SPECIES PRESENCE AND DISTRIBUTION OF SCLERACTINIA (CNIDARIA: ANTHOZOA) FROM SOUTH CAICOS, TURKS AND CAICOS ISLANDS

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ABSTRACT

The species presence and relative abundance of scleractinian corals was recorded on the narrow shelf of the Caicos Platform, off South Caicos Island, in the southeastern Bahamian archipelago. Belt transects were used to survey 100 m^2 at each of three topographic reef zones, namely "pavement" at 9 m, spur and groove at 18 m, and the forereef escarpment at 27 m depth. Thirty-three species were thus identified in situ. Including species of the environs, a total of 40 zooxanthellate and mostly hermatypic species were recorded. Three distinct coral assemblages were depicted. Low species richness, and a comparatively even distribution of individual abundances, characterized the coral assemblage at 9 m, influenced by the persistent wave impact of easterly Trade Winds. The coral assemblage at 18 m, spatially restricted to the spurs of the spur and groove topography, harbored the highest species richness and diversity, while exhibiting comparatively heterogeneous individual abundances. Outcrops, ledges, and sand chutes characterized the reef at 27 m, where the number of species decreased, yet the evenness of occurrence increased. *Siderastrea siderea* and *Porites astreoides* were among the most frequently occurring corals at all depths, indicating that they are eurybathic and inter-specifically competitive. *Agaricia* spp., *Montastraea annularis,* and *M. faveolata*, were abundant at depths of 18 and 27 m, where they constitute the main scleractinian framework builders. The general paucity of *Acropora* spp. and the lack of *Acropora cervicornis* accretions at mid depths is another attribute of South Caicos.

The coral reefs of the Caicos Islands, in the southeastern Bahamian archipelago, between 21° and 22°N, and 71° and 72°30′W (Fig. 1), have been scarcely documented. Surveys of the Bahamian region by Bunt et al. (1981) include data from a single 10 m transect, examined at 15 m depth, near East Caicos, and account for 28 species of sponges, scleractinian corals, octocorals, and hydroids. A description of reefal ridges, reef flats, and surficial sediment types of the Caicos Platform was given by Wanless and Dravis, (1989). Scleractinian abundance patterns of South Caicos were first described by Sullivan et al. (1994). Based on 15 to 30 m^2 examined at each of five distinct reef locations, they report the presence of 35 hermatypic scleractinians with a low percent cover relative to other regions of the Caribbean. Mumby et al. (1998) provide further data on biotic and abiotic surface cover of the South Caicos area, in a recent effort to gauge and evaluate remote sensing imagery.

Coral reefs fringe the Caicos Platform on the windward side of its eastern and northeastern islands, as well as on the leeward side of its northern and western islands (pers. observ.). The interior of the Caicos Platform is characterized by relatively barren tidal flats, lagoons, shallow subtidal areas with a few intermittent shoals (Wanless and Dravis 1989), and sediments ranging from oolitic grainstone to peloidal packstone-grainstone. These sediments are widely bioturbated by *Callianassa* (Wanless et al., 1988). Coral growth in these areas is predominantly associated with tidal channels adjacent to islands, but *Siderastrea radians* can also be found in lagoonal settings with sediment accumula-

