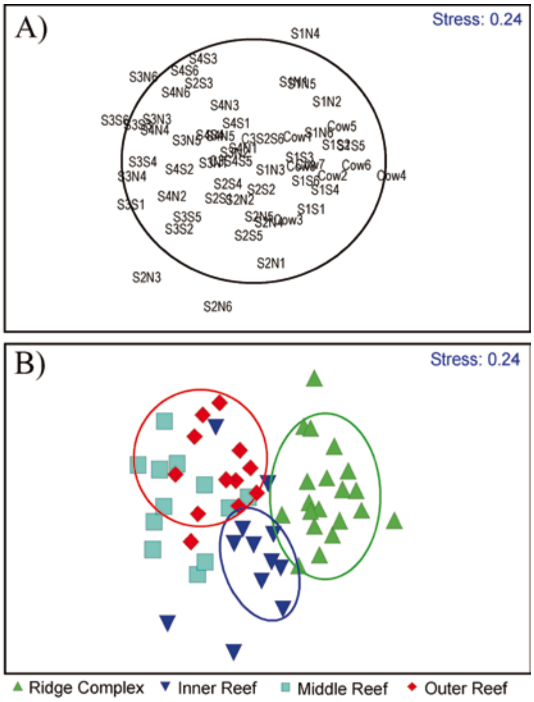


Fig. 10 Two-dimensional MDS plot of corridor 3 ecological data (**A**). Sites are coded as in Fig. 7. **B** transect location information combined with corridor 3 MDS ordination. *Ovals* are intended to guide the reader, and were drawn as interpreted by the authors

the macroalgae *Dictyota* sp. (29.21%) and *Halimeda* sp. (11.69%), and the alcyonacean *Pseudoplexaura* sp. (14.40%) had the highest contribution to within-group similarities. *B. asbestinum* (26.45%) and *E. caribaeorum* (13.59%), along with the sponge *Xestospongia muta* (19.33%), had the highest contribution to the similarity of the outer reef.

Habitat maps

Habitat maps produced for each corridor show seven different reef communities occurring in Broward County (Fig. 12). In the north, the ridge complexes have low proportions of living cover and are dominated primarily by sponges. Ridge complexes in the two south corridors have a greater proportion of living cover and are dominated by soft corals and either stony corals (corridor 3, Fig. 13A) or encrusting zoanthids (corridor 4, Fig. 13B). In corridor 3, the inner reef is dominated completely by soft corals. To the south (Corridors 3 and 4), the inner-reef community takes on community characteristics of both neighboring shallow and deep reefs, having a mixed fauna (Fig. 13C) with medium cover, and being dominated by both zoanthids (typical of shallow communities) and macroalgae (typical of deep communities). The deep reefs (middle and outer reefs) in all corridors had the highest proportion of living cover and were dominated mainly by macroalgae, except the outer reef in Corridor 4, which was dominated by massive sponges and soft corals (Fig. 13D, E).

Discussion

Spatial patterns

On the MDS plots, ridge-complex transects in the north (corridors 1 and 2) cluster distinctly from ridge-complex transects in the south (corridor 3 and 4). This difference is most likely controlled by the underlying substrate in each corridor. The ridge-complex communities in the north occur on flat pavements with little surface relief (< 1 m) and low live cover (Fig. 13F), while the ridge-complex communities in the south had a higher proportion of live cover and occur on structures with greater surface relief (1 m or more), which may be a combination of coral framework and cemented calcarenites.

The inner reef and middle reefs showed no apparent north–south trends in terms of community distribution, however on the outer reef, macroalgae dominated the benthos in corridors 1–3, surveyed in late spring, while sponges and soft corals dominated corridor 4, surveyed in late fall. The outer reef is one continuous structure, so that this difference may reflect seasonal algal dominance on the southern extreme.

The northernmost known thickets of *Acropora cervicornis* occur in the north of Broward County (Thomas et al. 2000; Vargas-Angel and Thomas 2002). These *A. cervicornis* patches provide a unique habitat on these shallow, flat pavements, and no active frame-building is evident. The distribution of these thickets is patchy (Thomas et al. 2000). They are commonly flanked by stable, uncemented *A. cervicornis* rubble zones. These characteristics may be the result of episodic disruptions caused by the frequent return of tropical storms, hurricanes, and winter storms associated with passing cold fronts (Muller and Stone 2001).

