ORIGINAL ARTICLE

Biodiversity, ecological structure, and change in the sponge community of different geomorphological zones of the barrier fore reef at Carrie Bow Cay, Belize

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Abstract

Changes in the relative abundance of benthic groups on the barrier fore reef at Carrie Bow Cay, Belize, point to a significant reduction of corals and an expansion of the sponge community in 1995–2009. Fifty-one species are now present in the four geomorphological zones of this reef: the low-relief spur-and-groove zone, the inner reef slope, the outer ridge, and the fore-reef slope (to a depth of 30 m). Five species are new additions to the sponge fauna reported for Belize, and six species account for 42.6% of the total assemblage: *Niphates erecta* (9.60%), *Aiolochroia crassa* (8.8%), *Niphates digitalis* (6.9%), *Callyspongia plicifera* (6.63%), *Aplysina archeri* (5.37%) and *Xestospongia muta* (5.37%). Species richness, average density, diversity and evenness indexes are statistically similar in these four zones but some species appear to be more dominant in certain areas. In the same 30 years, coral cover has decreased by more than 90%, while the octocoral cover has greatly increased (by as much as 10-fold in the low-relief spur-and-groove zone). Thus the Carrie Bow fore reef appears to be undergoing a transition from coral dominance in the late 1970s to algae dominance today, with other benthic groups such as sponges and octocorals showing signs of gradual recovery.

Introduction

Sponges have the highest biomass and species richness of the sessile benthic organisms on Caribbean reefs (Diaz & Rützler 2001). These reefs are home to more than 750 sponge species, with as many as 250 species reported for Cuba alone (Diaz *et al.* 2010). The reef system off Belize is of particular interest: first, because it is the largest barrier reef system in the Caribbean, and probably one of the most biodiverse; secondly, because it is impacted annually by hurricanes, as other Caribbean reefs, so that the consequences of this kind of perturbation can be studied in these systems; and thirdly, because the reef there has been under consistent observation since the early 1970s, enabling comparison of its condition then

and at present. Aerial surveys of the Belize reefs, including the Carrie Bow vicinity, provided information on reef structure and changes between 1978 and 1997, when the most striking change was the death of extensive thickets of *Acropora cervicornis* corals on all the Belizean reefs and the invasion of *Lobophora* algae on the resulting coral rubble and other parts of the substrate (Rützler & Macintyre 1982; Macintyre & Aronson 1997). The Caribbean Coral Reef Ecosystem, as a founding member of the Caribbean Community Productivity (CARICOMP) initiative, has recorded physical parameters and biological productivity data on the Carrie Bow reef since 1975, applying the CARICOMP protocol of measurements since 1990. CARICOMP data reported by Koltes *et al.* (1998) indicated the macroalgal cover had increased from 3.4%

in 1980 to about 45% in 1995, and the coral cover had decreased from 30% to 35% in the late 1970s to 12% in 1995. From observations along 10 transects measuring 10 × 1 m each, it was estimated that sponge coverage on the inner fore-reef slope of Carrie Bow Cay ranged between 1.4% and 3.3% in 1995.

An additional characteristic of these reefs not considered before is the topographic structural complexity of this barrier reef and the implications for the community structure of the phylum Porifera. In an early study of the geomorphology and biological communities seaward of Carrie Bow Cay, Rützler & Macintyre (1982) identified five major zones: lagoon, back reef, reef crest, inner fore reef, and outer fore reef. These were said to have developed largely in response to storm-generated water movement and depth. The inner fore reef gives way to the outer fore reef zone at the seaward edge of a low-relief spur and-groove formation (Rützler & Macintyre 1982). Here the reef slope changes abruptly from a gradual to a steep decline (25°), and the substrate consists largely of hard corals and sponges. In view of the marked structural differences between the inner fore reef and outer fore reef as well as the other zones, in this study we compare their sponge communities as to composition, richness, diversity, and density so as to determine whether they have experienced any significant changes over the past 30 years. The presence of a 650-m transect established at the time (marked permanently with a submarine cable and running from the shallow lagoon to the outer reef slope) has served as an important reference for observing temporal ecological changes on this reef, conditions we have taken advantage of in this work.

Methodology

Study area

The Belize Barrier Reef is the largest continuous reef system in the Western Atlantic, extending 257 km from Ambergis Cay south of Yucatán to the Gulf of Honduras; with its lagoon, it measures 10–32 km across. The reef complex consists of three regions as defined by biogeomorphic characteristics: the northern, central, and southern provinces (Burke 1982, 1993, cited by Koltes *et al.* 1998). Carrie Bow Cay lies in the central province 18 km offshore, at 16°48.1′ N and 88°04.9′ W and lies on the top of the Belize Barrier Reef (Fig. 1). The reef at Carrie Bow is separated from the main barrier trend by two channels, South Water Cut to the north (0.4 km wide and 4 m deep) and Carrie Bow Cut to the south (0.7 km wide and 5 m deep; Fig. 1). The present study took place in August 2009 and focused on four zones of the fore reef (outside the reef crest) as defined by Rützler & Macintyre

(1982): the low-relief spur-and-groove zone (SG), inner reef slope (IRS), outer ridge (OR), and fore-reef slope (FRS; Fig. 2).

The main characteristics of these zones are summarized in Table 1.