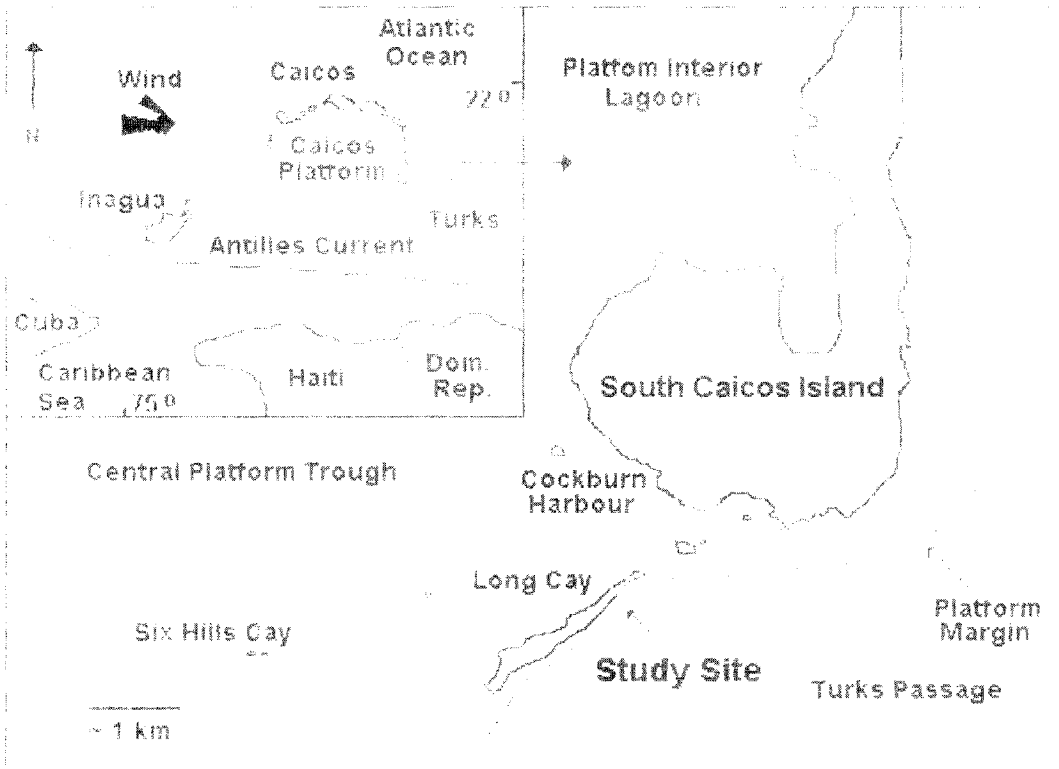

Figure 1. Location of South Caicos Island and the study site.

tions no deeper than 10 cm, often in close proximity to *Rhizophora mangle* stands (pers. observ.).

While international concern about the condition of coral reefs has augmented (Dight and Scherl, 1997; Spalding and Grenfell, 1997), there remains a paucity of records on the reefs in regions that lack research stations, yet receive increasing human use (see Cortés, 1997). In the Turks and Caicos Islands tourism has become the leading industry and primary user of coastal environments on the Islands of Providenciales, Grand Turk, and marginally South Caicos. But the industry is growing and evidence of direct anthropogenic disturbances includes scars from poor boating practices and gear loss. Fishermen's accounts of decreasing catch per unit effort, mainly in the extraction of *Strombus gigas* and *Panulirus argus*, indicate the possibility of faunal and algal phase shifts as documented in Jamaica (Hughes, 1994) and other Caribbean regions (Rogers, 1985). This study presents further insight into the coral reefs of the Turks and Caicos Islands. Scleractinian species presence and relative frequency of occurrence along the southern shelf, adjacent to South Caicos, are described and compared to other areas in the greater Caribbean. Bathymetric distribution patterns are discussed on the basis of local hydrodynamic parameters.

Methods

Study Site.—South Caicos is the southernmost island of the Caicos islands (Fig.1). The study site, located on the windward side of Long Cay, consisted of three distinct topographic zones (Fig.2). A low relief (≤1 m) platform or pavement extends seaward from 0 to 12 m of depth. Spur and groove formations of 1–1.5 m relief, span depths from 12 m to 18 m. Within the spurs, colony rugosity is up to 1.5 m. A steep forereef escarpment begins at 18 m, and drops to 2100 m, the Turks Passage. It is characterized by outcrops, sand chutes, and intermittent ledges.