Community structure

Despite having similar faunas (Goldberg 1973; Kinzie III 1973; Opresko 1973), the community structure of these reefs is remarkably different than reefs in other Caribbean areas such as the Florida Keys (Jaap 1984), the Bahamas (Lidell et al. 1997), Jamaica (Goreau 1959), the US Virgin Islands (Hubbard et al. 1993; Cox et al. 2000), and Puerto Rico (Loya 1976). Goldberg (1973) reported that certain important hermatypic scleractinia (namely *Porites porites* and *Diploria strigosa*) were absent, but both species were documented in this study. The only major reef-builder that seems to be lacking in this area is *Acropora palmata*, which was not found by Goldberg (1973) or in the present study. While Broward County reef communities have a fairly complete list of hermatypic coral species (30), the average coral size is small (typically < 50 cm diameter,

Table 5 Species causing similarities within groups and dissimilarities among groups based on Bray-Curtis similarity or dissimilarity indices in corridor 3. Species are liked in ascending order according to percent contributions to respective similarity or dissimilarity. Numbers to the right reflect cumulative percent contribution for each species

Group ridge complex		
Average similarity: 47.31		
Species	Cont. (%)	Cum. (%)
Montastrea cavernosa	28.26	28.26
Pseudoplexaura sp.	21.89	50.16
Group inner reef		
Average similarity 46.55		
Dictyota sp.	26.02	26.02
Palythoa caribaeorum	24.06	50.08
Group middle reef		
Average similarity 40.86		
Dictyota sp.	35.57	35.57
Erythropodium caribaeorum	11.45	47.02
Halimeda sp.	10.77	57.73
Group outer reef		
Average similarity: 48.97		
Dictyota sp.	29.36	29.36
Eunicea sp.	15.31	44.67
Pseudopterogorgia sp.	9.29	53.96
Groups ridge complex and inner reef		
Average dissimilarity: 64.64		
Dictyota sp.	7.41	7.41
Pseudoplexaura sp.	6.66	14.98
Montastrea cavernosa	5.86	19.94
Eunicea sp.	5.52	25.46
Pseudopterogorgia sp.	5.42	30.88
Briaeum asbestinum	5.19	36.07
Palythoa caribaeorum	4.86	40.93
Erythropodium caribaeorum	4,70	45.63
Siderastrea siderea	3.54	49.17
Amphimedon compressa	3.19	52.36
Groups ridge complex and middle reef		
Average dissimilarity 75.08		
Montastrea cavernosa	8.42	8.42
Dictyota sp.	6.79	15.21
Pseudoplexaura Sp.	5.09	20.30
Halimeda sp.	4.78	25.08
Palythoa caribaeorum	4.20	29.28
Briareum asbestinum	4.13	33.41
Eunicea sp.	4.07	37.48
Erythropodium caribacorum	3.80	41.28
Pseudopterogorgia sp.	3.05	44.32
Xestospongia muta	3.02	47.34
Amphimedon compressa	2.80	50.14

