PATTERNS OF SPONGE (PORIFERA, DEMOSPONGIAE) DISTRIBUTION IN REMOTE, OCEANIC REEF COMPLEXES OF THE SOUTHWESTERN CARIBBEAN[1]

by

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Abstract

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Sponge abundance data were obtained in depths from 2.5 to 22 m at Albuquerque Cays, Serrana Bank and Roncador Bank, three remote atolls of the Southwestern Caribbean Sea (San Andrés and Old Providence Archipelago, Colombia). Although the number of sponge species (96 overall, 52 to 61 per atoll) was comparable to that in reef areas in the continental shelves, the density (atoll means 22.5 to 58.3 ind.20m^{-2}) was noticeably lower, possibly due to lower amounts of suspended organic matter. Cluster and Correspondence Analyses of stations showed that sponge distribution patterns were apparently stochastic, both at small and large scale, and only weakly related to major environmental variables. Inverse Analysis, however, revealed that the majority of sponges had marked habitat preferences, but that their within-habitat distribution was patchy. Short-distance dispersal of free-living larvae and migration of adults by rafting, coupled to the remoteness of the atolls, implies that the identity and timing of arrival of propagules is a random event. Together, the local proliferation of founder populations and the haphazard effect of perturbations, give rise to a strong heterogeneity, in a scale of tens of meters to hundreds of kilometers, in the dominance within the same habitat type.

Key words: Sponges, Porifera, Distribution, Stochastic, Caribbean.

Resumen

Se obtuvieron datos de abundancia de esponjas en profundidades entre 2.5 y 22 m en Cayos Albuquerque, Banco Serrana y Banco Rondador, tres atolones remotos del Caribe suroccidental, (Archipiélago de San Andrés y Providencia, Colombia). Aunque el número de especies de esponjas (96 en total, 52 a 61 por atolón) fue comparable con el de arrecifes en plataformas continentales, la densidad (promedios por atolón de 22.5 a 58.3 ind.20m^{-2}) fue notablemente más baja, posiblemente debido a menores cantidad de materia orgánica en suspensión. Análisis de Clasificación y de Correspondencia de las estaciones mostró que los esquemas de distribución de las esponjeas son aparentemente estocásticos, tanto a pequeña como a gran escala, y apenas débilmente relacionados con las variables ambientales principales. Empero, Análisis Inverso reveló que la mayoría de las especies presentaron preferencias marcadas por el hábitat, pero su distribución dentro de cada uno fue en mosaico. Dispersión a corta distancia de las larvas y migración por balseo de los adultos, aunado a lo remoto de los atolones, hace que la identidad y el momento de arribo de propágulos sea un evento azaroso. Juntos, la proliferación local de las poblaciones fundadoras y el efecto azaroso de perturbaciones, producen una fuerte heterogeneidad, en una escala de decenas de metros a centenares de kilómetros, en la dominancia dentro de un mismo tipo de hábitat.

Palabras clave: Esponjas, Porifera, Distribución, Estocástico, Caribe.

Problem

Sponges are important benthic components of reef environments in the Caribbean Sea. They are quite abundant, and can grow especially large in the deeper parts of the reefs, below about 15-20 m; in shallow areas, they are usually found in cryptic, non-exposed sides of corals and hard substrata (**Goreau**, 1967; **Sarà & Valecet**, 1973; **Vasseur**, 1985; **Álvarez** *et al.*, 1990; **Díaz** *et al.*, 1990; **Schmahl**, 1990; **Schubauer** *et al.*, 1990; **Zea**, 1993a; **Maldonado & Young**, 1996a). These patterns are explained by the faster growth rates of photosynthetic organisms like algae and corals, which in well illuminated habitats, outgrow and smother sponge recruits and juveniles (**Wilkinson & Trott**, 1985; **Zea**, 1993a, 1993b). Strong turbulence from surge may also contribute in preventing sponges from becoming abundant or grow tall in shallow areas (**Sarà** *et al.*, 1979; **Schmahl**, 1990; **Muricy** *et al.*, 1991; **Parra & Zea**, submitted). Mid-depth (4-15 m), calm, slightly turbid reef lagoons may also harbor important sponge populations (**Wiedenmayer**, 1977; **Bonem & Stanley**, 1977; **Maldonado & Young**, 1998).

While carrying out baseline surveys of coral reefs in remote, oceanic islands and atolls of the Southwestern Caribbean Sea (see **Díaz** *et al.*, 1995; 1996a; 2000), it became evident that there was a great deal of heterogeneity in sponge composition and abundance in physiognomically similar stations within a given reef zone, more than expected from previous experience in continental reefs. In this paper, the patterns of sponge distribution and abundance in three remote, oceanic

Caribbean atolls are described, and their strong stochastic component is interpreted in terms of paucity of dispersal coupled to happenstance events after colonization.

Study area

The Archipelago of San Andrés and Old Providence, Colombia, comprises a series of oceanic islands, atolls and coral shoals lined up in a NNE direction and extending over nearly 500 km along the Lower Nicaraguan Rise off the Central American Continental Shelf (Fig. 1) (**Geister**, 1975; 1992; **Kocurko**, 1977; **Díaz** *et al.*, 1995; **Geister & Díaz**, 1996). Both geomorphologic and ecological zonation patterns are quite similar among these reef-complexes, governed mainly by the effect of a northeast trade wind fetch of over two-thousand kilometers (**Geister**, 1975, 1977, 1983; 1992; **Díaz** *et al.*, 1996b).

From east to west, five main geomorphologic features are evident in the upper atoll platform (Fig. 2). (a) An abrasional windward fore-reef terrace with poor coral development of mixed diversity, and profuse gorgonian growth. (b) The emergent windward peripheral reef of hydrocorals, zoanthids and crustose coralline algae. (c) The lagoonal basin with patch, ribbon and anastomosed reefs, dominated by the *Montastraea* spp. coral species complex. (d) A series of detached peripheral reefs, some crown with crustose coralline algal pavements or with ramose *Acropora palmata* and cerebroid *Diploria strigosa* corals, interspersed over the shallow areas of the leeward margin of the lagoon. (e) The leeward fore-reef terrace, rather bare in shallow sites and with diverse, developed

carpets of mixed coral species in deeper waters (see also **Díaz** *et al.*, 1996b, and **Sánchez** *et al.*, 1997).