Stations for this study were selected at 9, 18 and 27 m depth. At the 9 m station, the algae *Dictyota* spp. and *Lobophora* sp., the octocorals *Gorgonia* sp., *Pseudopterogorgia* sp., *Plexaura* sp., and encrusting colonies of the stony corals *Siderastrea siderea, Siderastrea radians, Stephanocoenia intersepta,* and *Porites astreoides* constitute the visually most common sessile macro benthos. It is the most turbulent station, influenced by a persistent incoming surge (Antilles Current, Trade Winds) and its reflection from Long Cay (Fig. 1). At the 18 m station, *Dictyota* spp., *Lobophora* sp., the sponges *Pseudoceratina crassa*, *Ectyplasia ferox*, *Neofibularia nolitangere*, and *Aplysina cauliformes*, the octocorals *Pseudopterogorgia* sp., *Plexaura flexuosa* and *Plexaura homomalla*, and the stony coral *Montastraea annularis* were visually common, while the 27 m station was characterized by *Lobophora* spp., the sponge *Aplysina archeri,* folios *Agaricia* spp., and *Montastraea favaeolata*.

DATA COLLECTION.—Records of species presence from approximately 400 snorkel- and SCUBA dives, carried out between September 1994 and August 1996, at various locations around South Caicos, Long Cay, and Six Hills Cay (Fig. 1), were compiled to a reference list for the area. A sample size of 20 m^2 was determined by plotting species per-area curves (Loya 1978) for each of the three selected depths. Using SCUBA, five 20 m transect lines were then nailed to the substratum, parallel to the shoreline and to each other at the 9 m, and 18 m stations. The transects were installed at 5 m intervals, resulting in a depth difference between the shallowest and the deepest lines of 0.5 m at the 9 m station, and 1 m at the 18 m station. At the 27 m station, such a layout would have incurred a 9 m change in depth. Therefore, transects were installed in a tandem position along the reef escarpment. Using 1-meter-long PVC pipes as visual reference, every scleractinian colony within 0.5 m of the transect was counted and identified in situ. Thus, a total of 300 m^2 reef surface were surveyed, 100 m^2 at each depth. Species that were observed between the stations, but did not occur in the transects, were also recorded.

Species identification was based on Cairns (1982), Goreau and Wells (1973), Humann (1994), Smith (1971), and Weil and Knowlton (1994). Fourteen solitary polyps could not be identified, and were not included in the subsequent data analysis. Individual colony boundaries were defined as the discontinuity of live coral tissue. Although this approach leads to high counts in columnar species such as *M. annularis* with partial mortality sensu Hughes and Jackson (1980), it is more replicable in dense and convoluted reef structures, than to define colony boundaries as skeletal entities. Each transect was surveyed up to 6 times until counts of species and individuals were consistent. Visual observations of colony size and percent live coverage were noted. Transect surveys were carried out from October to December 1995 and from March to April 1996.

COMMUNITY STRUCTURE ANALYSIS.— Counts of formas were pooled to single species counts prior to calculating species richness, species diversity (H', $\log_e$) as expressed by Shannon and Wiener (1948) and Pielou's (1966) evenness index (J') for each transect. Data were subsequently subjected to a hierarchical, agglomerative cluster analysis. The Bray-Curtis index was used as distance measure with centroid method of linkage (Digby and Kempton, 1987).

RESULTS

SPECIES PRESENCE AND DISTRIBUTION.—A total of 40 Scleractinia, from 22 genera and 10 families, were identified in the reefs off South Caicos (Table 1). Within the 300 m^2 surveyed in detail on the windward side of Long Cay, 33 species were recorded. Only 17 of these species were found at the 9 m pavement. They comprise encrusting species as *S. radians*, *D. clivosa*, and small colonies of massive corals as *S. intersepta* and *M. cavernosa*. The three most frequently occurring corals at this depth were *P. astreoides*, *S. siderea*, and *D. stokesii*, constituting over half of the coral colonies counted. The comparatively largest

Table 1. Coral species and their relative abundance at 9, 18 and 27 m. Additional coral species present around South Caicos, observed outside the belt transects.

