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SPONGES: AN ESSENTIAL COMPONENT OF CARIBBEAN CORAL REEFS

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ABSTRACT

Sponges are an important structural and functional component of Caribbean coral reefs. We support this statement with our data on sponge diversity, abundance, productivity, and participation in nutrient cycling from Carrie Bow Cay on the Barrier Reef of Belize and from comparative studies in other Caribbean locations. Sponges have at least six biological and ecological properties that make them an influential part of Caribbean coral-reef ecosystems: high diversity, higher than all coral groups combined; high abundance (area coverage) and biomass (weight, volume) that may exceed values for all other reef epibenthos in some areas and reef zones; capacity to mediate non-animal processes such as primary production and nitrification through complex symbioses; chemical and physical adaptation for successful space competition; capability to impact the carbonate framework through calcification, cementation, and bioerosion; and potential to alter the water column and its processes through high water filtering capabilities and exhalation of secondary metabolites. We conclude that thorough and informed study of sponges is indispensable when characterizing, assessing, or monitoring a coral reef.

The assessment and monitoring of Caribbean coral reefs have become of paramount importance in recent years owing to the increasing occurrence of maladies menacing this unique ecosystem (for instance, coral bleaching, disease, urban development, ship grounding, and oil spills). The recognition of the importance of sponges in these ecosystems is reflected in the inclusion of sponge abundance estimates, mostly in the form of area coverage, in major monitoring efforts of Caribbean coral reefs (Woodley et al., 1997). However, other aspects of sponge biology and ecology that, as we will argue, make sponges a unique component of coral reefs remain understudied or ignored in the any assessment, monitoring or restoration of coral reefs. Standardized accounts of the richness and composition of sponges in Caribbean coral reefs are few and restricted to local surveys (Wiedenmayer, 1977: Bahamas; Alvarez et al., 1990: Venezuela; Meesters et al., 1991: Curaçao and Bonaire; Alcolado, 1994: Cuba; Wulff, 1994: Caribbean Panama; Zea, 1994: Caribbean Colombia; Clifton et al., 1997: Caribbean Panama; Reed and Pomponi, 1997: Bahamas; Diaz, Smith and Newberry, in prep: Belize). Other scientific accounts of sponge diversity on reefs are qualitative only (e.g., de Laubenfels, 1936; van Soest, 1978, 1980, 1984; Zea, 1987). Objective statistics of sponge species richness, composition, and distribution that could aid to determine the health of a Caribbean coral reef are not available. The principal reason behind the traditional neglect of Porifera in reef diversity and ecology surveys is the lack of reliable field guides for this group. Despite a few attempts to remedy this situation (e.g., Rützler, 1978, 1986; Zea, 1987; Humann, 1992) sponges are still regarded as enigmatic creatures because identification requires tedious microscope preparations in addition to examining pictures and correctly identified color images are scarce. In this paper we present and compare biological and ecological data from the work of many authors including ourselves. We shall identify six major aspects of biology and ecology that make sponges an essential component of the reef ecosystem. Each of these aspects, diversity, abundance (area coverage and biomass), symbiotic associations with microorganisms, space competition, impact on the reef framework, and exchanges with the water column will be separately discussed.

Diversity

Sponges are among the most prominent coral reef groups, usually exceeding corals and algae in species number (Table 1, Fig. 1A). Numerous Caribbean coral reef sponges remain undescribed. The less explored deeper zones of Caribbean coral reefs hold the largest and least known sponge populations. For example, submersible observations from the 'deep fore reef escarpment' (60–150 m deep) in the Bahamas (212 collection sites throughout the Islands, 182 submersible and 28 ROV dives) revealed 206 taxa but only 146 described species (Reed and Pomponi, 1997). Likewise, sub-rubble communities (organisms living under coral rubble) in Curaçao and Bonaire are dominated by sponges representing 60% of all sessile cryptic species (220 of 367 species) (Meesters et al., 1991). Sponges are not only one of the most diverse components of coral reefs but promote diversity through their associated infauna. For example, 139 and 53 species, respectively, of crustaceans, ophiuroids, mollusks, and fishes were found inhabiting the interior cavities and canals in only two reef sponges, *Aplysina lacunosa* and *Aplysina archeri* (Villamizar and Laughlin, 1991).