Materials and methods

Three atolls, one in the southern side and two in the northern side of the Archipelago, were surveyed for sponge density on board R/V Ancón from INVEMAR, Santa Marta. The southernmost atoll, Albuquerque Cays, was surveyed during May to June 1994. The other two, Serrana Bank and Roncador Bank, were surveyed from May to June 1995. Five reef zones were sampled: (**1**) the deeper parts (15-22 m) of the windward fore-reef terrace (FT), (**2**) shallow (2.5-4 m), protected lagoonal patch reefs of the *Montastraea* spp. - *Acropora cervicornis* type (LS), (**3**) mid-depth to deep (4-14 m), lagoonal ribbon and anastomosed reefs of the *Montastraea* spp. type (LD), (**4**) shallow areas (6-9 m) of the leeward terrace with sparse coral growth (TS) and, (**5**) deep areas (15-18 m) of the leeward fore-reef terrace and the upper reef slope (TD). Neither at the windward peripheral reef (0-4 m in depth) nor at the shallow exposed *Acropora palmata* -*Diploria strigosa* lagoonal and leeward peripheral reefs (0-3 m in depth), detailed censuses of sponge density were carried out due to turbulence and shallowness.

Forty-two stations were surveyed by SCUBA, each spanning a plot of about 20 x 20 m of homogeneous coral composition, located in depths between about 2.5 m and 22 m. In each station, three 10 m-long chains were laid over the bottom, following its relief, in parallel to each other and to the depth contour. Individuals of each sponge species were visually counted by moving over a 1 m-wide belt transect along each chain. The width of the transect was judged by a hand-held, 1 m-long rod. Species were visually identified in the field, and fragments of those posing difficulties were collected for closer examination on board and in the laboratory. These are being deposited at the INVEMAR sponge collection. A list of all sponges found within the whole plot was also made. Additional reef community data were obtained by the author and other team divers, either from visual observations over the whole plot (total percent live coral cover, proportion of dead coral [from total live + dead], and total sponge cover), or from the percentage of chain links overlaying a given type of sessile organism (total percent cover of sponges, live coral, algal forms, or other animals). The latter data were obtained from the analysis of in-situ close-up video images recorded while swimming over the chains. Stations were ranked qualitatively from 0 to 3 in their degree of exposure to waves (0=null, 1=low, 2=mid, 3=high) according to their placement in relation to the

predominant direction of the wind and waves, and their depth. The median depth of each station was taken as a variable for the analyses. A rugosity index, representing the overall relief of the bottom, was calculated from the ratio of the total chain length (10 m) to the straight line between its extremes, which was measured in-situ with a metered tape. All data from the 3 belt transects were pooled in a single value. Sponge density was normalized as number of individuals in 20 m^2. The area censused in each station (3 belt transects combined) varied between 17.3 m^2 and 27.0 m^2. On average, only 69.7±2.1 % (±1 standard error) of the species observed in the entire area of each station were found within the belt transects (range 36 % to 100 %). However, as in most sponge communities (e.g. **Álvarez** *et al.*, 1990; **Díaz** *et al.*, 1990; **Valderrama**, 2001), there were a few to several abundant species, and many rare ones. Hence, the censused area was large enough to estimate the abundance of the dominant species in each station, and thus was considered representative to describe the local sponge community.

To determine whether the patterns of species composition and abundance of sponges across stations were related to reef zonation, environmental variables and other benthic community components, stations were grouped by Normal Cluster Analyses according to (1) species composition (Jackard's similarity index) and, (2) species density ($\log_{10}[x+1]$ transformation, Bray-Curtis distance index), in both cases using the unweighed pair group average clustering method (**Dunn & Everitt**, 1982; **Field** *et al.*, 1982; **Digby & Kempton**, 1987). Further ordination of stations was carried out on untransformed density data using Detrended Reciprocal Averaging –DRA (cf. **Pimentel & Smith**, 1985; = Detrended Correspondence Analysis, cf. **Hill**, 1979), with the option of down weighing the effect of rare species. DRA station scores for the first four axes were correlated to the environmental variables to find those possibly influencing the patterns of sponge distribution, and to raw species densities to find those species associated with the patterns. Non-parametric, Spearman rank correlation coefficients were used (**Siegel & Castellan**, 1988).

Species characteristic to the various reef zones were found using the **Kaandorp** (1986) and **de Kluijver** (1991) Inverse Analysis. Mean densities and frequencies of occurrence (percentage of stations where the species occurred) in each sampled reef zone were recalculated for each species. Characteristic species were those having 70% to 90% of their cumulative density (from highest to lowest) within a zone or group of zones (grouped according to geomorphology and/or environmental variables).

Total per-station sponge densities were compared between reef zones and atolls by a 2-way ANOVA and Scheffe's multiple comparisons tests. Given the scarcity of data for some of the zones, only the windward fore-reef terrace (FT), deep lagoon (LD) and leeward fore-reef terrace (TD) were compared in this test. Type III sums of squares were used to account for the unbalanced replication (**SAS Institute**, 1981). Homogeneity of cell (reef zone*atoll combination) variances and normality of data were checked by the Bartlett's and Kolmogorov-Smirnov tests, respectively (**Sokal & Rohlf**, 1981).

Results

Patterns of species distribution

Ninety six sponge species or morphotypes were found in the belt transects. The greatest overall densities (mean of all 42 stations) were found in *?Pseudaxinella zeai* (3.8 ind.20m^{-2}), *Ectyoplasia ferox* (2.5 ind.20m^{-2}), *Cliona* sp. 1 (a morphotype of the *Cliona aprica – C. langae – C. caribbaea* species complex, 2.5 ind.20m^{-2}), *Aplysina archeri* (2.2 ind.20m^{-2}), *Agelas dispar* (dark brown morphotype, 2.1 ind.20m^{-2}), *Agelas sventres* (1.9 ind.20m^{-2}), *Aka brevitubulata* (1.9 ind.20m^{-2}), *Scopalina ruetzleri* (1.8 ind.20m^{-2}), *Ailochroia crassa* (1.8 ind.20m^{-2}), *Aplysina fulva* (1.2 ind.20m^{-2}), and *Aplysina fistularis* (1.1 ind.20m^{-2}). The species with the highest abundances wherever they occurred were *Agelas sventres* (mean 27.1 ind.20m^{-2} in 3 stations), *? Pseudaxinella zeai* (mean 16.0 ind.20m^{-2} in 10 stations), *Agelas wiedenmayeri* (mean 12.5 ind.20m^{-2} in 3 stations), and *Ulosa funicularis* (mean 7.1 ind.20m^{-2} in 4 stations). The number of sponge species in the three transects of each station varied between 4 and 26, while total sponge density varied between 5.6 and 126 ind.20m^{-2}.