Species composition and abundance were recorded for sponges living exposed (noncryptic) in the four reef zones. In each zone, data were collected along three transects, each measuring 60 m^2 (30 m long × 2 m wide). These were laid at right angles to Rützler and Macintyre's submarine cable (Fig. 3) and placed at random in the four zones. The coverage of five benthic taxa and two substrate categories (corals, sponges, gorgonians, algae, tunicates, coral rubble and sand) was estimated using 35 frames 1-m^2, laid alternatively at opposite sides of each transect (up and down). Each frame was photographed and interpreted in the lab with the Coral Point Count with EXCEL EXTENSIONS (CPCe) Program, version 3.6 (Kohler & Gill 2006).

Data analysis

Species diversity and evenness for sponge assemblages in each zone were determined with the Shannon index (H′) and Pielou index (J), respectively. The average density, diversity, and evenness were compared among zones using a nonparametric analysis of variance (Kruskal–Wallis test) after checking for homogeneity of variance. Similarities were analysed (ANOSIM, one-way analysis) with the Bray–Curtis distance to test for significant differences in the composition of the sponge assemblages among zones. If differences were detected, the contribution of different species to average between-zones dissimilarity (discriminating species) and within-zone similarity (characteristic species) was assessed using similarity percentage (SIMPER) analysis (Clarke 1993) with the software PRIMER 6 (Plymouth routines in multivariate ecological research). The ordination technique used to explore these patterns was nonmetric multi-dimensional scaling (MDS). The SIMPER analysis and MDS were performed after removing species that contributed <1% to the dataset.

Results

Richness and species composition

A total of 41 sponge species and 789 individuals were counted along the 12 transects (Table 2). Ten more species were found outside the transects: *Agelas cerebrum* Assman, van Soest & Köck, 2001; *Agelas dilatata* Duchassaing & Michelotti, 1864; *Agelas sventres* Lehnert & van Soest, 1996; *Callyspongia* (*Callyspongia*) *densasclera*
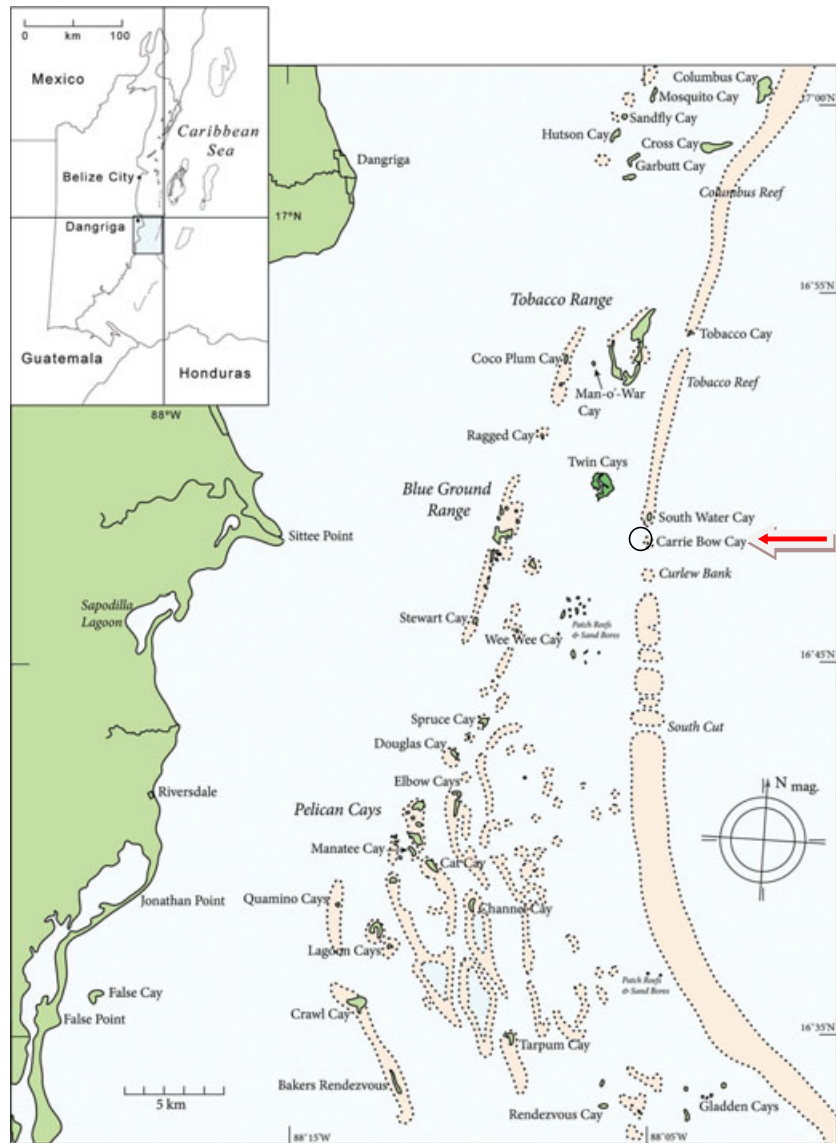
Fig. 1. Location of Belize Barrier Reef and other reef tracts (pink color) and Carrie Bow Cay (indicated with a black circle and a red arrow). From Rützler (2009).