Groups ridge complex and outer reef		
Average dissimilarity: 66.73		
Species	Cont. (%)	Cum. (%)
Dictyota. sp.	7.45	7.45
Montastrea cavernosa	5.51	12.97
Pseudoplexaura sp.	5.35	18.32
Xestospongia muta	4.96	23.28
Pseudopterogorgia sp.	4.94	28.22
Palythoa caribaeorum	4.86	33.08
Halimeda sp.	4.50	37.58
Briareum asbsetinum	4.35	41.93
Erythropodium caribaeorum	3.85	45.78
Eunicea sp.	3.35	49.13
Groups inner reef and middle reef		
Average dissimilarity: 64.69		
Palythoa caribaeorum	8.55	8.55
Halimeda sp.	5.10	13.64
Montastrea cavernosa	4.30	17.95
Pseudppterogorgia sp.	3.97	21.92
Eunicea sp.	3.81	25.73
Briareum asbestinum	3.62	29.35
Xestospongia muta	3.46	32.81
Amphimedon compressa	3.37	36.18
Pseudoplexaura	3.28	39.45
Erythropodium caribaeorum	3.22	42,67
Siderastrea siderea	3.12	45.80
Callyspongia vaginalis	2.78	49.58
Apylsina fulva	2.74	51.32
Groups inner reef and outer reef		
Average dissimilarity: 60.39		
Palythoa caribaeorum	9.73	9.73
Eunicea sp.	5.33	15.06
Xestospongia muta	4.60	19.65
Haiimeda sp.	4.58	24.23
Erythropodium caribaeorum	4.27	28.50
Pseudoplexaura sp.	4.07	32.57
Briareum asbestinum	3.84	36.41
Pseudopterogorgia sp.	3.60	40.01
Siderastrea siderea	3.43	43.44
Montastrea cavernosa	3.29	46.73
Plexaura flexuosa	3.17	49.90
Groups middle reef and outer reef		
Average: 57.25		
Montastrea cavernosa	4.74	4.47
Eunicea sp.	4.44	9.18
Xestospongia muta	4.31	13.40
Erythropodium caribaeorum	4.19	17.68
Pseudopterogorgia sp.	4.13	21.81
Pseudoplexaura sp.	3.97	25.78
Briaerum asbestinum	3.94	29.71
Halimeda sp	3.87	33.59

Fig. 13G) and relative percent cover by scleractinians is low (Table 7). Furthermore, although the *Montastrea annularis* species complex (*M. annularis, M. faveolata, M. franksi*) is present, it is not a dominant species in these communities as is typical in the wider Caribbean (Knowlton 2001), but are subordinate to *M. cavernosa*, which was the most abundant scleractinian. This difference has also been reported in other high-latitude (Bermuda; Laborel 1966) and turbid (windward Barbados, Lewis 1960) settings. Goldberg (1973) attributed this phenomenon to the proximity to shore and the deleterious effects of the large human population (i.e. increased runoff and sedimentation, sewage effluent) causing high turbidity and decreased light penetration, and these factors are cited as the cause of low coral cover on high-latitude reefs in Brazil (Laborel 1969; Castro and Pires 2001). Other similarities also exist between the high-latitude reefs described in this study and the Brazilian reefs. Castro and Pires (2001) describe the northeastern Brazilian reefs as long lines of "fringing reefs" expressed as coral communities growing on beach rock, with other parallel lines of reef

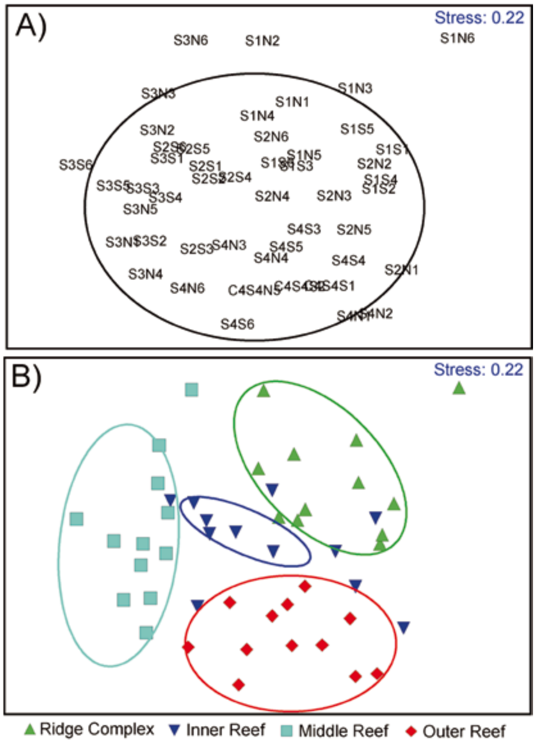


Fig. 11 **A** Two-dimensional MDS plot showing spatial relationship of corridor 4 benthic transect data, site coding as Fig. 7. **B** same MDS plot as **A** with each transect coded according to transect location information. *Ovals* are intended to guide the reader, and were drawn as interpreted by the authors

communities further offshore. This is very similar to the situation in corridors 1 and 2.