The Cluster Analysis of stations by the density of their constitutive sponge species (Fig. 3) yielded groups of stations with no consistent relationship to reef zone, depth, degree of wave exposure or atoll. The same occurred in the classification of station by species presence-absence (not shown). In the classification by density, some groups included stations located at one atoll, but belonging to different ecological regimes. For example, all stations of Group D were from Roncador, but across four different reef zones. Group C included mostly Serrana deep stations, but from both the calm lagoon and the wave-exposed, windward fore-reef terrace (Fig. 3).

In the ordination of the data by DRA, axis 1 accounted for 39.7% of the variance in sponge abundance, while axis 2 to 4 accounted for 25.1%, 18.9% and 16.4%,

respectively. This broad dispersion of variance among axes indicated a great deal of heterogeneity in sponge distribution patterns. Nevertheless, in contrast to the results by the Cluster Analyses, a weak pattern of distribution in relation to certain prevalent environmental conditions emerged with DRA. Stations of the five reef zones sampled both overlapped and were segregated in the ordination space of the first two DRA axes (Fig. 4A). Also, Roncador stations certainly segregated on one side (Fig. 4B), indicating a geographical component in sponge distribution and abundance. Stations were also slightly segregated by depth (Fig. 4C), and depth was significantly correlated to ordination axis 2 scores (r_2= +0.44, p=0.005, n=42), with the shallower stations located mainly on the lower side of the ordination space. The degree of wave exposure was also segregated in the ordination space (Fig. 4D), being significantly correlated to axis 1 scores, although in a lower degree than depth (r_1= +0.37, p=0.02, n=42). Other variables such as cover of live and dead coral, cover of algal forms, and rugosity, were not correlated to the ordination space. The density of only three sponge species was found to be correlated to axis 1 scores, and thus to the degree of wave exposure (*Aplysina archeri*, r_1= –0.73, p=0.0000; *Mycale laevis*, r_1= +0.32, p=0.04; *Aplysina, cauliformis*, r_1= –0.35, p=0.02), and only two were correlated to the second axis, and hence to depth (*Aplysina archeri*, r_2= +0.44, p=0.005; *Amphimedon compressa*, r_2= +0.33, p=0.04). The total cover of sponges was also significantly correlated to axis 2 (r= +0.37, p=0.02).

In Table 1, the results of the Inverse Analysis to find species characteristic to the various reef zones are shown. The rectangles mark those reef zones or group of zones (according to geomorphology and/or environmental variables) within which each species is characteristic, i.e., is included within 70% (boldfaced) to 90% (boldfaced italics) of its cumulative density (from greatest to lowest). Underlined data indicate that a species occurs in the reef zone in more than 60% of its stations. Overall mean densities per atoll are also included.

Twenty-one species were found to be eurytopic (Table 1A), living either in all reef zones (6 species) or in diverse and extreme environmental conditions. Remarkably, very few values are underlined, indicating that most species occurred in a few the stations at each reef zone.

For most of the remaining species, there were definitely certain ecological preferences. In Table 1B the 22 species characteristic to deep waters are highlighted. Note again, nevertheless, that only two species had a frequency of occurrence larger than 60% in one (*Niphates digitalis*) or

Table 1. Inverse Analysis. Mean density (± 1 standard error) for each sponge at each reef zone (across atolls) and each atoll (across reef zones). The rectangles mark those reef zones or groups of zones (according to geomorphology and/or environmental variables) to which each species is characteristic, i.e., including 70% (boldfaced) to 90% (boldfaced italics) of each species cumulative density (from greatest to lowest). Underlined data indicate that the species occurs in the reef zone in more than 60% of its sampled stations. A. Eurytopic species, B. Deep-water species. C. Fore-reef terrace species. D. Lagoon species. E. Shallow lagoon species. F. Leeward species. G.Species living in turbulent sites