Family and Species	9 m	18 m	27 m
ASTROCOENIIDAE			
Stephanocoenia intersepta	5.57%	7.10%	11.43%
POCILLOPORIDAE			
Madracis decactis		0.99%	5.99%
Madracis mirabilis	-	0.90%	-
Madracis formosa	-	-	2.21%
AGARICIIDAE			
Agaricia agaricites			
forma agaricites	-	13.31%	8.94%
forma danai	-	2.94%	2.15%
forma carinata	-	3.59%	2.60%
forma purpurea	-	-	0.40%
Agaricia humilis	-	0.99%	0.11%
Agaricia fragilis	-	2.55%	2.49%
Agaricia grahamae/lamarcki	-	-	2.88%
Leptoseris cucullata	-	0.47%	3.07%
SIDERASTREIDAE			
Siderastrea siderea	17.77%	15.38%	21.51%
Siderastrea radians	3.44%	0.90%	0.34%
PORITIDAE			
Porites porites			
forma porites	3.44%	1.25%	0.28%
Porites astreoides	34.22%	10.02%	15.34%
Porites branneri	2.65%	0.04%	-
FAVIIDAE			
Favia fragum	4.51%	1.08%	0.34%
Montastraea annularis	2.12%	24.64%	1.36%
Montastraea faveolata	-	6.67%	11.20%
Montastraea franksi	-	1.03%	0.34%
Montastraea cavernosa	6.36%	2.07%	2.43%
Diploria clivosa	0.79%	-	-
Diploria strigosa	1.32%	0.30%	-
Diploria labyrinthiformes	0.53%	-	-
Colpohyllia natans	0.53%	0.12%	0.17%
Manicina areolata	0.26%	0.12%	0.45%
MEANDRINIDAE			
Meandrina meandrites	1.32%	0.60%	0.68%
Dichocoenia stokesii	14.59%	1.68%	0.68%
MUSSIDAE			
Mussa angulosa	-	0.08%	-
Scolymia cubensis	-	0.08%	0.51%
Isophyllastrea rigida	0.53%	0.04%	0.06%
Isophyllia sinuosa	-	0.04%	-
Mycetophyllia danaana	-	0.21%	0.68%
Mycetophyllia lamarckiana	-	0.08%	0.06%
CARYOPHYLLIDAE			
Eusmilia fastigiata	-	0.73%	1.30%
Total Number of Species	17	29	26

Species absent in the transects, but present in South Caicos: ACROPOPRIDAE *Acropora cervicornis*, *Acropora palmata*, *Acropora prolifera*; CARYOPHYLLIIDAE *Tubastrea coccinea*; PORITIDAE *Porites colonesis*, *Porites porites forma divaricata*; MEANDRINIDAE *Dendrogyra cylindrus*; MUSSIDAE *Mycetopyllia ferox*