Lehnert & van Soest, 1999; *Chondrila caribensis* Rützler, Duran & Pantioni, 2007; *Cliona aprica* Pang, 1973; *Cliona tenuis* Zea & Weil, 2003; *Cynachirella kuekenthali* (Uliczka, 1929); *Ircinia campana* (Lamarck, 1816) and *Topsentia ophiraphidites* (de Laubenfels, 1934). The total count was 51 sponge species for this part of the Carrie Bow reef, representing 30% of the 188 species reported for all mangrove and reef habitats in this part of Belize (Diaz *et al.* 2010, http://marinespecies.org/porifera/). Five species are new additions to the sponge fauna reported for Belize: *Agelas* cf. *inaequalis* Pullitzer-Finalli, 1986, *Callyspongia (Cladochalina) armigera* (Duchassaing & Michelotti, 1864), *Callyspongia (Cladochalina) plicifera* (Lamarck, 1813), *Callyspongia (Cladochalina) densasclera* Lehnert & van Soest, 1999, and *Oceanapia bartschi* (de Laubenfels, 1934). The most abundant species on the reef

were *Niphates erecta* (77 individuals, 9.60%), *Aiolochroia crassa* (70 individuals, 8.8%), *Niphates. digitalis* (55 individuals, 6.9%), *Callyspongia (C.) plicifera* (53 individuals, 6.63%), *Aplysina archeri* (43 individuals, 5.37%), and *Xestospongia muta* (43 individuals, 5.37%). These represent 42.6% of the total abundance of the sponge assemblage. A total of 32 species (71.1%) appeared in both the low-relief spur-and-groove zone and outer fore reef, 19 of which were recorded in all four study zones.

Spatial variability

Species richness in the four reef zones was very similar (31–33 species). Furthermore, no significant differences were detected in the average density of individuals, average diversity index, or average evenness index among the
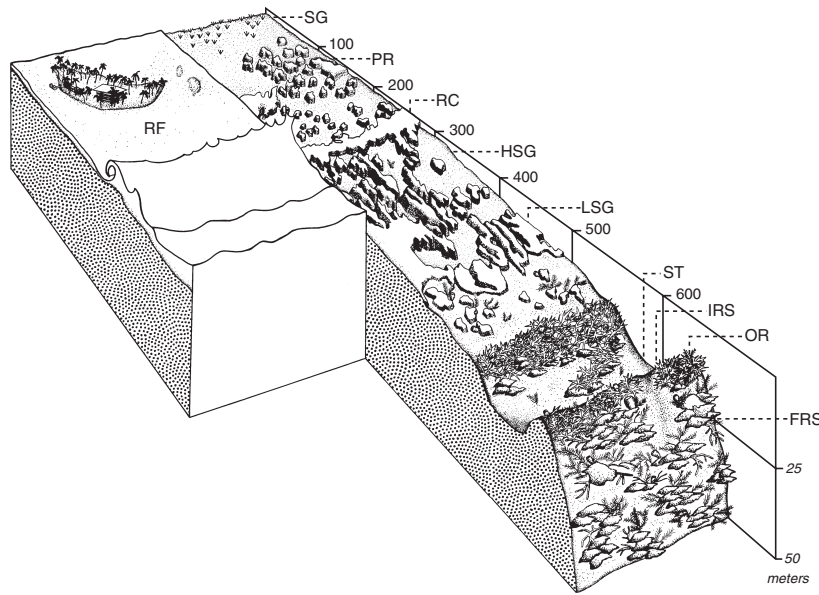
Fig. 2. Block diagram of reef zonation at Carrie Bow Cay (from Rützler & Macintyre 1982, fig. 31). FRS, fore-reef slope; HSG, high spur and groove; IRS, inner reef slope; LSG, lower spur and groove; OR, outer ridge; PR, patch reefs; RC, reef crest; RF, reef flat; SG, seagrass; ST, sand trough.

Table 1. Habitat characteristics of the four reef zones surveyed in the present study.

zone name and depth range	habitat description
low-relief spur and groove (LSG); 10–15 m	Coral spurs of low relief alternate with sandy grooves. Mostly sand-covered hardground with scattered coral heads, gorgonians, and sponges. *Acropora cervicornis* rubble covered by *Lobophora* sp. and *Dictyota* sp. Slope measures between 10° and 15°.
inner reef slope (IRS); 15–23 m	Reef slope of approximately 45°. Platy or leaf-like corals, such as *Agaricia agaricites* and *Leptoseris cucullata*, and tubular or vase sponges are the dominant species. Calcareous algae cover many coral surfaces. Sandy patches at the base of the slope.
outer ridge (OR); 12–14 m	Coral ridge densely covered by *Lobophora* sp., *Dictyota* sp., and *Amphiroa* sp. High abundance of gorgonians. Scattered colonies of *A. cervicornis* and *Porites astreoides*.
fore-reef slope (FRS); 15–30 m (reaches 50 m)	Reef slope of 50–70°. Bottom dominated by *Lobophora* sp. and calcareous algae. Scattered coral rubble. Various sponge species are widespread over the entire slope.

Fig. 3. Panoramic view of outer fore-reef slope. Transect line (white) tied to Rützler and Macintyre's submarine cable (indicated with a red arrow).

four zones (Table 3). However, some species were more dominant in particular reef zones. The most abundant species in the low-relief spur-and-groove zone was *Scopa-* *lina ruetzleri* (16.95%), followed by *Callyspongia (Cladochalina) plicifera* (10.73%), while *Niphates erecta* (10.95%) and *Niphates digitalis* (10%) were dominant on the outer ridge. *Aiolochroia crassa* (17.7%) was notably dominant on the inner reef slope and *N. erecta* (13.2%) on the fore-reef slope.