	Windward fore-reef terrace	Lagoon shallow (protected)	Lagoon deep	Leeward shallow terrace	Leeward fore-reef terrace	Albuquerque Cays	Serrana Bank	Roncador Bank
Code	FT	LS	LD	TS	TD	ALB	SER	RON
# of stations	8	3	21	2	8	10	15	17
C. Fore-reef terrace species								
Aplysina cauliformis, tubes	2,71 ± 1,11	-	0,29 0,17	-	1,43 ± 0,98	0,09 ± 0,09	0,68 ± 0,32	1,65 ± 0,61
Hyrtios proteus	0,11 ± 0,11	-	-	-	0,20 ± 0,20	0,16 ± 0,15	-	0,05 ± 0,05
Ircinia sp. 2, dirty	0,51 ± 0,27	-	-	-	0,34 ± 0,34	-	0,34 ± 0,19	0,10 ± 0,10
Mycale laxissima	0,21 ± 0,21	-	0,04 ± 0,04	-	0,22 ± 0,15	-	0,16 ± 0,11	0,11 ± 0,07
Phorbas amaranthus	0,42 ± 0,22	-	0,05 ± 0,05	-	0,67 ± 0,32	0,18 ± 0,11	0,11 ± 0,07	0,36 ± 0,17
Plakinastrella onkodes	0,20 ± 0,13	-	-	-	0,10 ± 0,10	0,08 ± 0,08	0,05 ± 0,05	0,05 ± 0,05
Pachypellina podatypa	0,35 ± 0,23	-	-	-	0,26 ± 0,26	-	0,11 ± 0,10	0,19 ± 0,13
?Psudaxinella ?n.sp.1	0,11 ± 0,11	-	-	-	0,12 ± 0,11	-	0,12 ± 0,07	-
Windward fore-reef terrace								
Agelas clathrodes	0,20 ± 0,13	-	-	-	-	-	0,11 ± 0,07	-
Aka coralliphaga	0,21 ± 0,21	-	-	-	-	-	0,11 ± 0,11	-
Agelas sventres	10,18 ± 6,10	-	-	-	-	-	0,37 ± 0,35	4,47 ± 2,87
Agelas sceptrum	0,09 ± 0,09	-	-	-	-	0,07 ± 0,07	-	-
Agelas wiedenmayeri	4,68 ± 2,77	-	-	-	-	0,30 ± 0,28	-	2,03 ± 1,31
Callyspongia plicifera	0,11 ± 0,11	-	-	-	-	-	0,06 ± 0,05	-
Clathria spinosa	0,11 ± 0,11	-	-	-	-	-	-	0,05 ± 0,05
Eurypon laughlini	0,20 ± 0,20	-	-	-	-	-	0,10 ± 0,10	-
Black indet. sponge	0,12 ± 0,11	-	-	-	-	0,09 ± 0,09	-	-
Geodia neptuni	0,54 ± 0,31	-	-	-	-	-	0,21 ± 0,15	0,07 ± 0,07
Halisarca coerulea	0,11 ± 0,11	-	-	-	-	-	0,06 ± 0,05	-
Jaspis sp. 1	0,10 ± 0,10	-	-	-	-	-	0,05 ± 0,05	-
Myrmekioderma gyroderma	0,10 ± 0,10	-	-	-	-	-	-	0,05 ± 0,05
Plakortis angulospiculatus	0,24 ± 0,16	-	-	-	-	0,07 ± 0,07	-	0,07 ± 0,07
Ptilocaulis marquezi	0,30 ± 0,30	-	-	-	-	-	-	0,14 ± 0,14
?Pseudaxinella ?n.sp. 2	0,20 ± 0,13	-	-	-	-	0,07 ± 0,07	0,06 ± 0,05	-
Pseudaxinella tubulosa	0,21 ± 0,21	-	-	-	-	-	0,11 ± 0,11	-
Strongylacidon sp. 2, red	0,11 ± 0,11	-	-	-	-	-	-	0,05 ± 0,05
Topsentia ophiraphidites	0,72 ± 0,72	-	0,04 ± 0,04	-	-	-	0,06 ± 0,06	0,34 ± 0,33
Leewaard fore-reef terrace								
Clathria bulbotoxa	-		-	-	0,36 ± 0,26	0,08 ± 0,08	-	0,12 ± 0,12
Encrust. indet sponge	-		-	-	0,11 ± 0,11	0,09 ± 0,09	-	-
Haplosclerida indet sp. 1	-		-	-	0,56 ± 0,56	-	0,30 ± 0,29	-
Xestospongia sp. 2	-		-	-	0,12 ± 0,11	-	0,06 ± 0,06	-
Xestospongia muta	-		-	-	0,19 ± 0,19	-	0,10 ± 0,10	-

two (*Ailochroia crassa*) reef zones. Thus, most of all these species, although always found in deep water, were patchily and sparsely found in the studied atolls.

Thirty-two species were characteristic to the fore-reef terraces (Table 1C), 8 found both in the windward and the leeward, 19 exclusive to the windward and 5 to the windward terraces. Again, the low frequency of occurrence is noticeable. Likewise, 14 species were characteristic to the lagoon, 2 in general, 1 to the shallow and 11 to the deep lagoon (Table 1D). There were also species found

preferentially in shallow waters, others in the leeward side of atolls, and still others in the most turbulent sites sampled (Table 1E to G).

The three atolls shared 32 species (Table 1). Overall, 59 species occurred in at least two atolls, while 37 were found exclusively in one atoll. A geographical component in the distribution of some species was evident: while Serrana and Rocandor Banks, closer together in the northern part of the San Andrés Archipelago, shared exclusively 14 species, Albuquerque, far to the south, shared exclusively only 7 species with Serrana and 4 species with Roncador. Interestingly, although Roncador Bank stations appeared segregated from Albuquerque and Serrana stations in the ordination space (Fig. 4B), it was not due to the presence there of many unique species (only 10 there, vs. 7 at Albuquerque and 20 at Serrana), but to differences in the abundance of most common forms (Table 1).

The conclusions of these analyses are that, besides some widespread and eurytopic species, most sponges have ecological preferences in relation to depth and degree of wave exposure, which are the main factors determining reef physiognomy. However, their occurrence in any given reef zone is rather heterogeneous and patchy at the scale of tens of meters to hundreds of kilometers. As one moved several tens to a few hundreds of meters within a physiognomically homogeneous reef zone, the pattern of dominance changed from one species to another; also, as one moved to another atoll in the same reef zone, yet another species, however widely distributed, was the numerical dominant. Additionally, no single proximate factor in the current bottom composition of the reefs (e.g.,

coral cover, coral death, algal cover, bottom rugosity, etc.) seemed to affect sponge distribution.

Total density and species richness

Differences between reef zones in total sponge density per-station also depended on the atoll (Fig. 5), due to a significant interaction between reef zone and atoll (2-way ANOVA comparing windward fore-reef terrace, deep lagoon and leeward fore-reef terrace zones across the 3 atolls, F=3.689, p=0.02). At the windward fore-reef terrace, Roncador had the greatest mean density (100.8 ind.20m^{-2}), while at the deep lagoon, the highest mean density occurred at Serrana (64.6 ind.20m^{-2}) (Fig. 5A). However, only at this latter zone there were significant differences in density between atolls (Scheffe multiple comparison, p<0.05). Overall (Fig. 5B), the windward fore-reef terrace and Serrana Bank showed the greatest density (69.4 ind.20 m^{-2} and 58.3 ind.20m^{-2}, respectively).