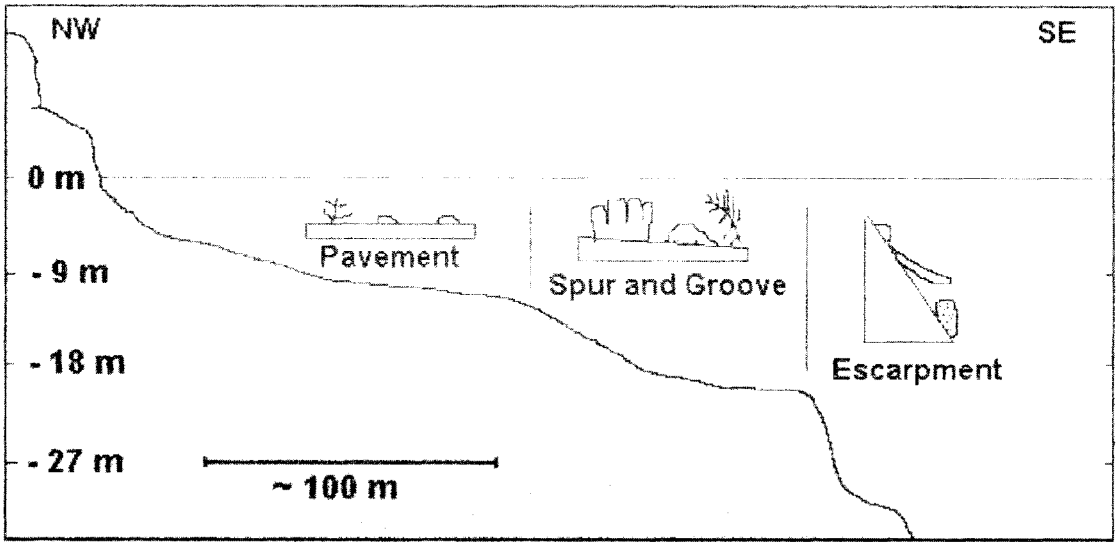

Figure 2. Diagrammatic profile of the study site, perpendicular to the shore of Long Cay, including schematic illustrations of benthic composition.

number of species was recorded at the 18 m spur and groove zone (Table 1, Fig. 1), where an increase in colony size and coral cover was also observed. *S. siderea* was again among the most abundant species, together with *M. annularis* and *A. agaricites.* The columnar colony morphology of *M. annularis* leads to the highest count of individuals per species at 18 m, based on the colony definition "discontinuity of live tissue", used here. It is likely that *S. siderea* and *A. agaricites* outnumber *M. annularis* at this depth, if skeletal entities were used as colony definition. Alternatively, the *A. agaricites* count is comprised of the identified form as *agaricites*, *danai* and *carinata*, which are considered to be distinct species by some researchers. The species presence records from the 18 m spur and groove zone, and the 27 m escarpment, differ in the lack of *P. branneri*, *D. labyrinthiformis* and *M. angulosa* at 27 m (Table 1). The absence of *P. branneri* at 27 m, and its rarity at 18 m, is considered to be an indication of this species depth limits. However, *D. labyrinthiformis* and *M. angulosa* were identified in parts of the reef deeper than 27 m. Deeper parts of the escarpment, at least up to 45 m, appeared similar in species composition. Tabular *M. faveolata* and *Agaricia* sp. increasingly dominated in terms of surface cover.

As species richness increased with depth, so did the number of forms and varieties per species (Table 1). Green, and reddish-brown varieties of *M. faveolata* composed the counts at 18 and 27 m. Folios and tabular morphotypes of the same species start occurring at approximately 30 m, and appear to dominate at depths of 45–60 m. Iridescence was observed in the reddish variety of *M. cavernosa*. At 18 m, two colonies of *D. labyrinthiformes* with peculiarly narrow, yet deep indentations along their meandering ridges were observed. Large colonies of *S. intersepta* (≥0.5 m diameter) were only found in deeper waters (≥20 m). All of these colonies hosted Serpulidae. *C. natans* colonies observed at 30 m had widened grooves.

S. siderea and *P. astreoides* were the bathymetric generalists. *S. siderea* had a persistently high number of colonies at the three depths examined. Similarly, *P. astreoides* was present at various depths, abundant in shallower and more turbulent waters with less