Although species diversity was much the same among zones, one-way ANOSIM analysis (R = 0.5139, P = 0.0008) showed significant differences in composition and relative abundance. Pairwise comparisons, with Bray–Curtis dissimilarity dBC, indicated less dissimilarity between the low-relief spur-and-groove zone and outer ridge (dBC = 53.82) than between the LSG and either the

Table 2. Abundance (number of individuals) of sponge species identified in 12 transects of 60 m², each laid in the low-relief spur-and-groove and outer reef zones in Carrie Bow Cay Reef.

species	abundance
1. *Agelas clathrodes* (Schmidt, 1870)	1
2. *Agelas conifera* (Schmidt, 1870)	27
3. *Agelas* cf. *inequalis* Pulitzer-Finali, 1986	1
4. *Agelas wiedenmayeri* Alcolado, 1984	27
5. *Aiolochroia crassa* (Hyatt, 1875)	70
6. *Siphonodictyum coralliphagum* Ruetzler	3
7. *Amphimedon compressa* Duchassaing & Michelotti, 1864	30
8. *Aplysina archeri* (Higgin, 1875)	43
9. *Aplysina cauliformis* (Carter, 1882)	11
10. *Aplysina fistularis* (Pallas, 1766)	39
11. *Aplysina fulva* (Pallas, 1766)	6
12. *Callyspongia (Cladochalina) plicifera* (Lamarck, 1814)	53
13. *Callyspongia (Cladochalina) armigera* (Duchassaing & Michelotti, 1864)	3
14. *Callyspongia (Cladochalina) vaginalis* (Lamarck, 1814)	6
15. *Chondrilla caribensis* Ruetzler, Duran & Piantoni 2007	1
16. *Cinachyrella kuekenthali* (Uliczka 1929)	3
17. *Cliona varians* (Duchassaing & Michelotti, 1864)	4
18. *Cliona caribbaea* Carter, 1882	7
19. *Cliona delitrix* Pang, 1973	20
20. *Ectyoplasia ferox* (Duchassaing & Michelotti, 1864)	24
21. *Geodia gibberosa* Lamarck, 1815	3
22. *Geodia neptuni* (Sollas, 1886)	20
23. *Ircinia felix* (Duchassaing & Michelotti, 1864)	21
24. *Ircinia strobilina* (Lamarck, 1816)	30
25. *Ircinia variabilis* (Schmidt, 1862)	1
26. *Monanchora arbuscula* (Duchassaing & Michelotti, 1864)	1
27. *Mycale laevis* (Carter, 1882)	8
28. *Mycale laxissima* (Duchassaing & Michelotti, 1864)	12
29. *Neofibularia notilangere* (Duchassaing & Michelotti, 1864)	4
30. *Niphates digitalis* (Lamarck, 1814)	55
31. *Niphates erecta* Duchassaing & Michelotti, 1864	77
32. *Oceanapia bartschi* (de Laubenfels, 1934)	1
33. *Petrosia pellasarca* (de Laubenfels, 1934)	14
34. *Plakinastrella onkodes* Uliczka, 1929	14
35. *Plakortis angulospiculatus* (Carter, 1882)	17
36. *Scopalina ruetzleri* (Wiedenmayer, 1977)	32
37. *Svenzea zeai* (Alvarez, van Soest & Ruetzler, 1998)	32
38. *Verongula gigantea* (Hyatt, 1875)	1
39. *Verongula reiswigi* Alcolado, 1984	7
40. *Verongula rigida* (Esper, 1974)	17
41. *Xestospongia muta* (Schmidt, 1870)	43
Abundance total	789

inner reef slope (dBC = 58.49) or the fore reef slope (dBC = 60.71). Also, the fore reef slope was less dissimilar to the inner reef slope (dBC = 53.8) than to the outer ridge (dBC = 56.48). Otherwise, the fore reef slope and inner reef slope showed a greater within-zone average similarity (62.54 and 54.27, respectively) than the low-relief spurs and outer ridge (50.28 and 50.97, respectively). As the MDS plots (Fig. 4) show, samples along transects from the two slopes show segregation (in the first axis) in comparison with the samples from the two ridges, whereas those from the outer reef slope show less dispersion and clear separation in comparison with samples from the low-relief spur-and-groove zone. Species contributing more than 10% to average within-zone similarity (characteristics species of each zone) are shown in Table 4.

The species showing most dissimilarity between zones (discriminating species) are shown in Table 5.

The pattern of average abundances of this species in each zone is shown in Fig. 5.

The species *A. crassa* and *Scopalina ruetzleri* contributed most to the overall difference between zones. *Aiolochroia* also showed the second highest relative abundance across zones (8.75%). This species was registered in 11 of the 12 transects, but with a statistically significant greater abundance on the inner reef slope (IRS). *Scopalina ruetzleri* occurred only on the ridges, with a noticeable high abundance on the low-relief spur-and-groove ridge (LRSG). *Niphates erecta* is the most abundant species in the area and shows a gradual and slight increase from the low-relief spur and groove to the fore reef slope (Table 5). Three of the remaining species were more abundant on the inner reef slope: *Agelas conifera*, *Amphimedon compressa*, and *Plakortis angulospiculatus*. There was a lower abundance of *Callyspongia (C.) plicifera* and *Ircinia strobilina* in this zone of the reef. Table 6 compares the discriminant species between zone pairs.

Coverage by the benthic components

The benthic cover on Carrie Bow reef consists in large part of algae (>60%), represented by *Lobophora variegata* (J. V. Lamouroux) and some dominant species of the genera *Dictyota*, *Halimeda*, and *Amphiroa*. Abiotic components of coral rubble are second in importance (Table 7). Hermatypic coral cover, on the other hand, is very sparse (≤7.25%), with no difference between the low-relief spur-and-groove zone and the outer fore reef zone. Octocoral and sponge cover is also low, with a slightly higher incidence of both on the outer reef slope than in the spur-and-groove zone. All in all, the barrier fore reef at Carrie Bow Cay appears severely stressed and in danger of becoming a seaweed community.