Regarding number of species, the total number was in general higher at Serrana for all reef zones, excepting the
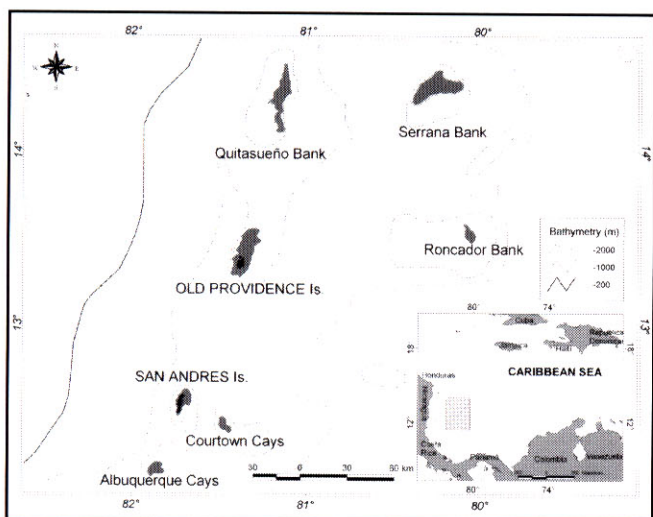

Figure 1 Map of the Southwestern Caribbean Sea with the location of Colombian islands, atolls and banks.
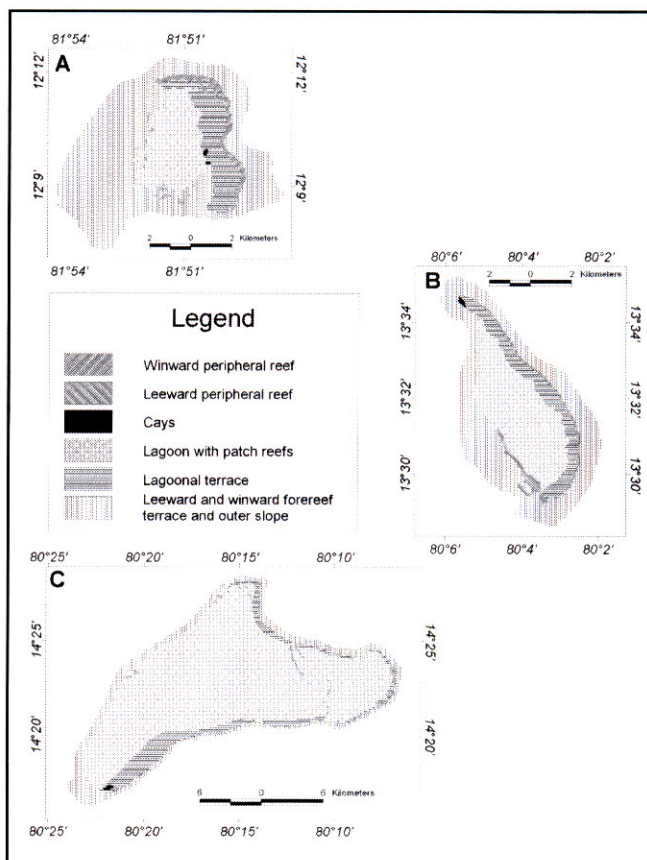

Figure 2. Geomorphologic features of studied atolls. A. Albuquerque Cays. B. Roncador Bank. C. Serrana Bank.

leeward shallow terrace (Figs. 5C), and in total (Fig. 5D, 74 species at Serrana vs. 52 at Albuquerque and 61 at Roncador). Also, as expected, in general the deeper reef zones held a greater diversity of sponges (Fig. 5D).

Discussion

The generally lower densities of sponges found at the studied atolls, in comparison to those found in reef areas on the continental shelves, are probably due to the effect of lower amounts of suspended organic matter in oceanic islands and banks. As most oceanic and continental Caribbean sponges are predominantly filter-feeding to mixotrophic (i.e., depend more on filtration than on photosynthates from endosymbionts, in contrast to Indo-Pacific oceanic sponges being predominantly photo-trophic), less suspended material in oceanic areas implies less food and hence lower densities (cf. **Wilkinson**, 1987;

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Group - Station - Atoll - Reef zone