Table 1. Species richness of conspicuous benthic components of coral reefs at various Caribbean localities. (sc) = soft corals, (as) = ascidians, (ma) = macroalgae, — = not reported.

Locality	Sponges	Hard corals	Others	References
Carrie Bow Cay, Belize	>300[1]	47	35 (sc)	Cairns (1982), Muzik (1982), Diaz et al. (in prep.)
Dos Mosquises Cay, Los Roques	60	58	—	Alvarez et al. (1991), Hung (1985), Croquer and Villamizar (1998)
South Florida	84[2]	36	—	Burns (1985), Schmal (1991)
Cuba	160	41	68 (sc)	Alcolado (1994), Menendez-Macia (in prep)., Garcia Parrado (in prep.)
Colombian Caribbean	6–15	3–6	0–2.8[3]	Zea (1994)[4]
San Blas, Panama	58	40	26 (sc) 97 (ma)	Clifton et al. (1997)
Curaçao sub-rubble habitats	156	7	41 (as), 1 (sc)	Meesters et al. (1991)[5]
Bonaire sub-rubble habitats	199	8	65 (as), 1 (sc)	Meesters et al. (1991)[6]

[1] Rützler, unpublished data

[2] Total diversity found in four reefs of Southern Florida (Triumph, Long, Ajax, Pacific), sponge diversity at each reef ranged between 37–49 species.

[3] Values shown represent range of mean number of species at three fringing reefs in the Colombian Caribbean of the Santa Marta area.

[4] The category for this study may include: Hydrocoral (1 spp.), unidentified gorgonian, actinian (1 spp.), bryozoans (2 spp.), tunicates (2 spp.), bivalves (1 spp.).

[5] Values shown represent total diversity in four sites, three between 4–6 m and one 35 m in depth. Species richness of sponges at each site ranged from 38–79.

[6] Values shown represent total diversity in five sites, four at 5 m and one at 25 m deep. Species richness of sponges at each site ranged from 38–49.