Table 3. Diversity and quantitative distribution of sponges in the reef zones studied.

parameter	LSG	IRS	OR	FRS	KW	P
no. of species/transect	21 (3)	18.3 (2.5)	18.7 (3.1)	21.3 (5.5)	1.51	0.68
total no. of species	33	30	33	31		
no. of individuals m^{-2}	0.98 (0.07)	1.16 (0.18)	1.17 (0.28)	1.13 (0.41)	1.24	0.74
total no. of individuals	177	209	210	204		
H' (diversity)	2.70 (0.24)	2.59 (0.05)	2.65 (0.16)	2.77 (0.25)	0.35	0.95
J (evenness)	0.89 (0.05)	0.89 (0.03)	0.91 (0.01)	0.91 (0.01)	1.46	0.69

Values in parentheses are the standard deviation and P is the significance value of the Kruskal–Wallis statistic (KW).
FRS = fore-reef slope; IRS = inner reef slope; LSG = lower spur and groove; OR = outer ridge.
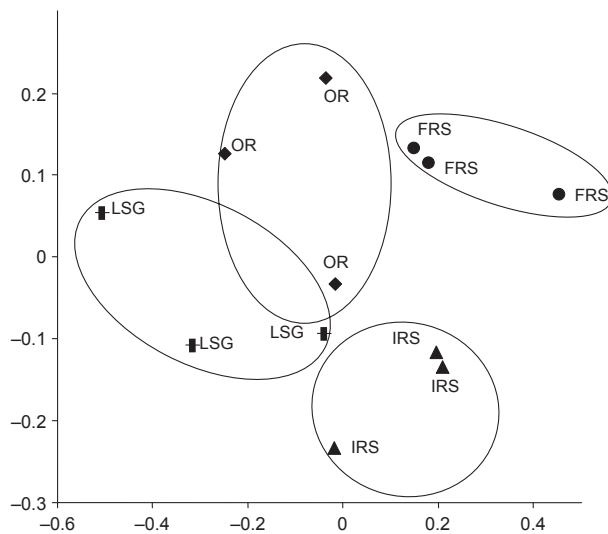
Fig. 4. Nonmetric multidimensional scaling ordination of transects at each of the four zones; stress = 0.22. FRS, fore-reef slope; IRS, inner reef slope; LSG, lower spur and groove; OR, outer ridge.

Discussion

Sponge community assemblage on Carrie Bow Reef

The species assemblage of sponges on Carrie Bow's fore reef is similar to that on other Caribbean reefs, with a large number of species but few individuals. There is also a small number of very abundant (dominant) species: *Aiolochroia crassa, Aplysina archeri, Callyspongia (Cladochalina) plicifera, Niphates digitalis, Niphates erecta,* and *Xestospongia muta. Niphates erecta* dominance has been observed elsewhere in the Caribbean, notably Dos Mosquises Key in Los Roques, Venezuela (Alvarez *et al.* 1985, Díaz *et al.* 1985), five other Los Roques locations (Villamizar, Diaz, Perez, Yranzo, Romero, in preparation), Golfo de Uraba reefs in Colombia (Valderrama & Zea 2003), Key Largo, Florida (Engel & Pawlik 2005), and Bocas del Toro, Panamá (Gochfeld *et al.* 2007). The sponge is a recognized opportunistic species noted for its eurytopic character (high tolerance to different environmental conditions) and high

Table 4. Analysis of percentage similarity (SIMPER) to detect the characteristic species responsible for within-zone similarity (similarities among transects for each zone). Only species with a percentage contribution ≥10% are reported.

| zone	species	As	As/DE(As)	contribution %	cumulative contribution %
LSG (As = 50.3)	*Callyspongia (C.) plicifera*	7.0	3.2	13.9	13.9
	Niphates digitalis	6.4	5.9	12.7	26.6
	Scopalina ruetzleri	6.4	0.6	12.6	39.2
IRS (As = 54)	*Aiolochroia crassa*	12.0	10.6	31.4	31.4
	Niphates erecta	5.7	4.3	12.5	43.9
	Aplysina archeri	4.0	6.0	10.0	53.4
OR (As = 50.9)	*Niphates erecta*	10	20.9	19.9	20.0
	Niphates digitalis	8.6	21.2	16.8	36.8
	Callyspongia (C.) plicifera	7.4	6.8	14.6	51.4
	Ircinia strobilina	7.1	4.3	13.9	65.3
FRS (As = 62.5)	*Niphates erecta*	9.1	2.5	14.6	15.0
	Amphimedon compressa	8.5	14.85	13.6	28.6
	Agelas conifera	7.4	15.1	11.8	40.4
	Plakortis angulospiculatus	6	2.5	10.1	50.0

As = average similarity; As/De(As) = ratio of average similarity to its standard deviation; FRS = fore-reef slope; IRS = inner reef slope; LSG = lower spur and groove; OR = outer ridge.