A  26  ALB  LD-------------------------------------------------I------I                                       I
A  31  ALB  LD------------------------------------------------I      I------------------I                     I
A  29  ALB  LD------------------------------------------------I           I-----I                             I
A  46  ALB  LD-----------------------------------------------------------I     I    I                         I
A  79  SER  LD--------------------------------I----------I           I-------I    I                           I
A  80  SER  LD--------------------------I            I-----------------I         I                            I
A  89  SER  LS--------------------------------I                                  I                            I
     ---------------                                                             I
B  28  ALB  LD---------------------------------I-------I                         I
B  33  ALB  LD-------------------------------I     I------------------------I    I
B  34  ALB  FT----------------------------------I              I--I          I   I
B  37  ALB  TD------------------------------------------------------I------I I   I
B  94  SER  FT-----------------------------------------------I-----I      I     I
B  97  SER  TD----------------------------------------------I            I     I
     ---------------                                                     I     I
C  83  SER  FT------------------------------I-----------------I          I-I   I----I
C 100  SER  LD------------------------------I         I-------I          I I   I    I
C 113  SER  LD--------------------------------I-----I     I--I     I I   I    I
C 114  RON  LD----------------------------------I      I  I   I I   I    I
C  87  SER  TD-------------------------------------I---------I I---------I I   I    I
C 101  SER  LD------------------------------------------I           I         I    I I   I    I
C  84  SER  LD-----------------------------I-------------------I     I         I-I  I    I
C  85  SER  LD----------------------------I                I-----I            I I  I    I
C  93  SER  LD-------------------------------------I----I                     I I  I    I
C  98  SER  LD-------------------------------------I                          I I  I    I
     ---------------                                                          I I  I    I
D 105  RON  TS----------------------------------------I                       I I  I    I
D 106  RON  TD------------------------------I-----I        I------------------I I I I    I II
D 109  RON  FT----------------------------I      I--------I              I    I I I---I  II
D 110  RON  LD----------------------------I                              I-----I I      II
D 116  RON  LD--------------------------------I---------I     I          I      I       II
D 117  RON  LD--------------------------I           I-------I I          I      II
D 122  RON  TD------------------------------------------I              I       II
     ---------------                                                   I       II
E  47  ALB  FT---------------------------------------------I--------I  I       I       II
E  91  SER  FT---------------------------------------------I        I  I       I       II
E 120  RON  FT----------------------------------------I-I            I--------I  II----
E 123  RON  FT-----------------------------------I I-----I           I          II
E 127  RON  TD--------------------------------I        I-------------I          II
E 121  RON  LD--------------------------------I                                 II
     ---------------                                                            II
F 107  RON  LS-------------------------------------I                            I----II
F 108  RON  LD----------------------------I----I                               I
F 118  RON  LS-------------------------I                                       I
     ---------------                                                           I
G  36  ALB  TD----------------------------------------------------I---------I  I
G  81  SER  TS----------------------------------------------------I          I----I
G 112  RON  LD--------------------------------------------------------------I
```

Atoll:
ALB = Albuquerque Cays
SER = Serrana Bank
RON = Roncador Bank

Reef Zone:
FT = windward fore-reef terrace
LS = lagoon, shallow protected
LD = lagoon, deep
TS = leeward shallow terrace
TD = leeward fore-reef terrace

Figure 3. Cluster Analysis of studied stations. Codes A to G are groups of stations defined by their analysis. For each station, its number, and the atoll and reef zone where they belong, are given.

Wilkinson & Cheshire, 1989; 1990). For example, mean sponge densities (measured with the same method employed here) of 87.2 ind.20m^{-2} have been found at Urabá Gulf, in the boundary between South and Central America in the Caribbean (Valderrama & Zea, submitted), in comparison to the per-atoll means of 22.5 ind.20m^{-2} to 58.3 ind.20m^{-2} found in this study. A similar pattern of greater densities in sites closer to continental runoff has been found in the ubiquitous Caribbean sponge genus

Ircinia (Parra & Zea, submitted). Northern Cuba offshore reefs also harbor larger populations (Alcolado, 1999). However, greater water transparency and lower suspended food in the oceanic atolls seem to favor high overall (e.g. *?Pseudaxinella zeai, Cliona aprica – C. langae – C. caribbaea, Aplysina archeri*) or local (*?Pseudaxinella zeai, Agelas wiedenmayeri, Ulosa funicularis*) densities of mixotrophic species with photosynthetic endo-symbionts (see Rützler, 1990; Vicente, 1990), while
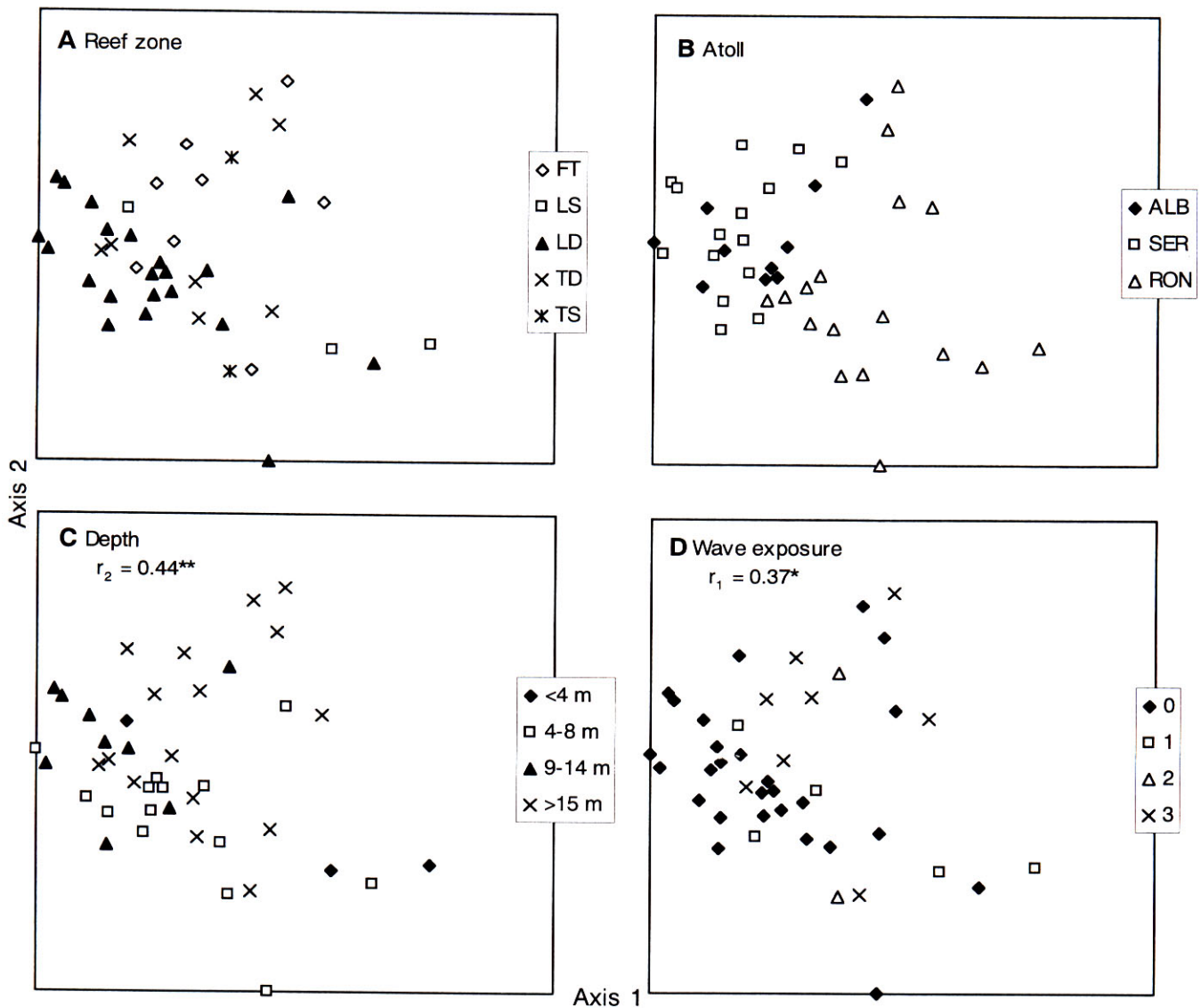
Figure 4. Detrended Reciprocal Averaging (DRA) ordination plot of the first two axes. For each plot, the points represent the position of each of the 42 stations in the ordination space; symbols represent reef zones (A), atoll (B), depth ranges (C), and degree of wave exposure (D). For wave exposure ranks, see materials and methods text. Reef zone and atoll codes are those of Fig. 3.