Factors influencing diversity and community structure

Diversity increased from north to south along the entire study area. Jordan-Dahlgren (2002) noted that several factors (larval availability and transport, ecological connectivity, substrate suitable for settlement, and local oceanic conditions) may explain observable gradients in alcyonacean communities. These factors need careful consideration in the current study because alcyonaceans were one of the dominant fauna, and typically contributed most to the within-group similarities of most reef communities. Substrate availability is fairly homogeneous in all locales and probably does not contribute to the north–south gradient in diversity.

Local oceanic conditions may play a role in determining some of the observed diversity gradients. Winter storm events produce heavy seas, leading to the frequent detachment and subsequent mortality (Kinzie 1973; Yoshioka and Yoshioka 1991) of the soft corals. The ridge-complex and inner-reef communities in the north are closer to shore and in more shallow water, where waves often break during storms. These areas had lower abundance and percent cover of alcyonaceans than the deeper reefs, which are not subject to breaking waves during storms. These seasonal disturbances, along with the area's susceptibility to hurricanes, are a likely control upon the distribution of alcyonaceans.

Although not investigated in this study, the abundance and distribution of alcyonacean larvae in this area may help to explain the observed diversity gradients. Alcyonaceans in this high-latitude setting can have a higher density of individuals than found in typical Caribbean reef communities (25.1 individuals/m^2; Goldberg 1973), so it seems logical that larval abundance is probably also high. Although virtually no reproductive data exits for the alcyonacean communities of Broward County, histological studies have shown that two common species (*B. asbestinum* and *E. caribaeorum*) have Stage III gametes present in their tissues by late spring (Vargas-Angel, personal communication). This indicates that spawning is likely to occur in mid- to late summer, in common with the Plexaurids in the Caribbean which typically spawn after the summer full moons (Brazeau and Lasker 1989; Beiring and Lasker 2000). If summer spawning occurs, the larval distribution along the reefs is likely to be influenced by localized currents. Soloviev et al. (2003) have observed the occurrence of a localized reversal in the general south to north flow of the Florida current in this area during late summer. This current reversal, and resultant north to south flow, may cause a concentrated distribution of planulae to the south during the spawning season when larvae are most abundant. As the reversal eventually weakens and flow returns to a north-running current, settling larvae can be re-dispersed from the concentrated area in the south to the northern extents of the reefs. Clearly, further investigation of this phenomenon is needed, however considering the physical and temporal scales involved, the described scenario seems likely. Whether temperature is a factor in limiting the community development of these high-latitude reefs is unclear. A two-year continuous record of monthly temperature data at 12 reef locations across all depth gradients (ranging from 5 to 20 m) yielded a minimum temperature of 20.2 °C and showed mean water temperatures (Fig. 14) to be well within the accepted limits for hermatypic coral growth and survival (Wells 1957; Macintyre and Pilkey 1969).

Water quality, in terms of turbidity and sedimentation, may play a role in determining community structure within this system. Goldberg (1973) considered that runoff and canal effluent as well as sewer outfalls with direct termination on the outer reef contribute to an increase in turbidity over these reefs, however little is known about sedimentation in this area. Although Loya (1976) found no clear trend between turbidity and coral size, his work did show that *M. cavernosa* was the most abundant reef-builder in areas with heavy sedimentation and high turbidity. Similarly, in experimental shading studies, *M. cavernosa* has been found to be more tolerant to reduced light levels than other dominant reef builders such as *M. annularis* complex or *A. cervicornis* (Rogers 1979; Brown

Table 6 Species causing similarities within groups and dissimilarities between groups based on Bray-Curtis similarity or dissimilarity indices in corridor 4. Species are listed in ascending order according to percent contributions respective similarity or dissimilarity. Numbers to the right reflect cumulative percent contribution for each species