Table 5. Results of a SIMPER analysis of the four zones combined with statistical tests for significant differences in average abundances for each species. The species are listed in order of their contribution to the average Bray–Curtis dissimilarity (54.8) of the four zones.

species	contribution	cumulative contribution%	average abundance (ind·transect^{-2})				total abundance
			LSG	IRS	OR	FRS	
Aiolochroia crassa	5.0	9.0	3.7	12.3	4	3.3	70
Scopalina ruetzleri	4.5	17.17	10	0	0.7	0	32
Callyspongia (C) plicifera	3.5	23.5	6.3	4.3	6	1	53
Niphates erecta	3.2	35.11	3.33	5.67	7.67	9	77
Ircinia strobilina	2.4	68.31	2.7	1.7	5.3	0.3	30
Amphimedon compressa	2.4	63.98	0.7	2	1.3	6	30
Agelas conifera	2.2	76.51	0.7	1.7	1.3	5.3	27
Plakortis angulospiculatus	2.1	80.34	0.7	0.3	0	4.7	17

For each species, shaded and unshaded average abundances indicate zones that differ significantly from each other.
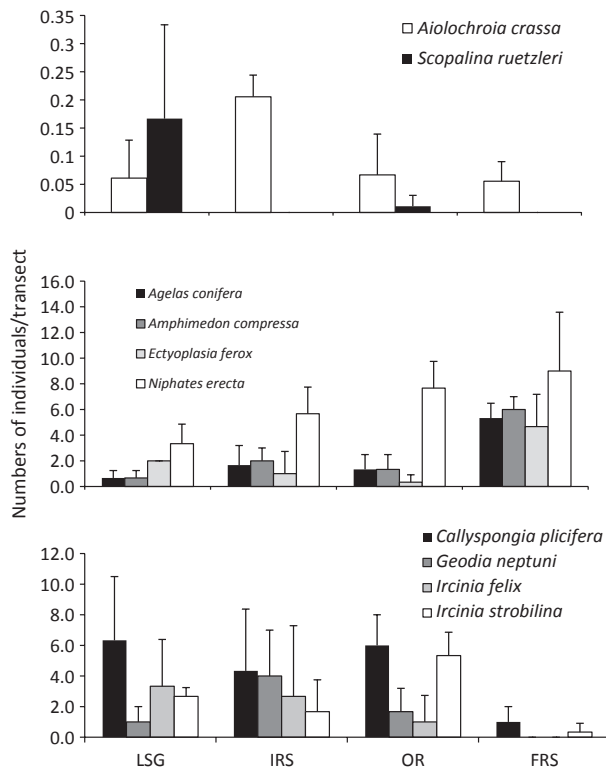
Fig. 5. Average abundance of the sponge species for the four zones studied at Carrie Bow Cay in 2009. FRS, fore-reef slope; IRS, inner reef slope; LSG, lower spur and groove; OR, outer ridge.

population recovery when decimated by storms (Valderrama & Zea 2003, Stevely *et al.* 2011). Being chemically undefended, *Niphates* species are palatable to predatory fishes, but they have a higher growth rate than unpalatable species (Pawlik 2011). The same could be true for *A. crassa*, which has the highest frequency of occurrence in this study (although a lower relative abundance than *N. erecta). Aiolochroia crassa* is also among the dominant

species in Los Roques in the Southern Caribbean and Isla de Aves in the Northeast Caribbean (Villamizar *et al.* in preparation). A study of sponge distribution in three oceanic reef complexes in the Southwestern Caribbean has found that only two species exceed a 60% frequency of occurrence in that location, *N. digitalis* in one reef complex and *A. crassa* in two (Zea 2001). Some aspects of the life history of *A. crassa* may account for its wide distribution, particularly its antifouling properties (Kelly *et al.* 2005, Pawlik *et al.* 2008) and its antipredatory defense (Pawlik *et al.* 2008). Both are advantageous traits on frequently disturbed reefs with a high macroalgae cover, such as those at Carrie Bow Cay. These various biological and ecological characteristics could explain the wide dominance of these two sponges on reefs and in other marine habitats. However, this needs further exploration.

Comparison of sponge community parameters between reef zones

Water depth, distance from the island shore, and structural differences between the four reef zones in the study area appear to have no significant effect on the number of species (30–33), average density of individuals, and average diversity and evenness indices. This similarity could be related to the nearly uniform reef bottom in the four zones (homogeneity), all of which have lost much of their coral reef framework, have a very sparse cover of live coral, and a high proportion of macroalgae and coral rubble (Table 7). The heterogeneity of substrate is thought to be a very important factor for the settlement of sponges, as the more heterogeneous the substrate is, the more species it can support (Sará & Vacelet 1973). The more exposed habitats on the Carrie Bow reef are probably structurally less complex than 20 years ago (more homogeneous). However, other factors, as yet unknown, may be at play on the outer reef slope, where

Table 6. Species responsible for the differences between zones of sponge communities (according to their average abundance).

	low-relief spur and groove	inner reef slope	fore reef ridge
low-relief spur and groove	*Scopalina ruetzleri* *Aiolochroia crassa* *		
outer ridge	–	*Aiolochroia crassa*	
fore reef slope	*Scopalina ruetzleri* *Callyspongia (C) plicifera* *Ircinia strobilina* *Amphimedon compressa** *Agelas conifera** *Plakortis angulospiculatus**	*Aiolochroia crassa* *Callyspongia (C) plicifera* *Ircinia strobilina* *Amphimedon compressa** *Agelas conifera** *Plakortis angulospiculatus**	*Scopalina ruetzleri* *Callyspongia (C) plicifera* *Ircinia strobilina* *Amphimedon compressa** *Agelas conifera** *Plakortis angulospiculatus**

An asterisk indicates the species is more abundant in the zone specified in that row; those without an asterisk are more abundant in the zone of the corresponding column.