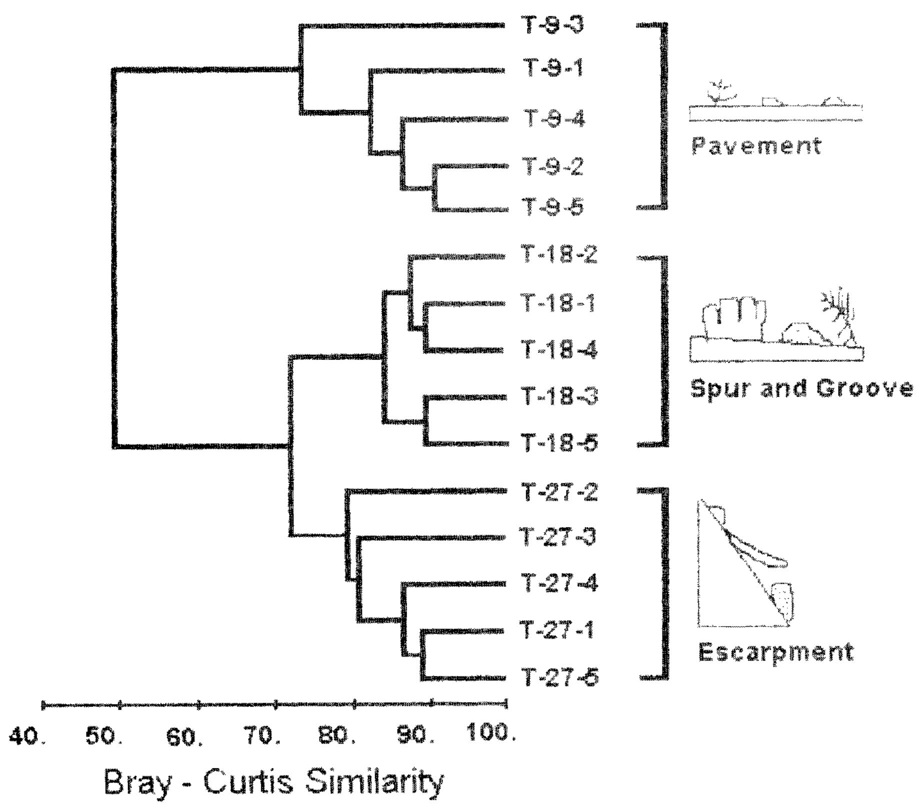

Figure 3. Differentiation of coral assemblages at 9, 18 and 27 m.

apparent spatial competition. *S. siderea*, by contrast, abounded in deeper and denser coral assemblages.

Community Structure.—Three coral assemblages could be differentiated (Table 2, Fig. 3). Each assemblage corresponds to a particular morphological reef zone. The pavement coral assemblage at 9 m (Table 2), had the comparatively lowest species richness (17) and species diversity as expressed by the Shannon and Wiener index (H' = 1.83–2.19), and the most homogeneous distribution of individuals per species (J' = 0.71–0.89). The spur and groove formations at 18 m had the overall highest species richness (29), higher diversity (H' = 2.18–2.29) than the pavement, but displayed the most heterogeneous frequency of occurrence among individual species (J' = 0.71–0.75). Despite equal differences in depth between the three stations, the coral community of the escarpment is similar to that of the spur and groove formation (Table 2), with slight increases in diversity (H'=2.21–2.35), and evenness (J' = 0.73–0.78).

Discussion

Species Presence.—All 32 species previously recorded by Sullivan et al. (1994) were also identified in this study, which reports 40 species. The discrepancy in species richness is due to the larger area surveyed here, and differences in species definition, as in the case of the *M. annularis* species complex (see Weil and Knowlton, 1994). However, accounts of *Agaricia tenuifolia* (Sullivan et al., 1994) could not be confirmed. In situ differentiation of *Agaraicia* spp. is often difficult, but based on a reappraisal of Sullivan's study sites

Table 2. The number of species (species), number of colonies (colonies), Shannon Wiener index of diversity (H'), and Pielou's evenness index (J') for each of the transects 9–1 through 27–5, and ANOVA for each depth.