Group ridge complex		
Average similarity: 38.65		
Species	Cont. (%)	Cum. (%)
Palythoa caribaeorum	28.74	28.74
Eunicea sp.	14.91	43.65
Erythropodium caribaeorum	10.52	54.23
Group inner reef		
Average similarity: 40.97		
Palythoa caribaeorum	32.55	32.55
Erythropodium caribaeorum	22.27	54.83
Group middle reef		
Average similarity: 42.72		
Dictyota sp.	29.21	29.21
Pseudoplexaura sp.	14.40	43.61
Halimeda sp.	11.69	55.30
Group outer reef		
Average similarity:39.41		
Briareum asbestinum	26.45	26.45
Xestospongia muta	19.33	45.79
Erythropodium caribaeorum	13.59	59.37
Groups ridge complex and inner reef		
Average dissimilarity: 65.24		
Dictyota sp.	7.27	7.27
Montastrea cavernosa	5.32	12.59
Eunicea sp.	5171	17.80
Briareum asbestinum	4.56	22.36
Pseudopterogorgia sp.	4.45	26.81
Pseudoplexaura sp.	4.27	31.08
Plexaura flexuosa	4.09	35.17
Erythropodium caribaeorum	3.93	39.10
Niphates erecta	3.61	42.71
Aplysina fistularis	3.49	46.20
Montastrea annularis	3.17	49.37
Amphimedon compressa	3.07	52.44
Groups ridge complex and middle reef		
Average dissimilarity: 73.52		
Dictyota sp.	7.05	7.06
Palythoa carlbaeota.	6.01	13.07
Halimeda sp.	5.34	18.41
Montastrea cavernosa	3.99	22.40
Briareum asbestinum	3.86	26.26
Erythropodiumcaribaeorum	3.72	29.98
Eunicea sp.	3.66	33.64
Pseudopterogorgia sp.	3.42	37.06
Pseudoplexaura sp.	3.39	40.45
Xestospongia muta	3.33	43.78
Plexaura flexuosa	2.98	46.76
Niphates erecta	2.96	49.72
Apylsina fistularis	2.70	52.42

Groups ridge complex and outer reef		
Average dissimilarity: 75.68		
Species	Cont. (%)	Cum. (%)
Xestospongia muta	6.30	6.30
Palythoa caribaeorum	5.85	12.15
Briareum asbestinum	5.30	17.45
Montastrea cavernosa	3.89	21.34
Eunicea sp.	3.89	25.23
Erythropodium caribaeorum	3.82	29.05
Pseudopterogorgia sp.	3.42	32.47
Niphates digitalis	3.36	35.83
Pseudoplexaura sp.	3.17	39.00
Amphimedon compressa	3.07	42.07
Plexaura flexuosa	2.94	45.01
Coralline algae	2.88	47.89
Niphates erecta	2.87	50.76
Groups inner reef and middle reef		
Average dissimilarity: 67.96		
Palythoa caribaeorum	7.81	7.81
Halimeda sp.	5.90	13.71
Dictyota sp.	5.12	18.83
Erythropodiumcaribaeorum	4.39	23.22
Pseudoplexaura sp.	4.35	27.57
Pseudopterogorgia	4.30	31.87
Briareum asbestinum	3.81	35.68
Eunicea sp.	3.76	39.44
Xestospongia muta	3.70	43.14
Niphates erecta	3.11	46.25
Montastrea annularis	3.06	49.31
Ectoplasyia ferox	2.56	51.87
Groups inner reef and outer reef		
Average dissimilarity: 72.33		
Palythoa caribaeorum	7.36	7.36
Dityota sp.	6.70	14.06
Xestospongia muta	6.21	20.27
Briareum asbestinum	5.86	26.13
Eunicea sp.	3.72	29.85
Niphates digitalis	3.65	33.50
Peudopterogorgia sp.	3.56	37.06
Pseudoplexaura sp.	3.52	40.58
Erythropodium caribaeorum	3.43	44.01
Aphimedon compressa	3.27	47.28
Siderastrea sidera	3.19	50.47
Groups middle ridge and outer reef		
Average dissimilarity: 72.15		
Dictyota sp.	9.15	9.15
Halimeda sp.	4.84	13.99
Erythropodium caribacorum	4.24	18.23
Briareum asbestinum∼	3.98	22.21
Pseudopterogorgia sp.	3.70	25.91
Xestospongia muta	3.57	29.48
Niphates digitalis	3.23	32.71
Pseudoplexaura sp.	3.16	35.87
Eunicea sp.	3.06	38.93
Amphimedon compressa	2.83	41.76
Siderastrea siderea	2.81	44.57
Niphates erecta	2.71	47.28
Unidentified Sponge	2.41	49.69
Coralline algae	2.36	52.05