Table 7. Average percent cover and standard deviation by benthic organisms and substrates on the inner and outer fore reef at Carrie Bow Cay, Belize; August 2009. The abiotic category represents sand and coral rubble; the algae include macroalgae and turf algae over sand or dead coral.

	benthos		component		
site	algae	sponges	Hermatypic Scleractinia	Gorgonacea	Abiotic substrata
low-relief spur- and-groove zone	61.19 ± 27.09	2.63 ± 5.02	7.25 ± 4.83	5.22 ± 4.32	23.30 ± 27.24
fore reef slope	70.99 ± 9.27	4.61 ± 4.61	5.48 ± 4.68	8.29 ± 6.33	27.26 ± 17.94
P-value (n = 35)	0.05	0.09	0.13	0.02	0.48

The statistical significance (P-value) of the mean difference is reported.

many crevices and cryptic caverns harbor a distinct and diverse sponge community. Sponge density in the Carrie Bow low-relief spur-and-groove zone and outer fore reef zone is not unlike that observed in a structurally similar habitat extending from the back reef to outer reef at South Water Cay, located about 1 km north of Carrie Bow Cay. Densities there range from 0.21% to 1.25% (Wilkinson & Cheshire 1990). However, results at Carrie Bow are not entirely comparable because no surveys were made of its back reef. Average densities at Carrie Bow are rather low (0.98–1.17 ind·m^{-2}) compared with those at other Caribbean locations, although values vary greatly from one location to another. They range from 3.3 to 17.5 ind·m^{-2} on reefs in the Florida Keys (Schmahl 1990) to 5 ind·m^{-2} on Dos Mosquises Sur, a reef at Los Roques, Venezuela, Díaz *et al.* 1985), but that figure appears to have dropped to <2 ind·m^{-2} in recent surveys (Villamizar *et al.* in preparation). In Cuba, lower densities are in the range of 3.5–3.3 sponges·m^{-2} (Alcolado 1999), but in the Gulf of Urabá, Colombia, they range from 0.175 to 13.325 sponges·m^{-2} (Valderrama & Zea 2003), probably in response to terrigenous nutrient input. At the high end, values from Bocas del Toro, Panamá, average 38.1–90.7 ind·m^{-2} (Gochfeld *et al.* 2007). However, note that the estimated standard at the last three study sites is close to 50%. As already mentioned, sponge richness, abundance, and density at depths of 10–30 m

are similar in all four zones investigated at Carrie Bow. By contrast, these characteristics increase with depth on Davies Reef (Queensland, Australia; Wilkinson & Evans 1989). As widely established, the structure of reef sponge communities depends in large part on environmental conditions (light, currents, turbulence, slope, and substrate availability and type), and to a lesser degree on biological interactions (recruitment, predation, competition). There is also a strong correlation between sponge distribution and factors that change with depth (*i.e.* turbulence, light intensity, and competition with photosynthetic, fast-growing organisms; Valderrama & Zea 2003). In general, species richness and density tend to be low in shallow environments exposed to waves and high light intensity, and gradually increase with depth (Alcolado 1979, Díaz *et al.* 1985, Schmahl 1990; Zea 2001). After examining combinations of diversity and equitability indices for sponge communities at 112 sites (pairs of H' and J), Alcolado (1992) proposed 11 'environmental inference zones or classes' of ecological situations. Since diversity and equitability indexes are similar in all four zones examined at Carrie Bow, it can be said that they are subject to approximately similar ecological conditions, defined by Alcolado as 'moderately severe and constant' (number 8 in his inference diagram). Where the four zones at Carrie Bow do differ markedly is in the species composition or relative abundance within each

reef section. *Scopalina ruetzleri*, for example, was present only on the outer ridge and in the low-relief spur-and-groove zone, whereas *Aiolochroia crassa* was highly dominant on the inner reef slope. By the same token, *Callyspongia (Cladochalina) plicifera* and *Niphates digitalis* are characteristic of the ridges (LSG and OR), where they occur in higher abundance than on the slopes (IRS and FRS). On the other hand, *Niphates erecta* shows a clear pattern of increasing abundance from the low-relief spur-and-groove zone to the outer fore reef. The distribution or absence of these species in the different zones of the reef seems to depend on the depth gradient of the slopes, with its accompanying changes in light intensity, sedimentation, and currents. Therefore population analysis (relative abundance, density, size structure, etc.) may be a better indicator of environmental conditions at different sections of the reef than community parameters (such as richness, diversity or equitability) – at least for the species just mentioned. At the same time, the influence of hazard or stochastic processes cannot be overlooked in the structural development of these systems. Such influences would include hurricanes in the West Caribbean (physical disturbance) and the unpredictable availability during larval dispersal of bare hard substrate for colonization. When Zea (2001) compared sponge communities in three remote oceanic reef complexes of the Southwestern Caribbean, distribution patterns appeared to be stochastic, both at small and large scales, and only weakly related to major environmental variables. By contrast, sponge distribution at the Carrie Bow study sites does not seem strongly stochastic. Certain species are clearly more abundant in specific zones – *S. ruetzleri* at the LSG, *A. crassa* at the IRS, *N. digitalis* and *N. erecta* at the OR, and *Amphimedon compressa*, *Plakortis angulospiculatus* and *Agelas conifera* at the FRS. The cryptic habitats in these reef regions, especially on the reef slopes (where platy corals are predominant), obviously need further investigation to complete the picture of their sponge-associated communities.