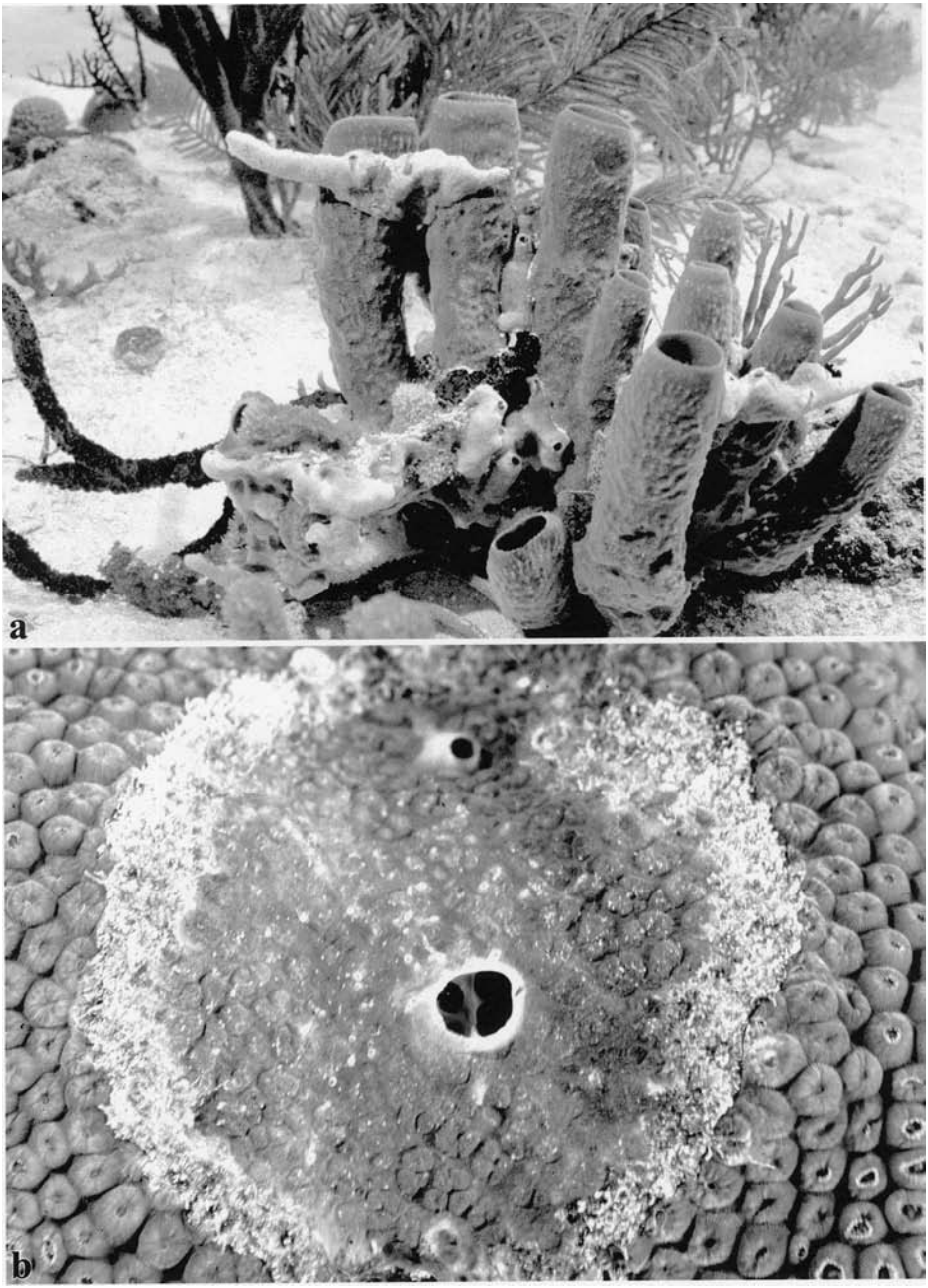

Figure 1. Sponges play important roles in Caribbean coral reef communities including space competitors, bioeroders, reef consolidators, food source for fishes, primary producers, and nitrifiers. a) Diverse assemblages of sponge species representing a large portion of coral reef living tissues can be found in small reef areas. In this picture, five species are found growing together in a sand channel in Belize: *Callyspongia vaginalis*, *Scopalina ruetzleri*, *Iotrochota birotulata*, *Holopsamma helwigi*, and *Niphates erecta*; b) Boring sponges of the genus *Cliona* can be very destructive in some reefs. In this picture *Cliona delitrix* is attacking a colony of *Montastrea cavernosa* .

ABUNDANCE (AREA COVERAGE)

Sponge abundance, estimated from area cover, varies along depth gradients and between reef geomorphologic zones. At Carrie Bow Cay on the Belize barrier reef, demosponges reach their highest area coverage at both the deepest reef zone (outer fore reef, >30 m) with 10% and 29 species, and the shallowest reef zone (high spur and groove, <10 m) with 7.3% and five species (Diaz, Smith and Newberry, in preparation). Estimates in other areas of the reef varied 2–7% (Low Spur-and-Grove zone, 10–15 m: 3.5%; Inner Reef Slope, 20–25 m: 7%; Outer Reef, 20–30 m: 5.6%). Studies carried out in various Caribbean coral reefs show cover by sponges of up to 24% on hard substrata in light-exposed, open reef habitats and up to 54% in cryptic, low-light sub-rubble habitats (Table. 2). Sponges are among the four most abundant (in terms of area coverage) organisms in Caribbean coral reefs, along with algae, scleractinian corals, and octocorals. In sub-rubble habitats, sponges are the most important group in terms of cover with an average of 30% (12–54%), followed by crustose algae and bryozoans (Meesters et al., 1991). In deeper open-reef areas, demosponges commonly increase their abundance and diversity consid-

Table 2. Abundance of major coral reef groups at various Caribbean localities. Abundance expressed as the range of mean area coverage (%) for each group from the total studied area. (— = not reported).

Locality/Study	Sponges	Algae	Hard corals	Soft corals	Depth (m)
Carrie Bow Cay, Belize Diaz et al. (in prep)[1]	2–10	2–55	16–30	1–14	0–30
Caribbean-CARICOMP Woodley et al. (1997)[2]	0.1–13	11–94	2–43	0.2–26	10–3
Colombian Caribbean Zea (1994)[3]	5–24	46–64	21–44	0–4[4]	17–22
Lee Stocking Is., Bahamas Lidell et al. (1997)[5]	1–6	60–90	3–23	–	<50
Lee Stocking Is., Bahamas Lidell et al. (1997)[5]	0–11	3–78	0.2–6	–	50–250
Curaçao (sub-rubble com.) Meesters et al. (1991)[6]	22–54	8–36	0.4–3	–	4–6
Curaçao (sub-rubble com.)[7]	52	14	0.2	–	35
Bonaire (sub-rubble com.)[7]	13–17	3–21	0.1–1.3	–	5
Bonaire (sub-rubble com.)[7]	21	12	4.1	–	25

[1] Organisms abundance was estimated laying a square-meter quadrant, along 3–4, 10 m long transects, perpendicular to the slope, at each of six reef zones 13.