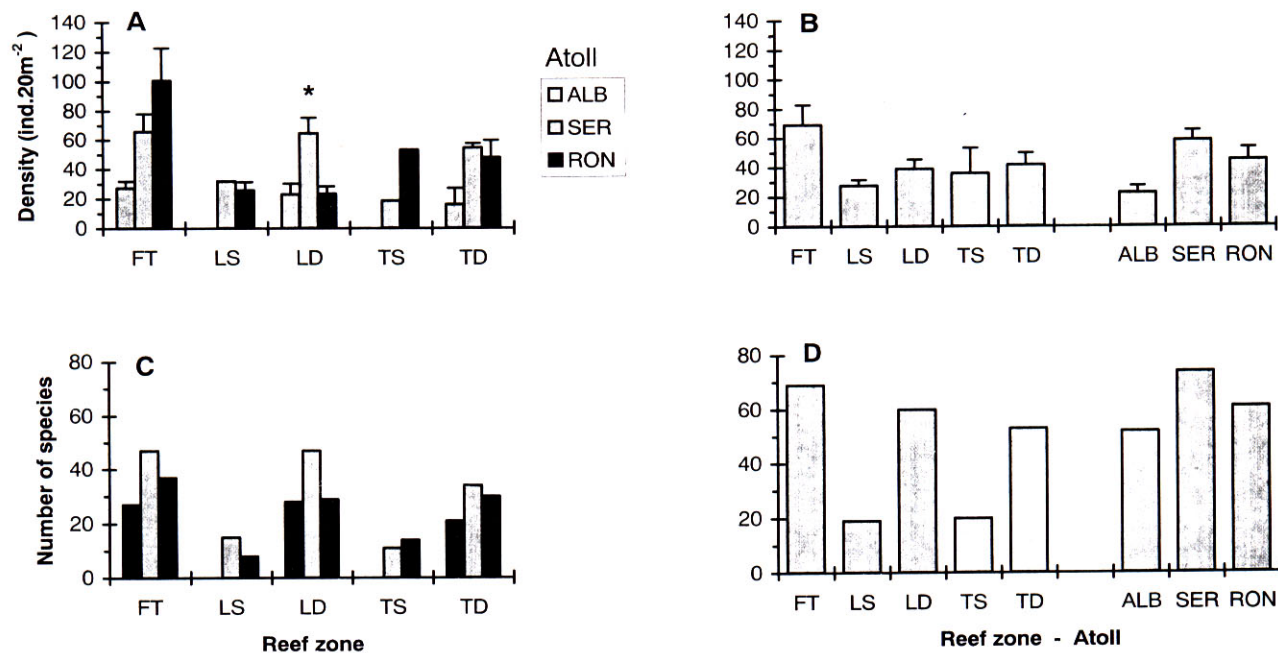
Figure 5. Mean sponge density (A) for each reef zone within each atoll, and (B) overall for each reef zone and atoll (error bars are +1 standard error). Total number of sponge species (C) for each reef zone within each atoll, and (D) overall for each reef zone and atoll. *= atoll significantly different from the others at a given zone (Scheffe multiple comparison within the reef zone, P<0.05, after two-way ANOVA comparing only FT, LD and TD zones). Codes as in Fig. 3.

entirely heterotrophic sponges are more favored in areas exposed to continental runoff (see **Valderrama**, 2001, **Valderrama & Zea**, submitted).

In contrast to density, species richness in the studied oceanic atolls is not particularly different from other oceanic or continental areas. This occurs because the density is more evenly spread among several species in the atolls, being more concentrated in a few species in other denser areas (see **Valderrama & Zea**, submitted).

Usually, most studies of sponge distribution patterns within a type of community (e.g., reef, rocky shore, seagrass, mangrove, soft bottom) have found a close relationship between these patterns and the predominant, local or widespread, abiotic and/or biotic environmental variables. Recurrent and consistent patterns of sponge distribution at a small to mid scale (e.g., centimeters to hundreds of meters) have been attributed to various environmental variables, the most important being the depth gradient (wave-exposure, abrasion, light regime and

competition with photosynthetic organisms, contrasting surface water conditions), the availability of vertical to overhanging and cryptic habitats, closeness to runoff or pollution sources, distance from shore, and larval behavior and dispersal (e.g., **Rützler**, 1972; **Sarà & Valecet**, 1973; **Vasseur**, 1985; **Alcolado & Herrera**, 1987; **Alcolado**, 1985; 1989; **Muricy**, 1989; **Wilkinson & Cheshire**, 1989; **Álvarez et al.**, 1990; **Díaz et al.**, 1990; **Schmahl**, 1990; **Muricy et al.**, 1991; **Zea**, 1993a; **Maldonado & Young**, 1996a; **Uriz et al.**, 1998; **Lehnert & Fischer**, 1999; **de Voogd et al.**, 1999; **Valderrama**, 2001). However, some studies have hinted a degree of heterogeneity at both larger and smaller scales, unexplained by the direct effect of environmental variables. At the larger scale, for example, **Reed & Pomponi** (1997) found that the diversity of deep reef and upper continental slope throughout most of the Bahamas is highly variable despite the similarity of the environmental variables across the full geographic range. In summarizing sponge distribution patterns across several Cuban reefs, **Alcolado** (1990) found it difficult to predict

which species would dominate in any given reef site not continuously subjected to extreme conditions (e.g., turbulence, pollution). **Alcolado** (1999), also reported the existence of a stochastic component of species distribution, especially in deep (>10 m) reef localities, throughout a 456 km-long reef tract off Northern Cuba. **de Voogd** *et al*. (1999) were able to attribute cross-shelf sponge distribution patterns Indonesian reefs to several environmental variables, but found heterogeneity in the distribution of species in a relatively large subset of the sampled stations. **Panzini & Pronzato** (1985) encountered unpredictable sponge distribution patterns across rather uniform sea-grass meadows in the Mediterranean. **van Soest** (1993) found dramatic changes in species composition and abundance in similar soft bottoms in the Mauritanian shelf in West Africa, due in part to a restricted exchange of larvae across a mud barrier separating them. Unexplained heterogeneity at small scales has also been shown in several studies (e.g., **Alcolado**, 1979; **Muricy** *et al*., 1991; **Rützler** *et al*., 2000), usually attributed to the synergistic effect of various environmental variables or to the consequences of small-scale random factors related to larval dispersal and settlement (e.g., **Zea**, 1993b; **Uriz** *et al*., 1998). Also, a great deal of local heterogeneity in species composition may be due to a high rate of individual (and partly of species) turnover through time, as some die and others recruit and grow (**Hughes**, 1996; **Wulff**, 1999). Hence, the degree of unexplained heterogeneity at a given scale depends on the balance between the various deterministic vs. stochastic processes shaping community structure (see **Alcolado**, 1999).

At the studied atolls, neither in the classification of stations by presence-absence of species, nor in the classification or ordination by species density, was there a clear pattern of sponge distribution in relation to major environmental variables at small (within reef zones) and large (across zones, between atolls) scale. Usually, presence-absence classification or ordination give information on the higher-scale processes affecting communities, while abundance classification or ordination yield a lower-scale effect of recent perturbation and recolonization events (**Allen & Starr**, 1982). In this case, a strong stochastic component in species distribution was evident at both scales. One could argue, on the other hand, that this lack of consistency in distribution is the result of not having normalized density data in terms of availability of those particular microhabitats that sponges prefer (e.g., crevices, bare substratum, etc.) (**Alcolado**, 1979; **Díaz** *et al*., 1990; **González**, 1992). However, physiognomic features did not vary much within habitats both within and among atolls, due to the strong effect of