Temporal community changes on Carrie Bow Reef

Since 1977 the communities and substrates of the Carrie Bow reef appear to have undergone many changes, as established in the early 1990s in a survey of the fore reef zones along a research transect starting at a depth of 14 m (Macintyre & Aronson 1997). In 1978 the shallower section of the outer ridge was covered by live *Acropora cervicornis*, but by the 1990s it was covered mainly by *A. cervicornis* rubble and the algae *Lobophora variegata*. A high cover of macroalgae was also observed in the present study, *L. variegata* being one of the most abundant (average coverage of the reef bottom: 55.41–61.19%). How-

ever, sponges and octocorals were also fairly abundant in this zone. In the 1990s the fore reef slope supported platy growths of *Montastraea annularis* (probably *Montastraea faveolata*) (Macintyre & Aronson 1997), but no mention is made of sponges in this zone. However, in our 2009 survey, sponge coverage in exposed habitats approached 4.61% (Table 7). The inner reef slope showed striking changes as well, from a substrate dominated by thickets of *A. cervicornis* in the 1970s to *M. annularis* with columnar growths and *A. cervicornis* rubble covered by *Lobophora* in the 1990s. By 2009 the low-relief spur-and-groove zone was supporting a variety of sponges and octocorals, as well as a dense cover of *L. variegata*. Interestingly, in the 1990s the substrate of the inner ridge consisted of a hardground dominated by octocorals and scattered coral heads and sponges, much like the conditions just described in the LSG almost 20 years later, although a dense cover of macroalgae was also present in this zone at the later date. The changes in relative abundance of benthic groups become even clearer when the coverage of corals, octocorals, sponges, and algae in 1995 (CARICOMP data, Table 8) is compared with that in 2009 (Table 7). Coral coverage has decreased by more than 90% since 1995, whereas octocoral cover has increased almost 10-fold (in the LSG) in the same period. The sponge cover has also increased since 1995, and the extent of the abiotic component has increased as well.

All information to date, including ours, indicates that the Carrie Bow reef is in a transition phase, changing from coral dominance in the late 1970s to algae dominance today, and that other benthic groups, such as sponges and octocorals, are undergoing a slow recovery. Because corals are the main builders of reef frame structure, the disappearance of *A. cervicornis* from Belizean reefs is of wide concern. Its demise was attributed to an outbreak of white-band disease in the 1980s (Peters 1993; Aronson & Precht 1997; Macintyre & Aronson 1997), as occurred on other Caribbean reefs. However, by 2009 some healthy patches of *A. cervicornis* colonies were beginning to appear, which suggests a partial recovery of

Table 8. Percent cover of benthic organisms at CARICOMP Coral Reef Sites I and II, Carrie Bow Cay, Belize; August 1995. Mean of five 10-m transects per site surveyed as part of semiannual CARICOMP monitoring (see CARICOMP 1994, for a description of methods). Algae include macrophytes (fleshy and calcareous), turf algae, and cyanophytes. Both sites are in the inner reef.

	benthos		component		
site	algae	sponges	Hermatypic Scleractinia	Gorgonacea	Abiotic substrata
I	65.8	1.4	12.3	2.3	18.2
II	52.7	3.3	20.9	1.0	22.2

this species on the Carrie Bow reef. The decline of coral species on Belizean reefs could be due to other factors as well. As McField (1999) has pointed out, many reefs in the Caribbean bleached repeatedly throughout the 1980s and early 1990s, whereas the reefs of Belize did not suffer a widespread bleaching event until the summer of 1995, when approximately 10% of all coral colonies were affected by some partial tissue mortality. Although Carrie Bow Cay is not included among McField's study sites (11 sites along the Belize Barrier Reef), this result can be extended to it. According to Rützler & Macintyre (1982), the inner fore reef (1–12 m deep) is strongly affected by storm waves and waves related to normal trade winds, whereas the outer fore reef (>12 m deep) is affected only by long period storm waves. At least eight hurricanes have struck Belize since 1998 (Mitch, Keith, Iris, Dean, Alberto, Karl, Alex, and Richard), probably with considerable impact on the barrier reef, including Carrie Bow, in some instances. When Hurricane Mitch made landfall on the Honduras coast in October 1998, for example, its consequences were felt in the Belizean reefs. Data from the Coastal Zone Color Scanner (CZCS) sensor aboard the Nimbus-7 satellite and SeaWiFS imagery show that terrestrial enrichment is a possible mechanism for massive smothering of a reef by sediments and simultaneous fertilization (Andrefouet et al. 2002). The time series revealed unsuspected connectivity patterns along the Meso-American barrier reef system that leave no doubt as to the consequences of such events for the structure of reef communities. So far, the extent of the damage caused by these hurricanes on the inner or outer fore reef of Carrie Bow Cay is not fully known, but such events may well be responsible for much of the missing physical structure of the reef.

Conclusions

The benthic community of the reef at Carrie Bow Cay is in a phase of transition, as is the case for many Caribbean reefs. The Carrie Bow reef is strikingly dominated by macroalgae and coral rubble, but a diverse sponge community of low density is also present, alternating with octocorals and, to a lesser extent, hard corals. Species richness, density of individuals, diversity, and evenness of sponge community do not differ in the four zones studied (LSG, IRS, OR, FRS). However, there are significant differences in composition and relative abundance of sponge species, as indicated by the Bray–Curtis dissimilarity index (54.8) calculated for the four zones. The differential abundance of species in these zones suggests that the distribution and abundance of sponge species are mainly of a deterministic nature. The relative importance of the different environmental and biological

factors acting on this sponge community has yet to be established.

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