and Howard 1985). The higher light requirements of *A. cervicornis* may explain why colonies seem to thrive in extremely shallow areas, but are virtually absent below 10 m. These studies also offer an explanation for the dominance of *M. cavernosa* on the Broward County reefs (Fig. 13H). The sewer effluents cited by Goldberg (1973), four of which have direct outfall on the eastern edges of the outer reef, are likely to increase nutrient availability

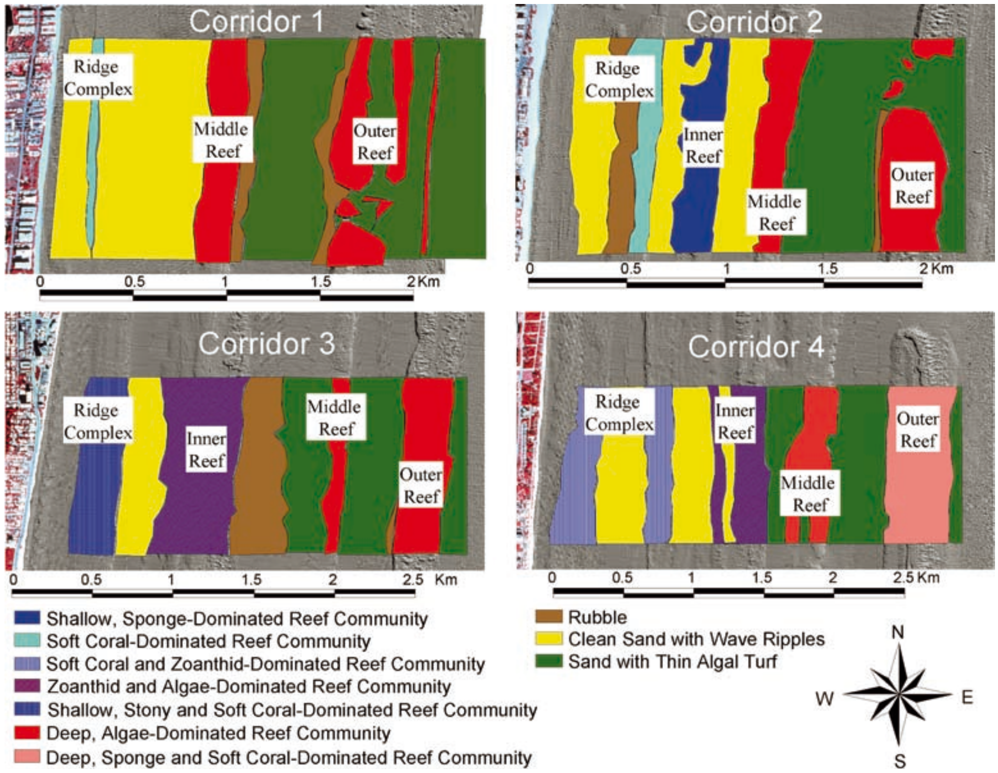


Fig. 12 Final habitat classifications for all four study corridors

and may explain the dominance of macroalgae on the outer reef in three of the four corridors.

Disturbance by hurricanes and major storms may also play a large role in determining the structure of these reef communities. Connell (1978) suggested that high levels of disturbance can cause decreased diversity, and Burns (1985) attributed low abundance of corals and low diversity to frequent disturbance by storms in the northernmost Florida Keys. Using the average of two different models (Simpson and Lawrence 1971; Muller and Stone 2001) and based on 100 years of storm data, this area was found to have the lowest mean recurrence interval of severe hurricanes (18 years for category 3 or stronger) and major storms (7 years for tropical storm strength or greater) in the continental United States. For comparison, Key Largo, the area of Florida with the most extensive reef development (Marszalek et al. 1977), has mean recurrence intervals of about 21 years for severe hurricanes and 8 years for all major storms (Simpson and Lawrence 1971; Muller and Stone 2001).