Transect	Species	Colonies	H'	J'
9–1	12	83	1.89	0.76
9–2	13	90	1.83	0.71
9–3	11	69	1.97	0.82
9–4	11	61	2.13	0.89
9–5	14	74	2.19	0.83
18–1	22	556	2.26	0.73
18–2	21	444	2.29	0.75
18–3	22	392	2.22	0.72
18–4	21	508	2.18	0.71
18–5	21	406	2.22	0.73
27–1	21	310	2.29	0.75
27–2	19	278	2.31	0.78
27–3	18	458	2.21	0.76
27–4	18	295	2.19	0.75
27–5	24	425	2.35	0.74
ANOVA	F = 43.36 df 12 P < 0.001	F = 50.7 df 12 P < 0.001	F = 15.54 df 12 P = 0.002	F = 3.92 df 12 P = 0.048

and the extensive surveys around South Caicos, previously reported *A. tenuifolia* are considered *A. agaricites* forma *danai.*

Solenastrea and *Oculina* have not yet been recorded from South Caicos. This may indicate a zoogeographic trait of these genera. Another attribute of South Caicos may be the relatively high abundance of *P. branneri* as depicted in Humann (1994), or "*Porites branneri*" sensu Weil (1992). It composed 2% of the colonies counted at the 9 m station, and is a common benthic component in sea grass beds among short stands (<5 cm) of *Thalassia testudinum* and *Syringodium filiforme* (pers. observ.).

Forty-eight hermatypic scleractinian corals were documented on the reefs of Discovery Bay in Jamaica, which is considered the center of diversity in the Atlantic (Goreau and Wells, 1973; Stehli and Wells, 1971). Fricke and Meischner (1985) report only 17 species in the Bermudian reefs characterized by the absence of the genera *Acropora*, *Mycetophyllia, Mussa and Colpophyllia* (Veron, 1995). Latitudinally, the Caicos islands are situated between these two locations. With an increase in distance from the center of diversity, a decrease in species could thus be expected.

Obviously, the "promotion" of ecomorphs to species (see *Montastraea* in Weil and Knowlton, 1994; *Porites* in Jameson, 1997), as well as the "demotion" of a species complex to a single species (e.g., *Agaricia* in Zlatarski and Estallela, 1982; *Scolymia* in Fenner, 1993) often undermines the usefulness of earlier field records of species presence and abundance (Knowlton et al., 1992). Ideally, field surveys should include forms and varieties. Data sets would remain valuable whenever growth forms are redefined as species, or the taxonomic position of a coral is changed.

COMMUNITY STRUCTURE.—Bathymetric species distribution and abundance patterns allow the differentiation of coral assemblages between 9 and 27 m (Table 3), reflecting variations of abiotic and biotic parameters. At 9 m, water movement causes a sea floor void of loose coral rubble or sediment accumulations. Turbulence and scouring can limit the settlement and growth of corals (Brown, 1997; Geister, 1977; Sheppard, 1982) and are probably the main physical control of coral growth at 9 m. The species that do tolerate the conditions at the 9 m station (Table 1), occur in comparatively even numbers (Table 3). At 18 m, moderate or "intermediate levels" of water movement sensu Connell (1978), allow a greater variety of corals to flourish. However, suitable hard substrates for coral settlement are limited to the spurs of the spur and groove topography. As sediments are transported along and into grooves, the spurs become the "hard substrate islands" for coral settlement. Limited spatial resources thus contribute to an increase in spatial competition (see Lang and Chornesky, 1990), a potential cause for the increase in heterogeneity of relative abundances evident at 18 m (Table 3). At 27 m, limitations to coral growth again increase, shifting from turbulence to sediment run-off washed across the escarpment by along-shore currents, and the depth limits of zooxanthellate corals. Sheet-like growth forms typical of deeper reefs with lower light regimes (Goreau, 1959; Jackson, 1991) also characterize the escarpment in South Caicos where *M. faveolata* outnumbers its cogener *M. annularis* at 27 m, and *M. faveolata* and *Agaricia* sp. form tabular colonies of up to 3 m in diameter.