the predominant turbulence in shaping atoll reef geomorphology (**Díaz** *et al*., 2000). In addition, abundance patterns were neither correlated to reef bottom components (which may somehow reflect availability of microhabitats), nor to bottom rugosity (which is correlated to availability of crevices).

The strong stochastic component of sponge distribution at the studied atolls can be interpreted in terms of dispersal. It has become evident that many sponge larvae do not disperse far from their mother. Some have negatively buoyant eggs that drop to the bottom after external fertilization, or that are released in strands of mucus which sink to the bottom close to their mother; yet some others have crawling larvae (**Reiswig**, 1976; **Ayling**, 1978, 1980; **Hoppe & Reichert**, 1987; **Hoppe**, 1988; **Fromont**, 1988; **Ilan & Loya**, 1990; **Maldonado & Young**, 1996b; **Maldonado** *et al*., 1997; **Uriz** *et al*., 1998; for cases of longer larval life see e.g., **Ilan & Loya**, 1988; **Kaye & Reiswig**, 1991; **Uriz** *et al*., 1998). One also finds a trend of greater larval recruitment where the adults live in higher densities (**Zea**, 1993b), and of higher young mortality with longer swimming by the larvae (**Maldonado & Young**, 1999). Also, sponge larvae are seldom found in planktonic tows, and a bottom plankton sampler is needed to capture them (**Sarà & Vacelet**, 1973; **Rützler** *et al*., 1980). This short-distance dispersal occurs in many non-solitary animals such as some stony corals, soft corals, bryozoans, and tunicates (**Jackson**, 1986). It implies that adults may be aggregated at a scale of decimeters to meters (e.g., **Díaz** *et al*., 1990; **Alcolado**, 1989). Additionally, processes at the small scale may generate patterns at the larger scale. **Uriz** *et al*. (1998) found that the discontinuous geographic distribution and localized small-scale aggregation of one species of sponge in the Mediterranean were related to the very short-distance dispersal of its crawling larvae, while the geographical ubiquity and small-scale randomness of another species were due to larvae with greater dispersal capabilities.

The studied atolls, of Miocene origin (**Geister**, 1975; 1992), presumably were formed sufficiently long ago to allow the opportunity of most common Caribbean sponge species to be present, as it was found during this study (see species lists on Table 1), arriving as larvae or as adults drafting in floating objects (cf. **Jackson**, 1986). However, given the presumed generalized paucity of dispersal, coupled to the relative remoteness of these atolls, the identity and timing of arrival of propagules becomes a random event. Thus, at the larger scale (hundreds of km), differences in species dominance between atolls are to be expected. Also, once a species arrives, it can spread locally

conforming a founder population. Hence, at a lower spatial scale (in reef zones within atolls), a patchiness in the density and dominance, as the one found, is to be expected. Moreover, after major disturbing events, like hurricanes, storms or epizootics, localized and discriminated extinctions can occur, as well as random dispersal by breaking and reattachment (**Wilkinson & Cheshire**, 1988; **Wulff**, 1995; 1999; **Wilkinson & Thompson**, 1997), allowing survival of some species or recolonization of a random sample of the spatially adjacent species pool, adding to the heterogeneity of sponge distribution. Hence, the strong stochastic component in sponge distribution created at lower scales (local colonization and perturbation) also has a strong effect at the higher scale in the studied atolls. This contrasts with the temporal stability of sponges at the community level (in terms of total cover, richness and diversity) in Jamaican deep reefs, which is maintained by constant recruitment and steady mortality (**Hughes**, 1996). Remoteness and greater exposure to waves and storms enhance the stochastic trends in sponge distribution in these atolls, in comparison to other areas.

At present it is difficult to interpret the striking difference in total sponge density among atolls, overall and for a given reef zone. Perhaps past disturbance events have lowered density; the lowest overall density at Albuquerque could have been a result of the near pass of Hurricane Joan in 1988. Also, the wide and open lagoon of Serrana Bank may allow a longer residency time of the waters and thus greater opportunity for planktonic blooms to occur and remain, providing additional food for benthic filter feeders.

Despite the strong stochastic component in sponge distribution, most species were found to have a certain preference for one or more reef zones, especially in relation to depth and degree of wave exposure, which are the main factors determining general reef physiognomy. This shows that predominant, biotic and/or abiotic environmental variables are also affecting sponge distribution in various ways. As expected, deeper reef areas hold a greater number of species and usually a greater density than shallower areas. On the other hand, current reef physiognomy and composition, which is the result of recent widespread disturbances (see **Zea et al.**, 1998) does not seem to be affecting sponge distribution, at least at the spatial and temporal scale it was studied, although an increase in sponge density may be expected as recent coral death continues to free hard bottom space (**Zea**, 1994, but see **Hughes**, 1996).

These results call for caution when using sponges as as bioindicators. Stochastic heterogeneity at various scales can confound results of simple observational studies comparing "pristine" with "impacted" sites. As is already being explored (e.g., **Alcolado & Herrera**, 1987; **Muricy**, 1989; **Muricy et al.**, 1991; **Zea**, 1994), it is first necessary to take into account the degree of response of the sponge community in general, and species in particular, to local deterministic forces.

Acknowledgments

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