Some interesting parallels exist between Broward County and other high-latitude settings. The community structure on these northern high latitude reefs (25°58′N to 26°19′N) is dominated by soft corals, possibly in response to wave action (among others) as forcing factor. A similar situation is observed on southern high-latitude reefs in South Africa (to 27°50′S), where community structure is also clearly dominated by alcyonacea in response to strong wave action (Riegl et al. 1995). Growth strategy of the respective soft corals is different, however: they are upright and flexible in the Atlantic fauna, compared to flat, soft and sprawling in the Indo-Pacific fauna. South of the major South African coral areas, on Aliwal Shoal, hard coral cover falls to similarly low levels as in Broward County (unpublished pers. obs., and Schleyer 1998), while soft coral cover remains high. Both Florida and South Africa are within the influence of a western boundary current (the Gulf Stream in Florida, and the Agulhas Current in South Africa), which may be a large-scale control for such a pattern of high-latitude faunal attenuation. Which exact factors are at play is, however, yet unknown. In Australian high-latitude reefs, a different pattern is observed. Within Queensland, soft coral cover increases towards high latitudes, but this trend is reversed into even higher latitudes (Harriott and Banks 2002). Much remains to be learned about the dynamics of high-latitude reef communities.

Conclusions

Community structure on the reefs of Broward County is highly variable according to location and associated physical factors. Generally, the proportion of living coral cover increases seaward, with the outer reef typically having the highest values. For the nearshore ridge-complex communities, those in the north have lower live cover and are dominated mainly by sponges. In the south, the ridge-complex communities have greater live cover, and are dominated by alcyonaceans, scleractinians, and encrusting zoanthids. Inner-reef communities are dominated by mixed faunal assemblages typical of