The decline of particular coral species, and consequent changes in community structure in the greater Caribbean, have been well illustrated for *Acropora palmata* and *Acropora cervicornis* (Lewis, 1984; Aronson and Precht, 1997; Greenstein et al., 1998). In South Caicos, the brittle *Acropora* spp. are most negatively affected throughout their depth rang by the persistent wave impact powered by easterly Trade Winds. On this windward location, *Acropora* spp. are absent above, and rare below, 9 m. Similarly, Sullivan et al. (1994) describe the absence of *A. cervicornis* accretions at mid-depths. *A. cervicornis* thickets do exist on the leeward side of Long Cay and isolated colonies of *A. cervicornis* can be seen on sand patches at depths of approximately 20 m on the windward side of Long Cay.

Nevertheless, sub-fossil *A. cervicornis* branches of up to 6 cm in diameter form a loosely packed stratum, of undefined breadth, underneath approximately 1–2 m of reef structure, to the East of Cockburn Harbour. It can therefore be assumed that *A. cervicornis* was a more substantial component of older reefs than it is today. Considering reef accretion rates of Holocene reef structures, as discussed and compared in Aronson and Precht (1997), the *A. cervicornis* layer mentioned here can not be linked to the drastic decline of this species within recent decades, yet falls well within time periods of human activity in South Caicos (see Jackson, 1997). Natural disturbances such as hurricanes and disease also remain among the possible causes for the apparent discrepancy between the current and past abundance of *A. cervicornis*. Similar trends may be discernible for *A. palmata* which has a rather narrow depth range, and whose recent declined in dominance was reported from Barbados (Lewis, 1984). *A. palmata* frameworks fringe tidal channels of Cockburn Harbour. This species is also a principal framework element of patch reefs located on the wider shelf along the eastern side of South and East Caicos. However, in 1996 live coral cover on these reefs averaged 3% including *A. palmata*, which had practically disappeared in some areas (pers. observ.).

While measures of biological diversity elucidate the composition of coral assemblages and their comparison on a local scale, direct comparisons of such quantitative data and indices from distinct locations in the Caribbean and Western Atlantic are difficult. Hydrological parameters, the examined depth range, and sampling techniques applied by investigators vary substantially among the studies from Barbados (Ott, 1975), Jamaica (Goreau, 1959; Huston, 1985), Panama (Porter, 1972) and Puerto Rico (Loya, 1976), as reviewed by Liddell and Olhorst (1987). The same holds true for the studies from Colombia (Antonius, 1972), Costa Rica (Cortés and Guzmán, 1985), Curaçao (Bak, 1975), Florida (Burns, 1985), Mexico (Jordan et al., 1981), the northeastern Caribbean (Edmunds et al., 1990), Venezuela (Antonius, 1980) and other works already cited here. It can be said that as in Panama (Porter, 1972; Guzmán et al., 1991), Jamaica (Houston, 1985; Liddell and Olhorst, 1987), and Saba (Edmunds et al., 1990), the higher diversity values determined for South Caicos can be attributed to an "edge effect". In South Caicos favorable conditions around 20 m depth include (a) levels of turbulence that are evidently not an impediment to coral settlement and colony growth, (b) low levels of turbidity coupled with low precipitation (Wanless et al., 1988) and corresponding terrestrial run-off, course sediments (Wanless et al., 1988) which settle within 1–2 d after resuspension from storm events (pers. observ.), and (d) along-shore currents of the Turks Passage inducive to upwelling. Similarly, coral cover is highest between 20–45 m depth, and, although not measured here, certainly exceeds the values of 1.6–6.5% reported for shallower locations by Sullivan et al. (1994).

In conclusion, the South Caicos coral community harbors a comparatively large variety of species in a small area. Suitable hard substrates for coral growth are predominantly on the windward, narrow shelf of the Caicos Platform. There, persistent hydrodynamic disturbances limit coral growth, at least up to depths of about 20 m, where *M. annularis*, *M. faveolata*, and *Agaricia* spp. are currently the main scleractinian components. *S. siderea* and *P. astreoides* are consistently numerous at all depths and thus the most eurybathic species of South Caicos.

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