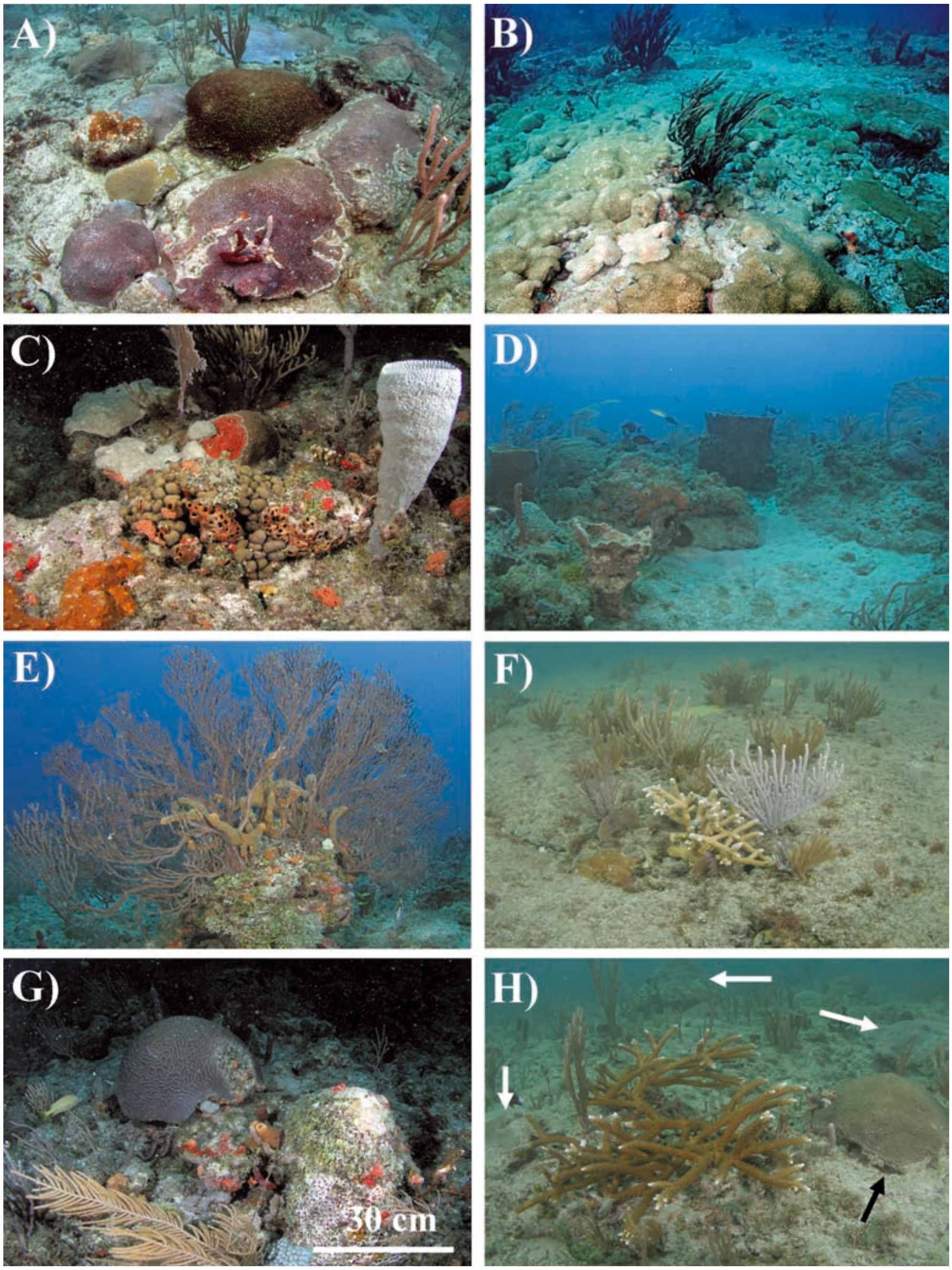


Fig. 13 Photo mosaic showing: **A** high cover of scleractinian corals on the inner reef of corridor 3; **B** high percent cover by the encrusting zoanthid *Palythoa caribaeorum* on the inner reef of corridor 4; **C** mixed faunal assemblage typical of the middle reef of corridor 4; **D** typical outer-reef community with tall alcyonacean fauna and the massive sponge *Xestospongia muta*; **E** *Icilligorgia schrammi*, a common alcyoncacean on the outer reef; **F** flat, low-cover pavement typical of northernmost ridge complexes; **G** small size (note scale) of common scleractinians *Montastrea cavernosa* (mostly dead in *foreground*) and *Diploria labyrinthiformes* (*background*); and **H** *Acropora cervicornis* colony surrounded by more dominant *M. cavernosa* colonies (*arrows*)

both neighboring shallow (ridge complex) and deep (middle and outer) reef communities. Macroalgae, massive sponges, and alcyonaceans are dominant on the deep reefs.

Table 7 Percent (%) cover of Scleractinians on each reef community throughout all study areas

	Ridge complex	Inner reef	Middle reef	Outer reef	Mean
Corridor 1	3	N/A	6	3	4
Corridor 2	2	1	2	4	2.25
Corridor 3	13	5	4	4	6.50
Corridor 4	6	3	4	4	4.25
Mean	6	3	4	3.75	

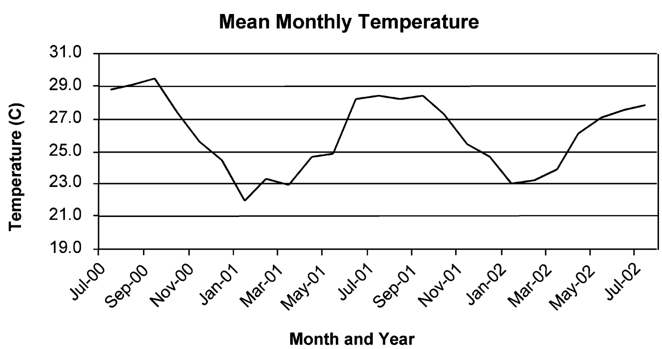


Fig. 14 Two-year mean monthly temperatures. Data from 12 reef locations off Broward County, Florida

Although these reefs provide habitat for many hermatypic corals, the colony size is small. The annual temperature range is within the limits for growth of scleractinia and may therefore have little effect on community structure, and indications are that water quality, sedimentation, and hurricane recurrence should be examined further as possible determinants of community structure in this area.

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