[2] Values determined in the mixed zone of the reef, in eighteen Caribbean localities. Abundance was estimated on the mixed zone of reef, with five to ten horizontal 10 m transects, perpendicular to the slope.

[3] Values shown represent range of mean cover of hard substrata at three fringing reefs in the Colombian Caribbean at the Santa Marta area. Data obtained by the point count method by laying 5 (20 m long) chain transects, with points every 10 cm (200 points/transect).

[4] This category may include: Hydrocoral (1 spp.), Unidentified gorgonian, actinian (1 spp.), Bryozoans (2 spp.), tunicates (2 spp.), bivalves (1 spp.).

[5] Values determined at nine depth intervals. Abundance was estimated at each depth, with eleven horizontal transects at each depth interval in shallow depth intervals (10, 20, 30 and 50 m) or a 100 m transect for the deeper areas (50, 75, 100,150, 200 and 250 m), and 100–121 photographs at each transect (0.2 m^2).

[6] Values shown represent range of total cover (%) per taxon under coral rubble (sub-rubble habitat), with sample areas of 0.3–0.7 m^2. Cover was estimated by laying a 100 cm^2 quadrat a minimum of 30× and surveying all the area under it.

[7] Same reference than the previous study.

erably (Alcolado, 1994; Zea, 1994;Woodley et al., 1997; Diaz, Smith and Newberry, in prep.). Among the reasons for this trend is the decrease in abundance of space competitors, such as algae and hard corals, caused by the lower light intensity and, possibly, higher sediment exposure (Alcolado, 1994; Zea, 1994). Another selective factor may be that some sponge species seem to thrive in mildly organically polluted areas while other groups such as hard corals decline in abundance (Alcolado, 1994; Zea, 1994).

Abundance (Biomass)

Biomass estimates of sponge abundance are even less used than area coverage estimates. Nevertheless, the existing data for biomass or standing stock on Caribbean reefs indicate that sponges may surpass most other conspicuous reef organisms such as corals and algae (Rützler, 1978). Wilkinson (1989) compared the size of sponge populations between three coral reef types in the Caribbean which he classified according to their distance and separation from the mainland: Inner reefs, middle reefs and outer reefs. The highest biomass (wet weight) values are from inner reefs (1011–2458 g m^{-2}), followed by middle reefs (99–1354 g m^{-2}), and outer reefs (368–702 g m^{-2}). At Carrie Bow Cay, just one sponge species, *Pseudaxinella? zeai*, presents mean biomass values (as total dry weight) of 8.9–439.6 g m^{-2} along depth gradients and between reef geomorphologic zones (Rützler and Macintyre, 1982; Diaz and Ward, 1997). This species attains the highest mean biomass values at the inner reef slope, 20–30 m (87.9 g m^{-2}, 0.25 ind m^{-2}) and at the fore-reef slope, 30–37 m (439 g m^{-2}, 0.98 ind m^{-2}). In sub-rubble communities (Meesters et al., 1991) of Curaçao and Bonaire, sponges had an average biomass of 300 g m^{-2} ash-free dry weight. Comparing these numbers with an estimated average biomass value for a coral reef system of 391 g m^{-2} (Polovina, 1984; Hawaiian Archipelago, all taxa including vertebrates combined) demonstrates the importance of sponges in sustaining the large standing biomass on Caribbean coral reefs. Overall, Caribbean sponges have five to six times greater biomass than Great Barrier Reef sponges at comparable locations (Wilkinson, 1989; Wilkinson and Chessire, 1990).

Biomass is a more realistic measure of sponge abundance than area cover, mainly owing to the large diversity of shape and volume of sponge specimens with species, growth form, and age. Ultimately, oxidizable carbon is considered the most realistic measure of the energy stored in a crop. Biomass estimates of Caribbean reef sponges show that organic carbon content is species-specific and ranges 14–34% of the dry weight (Rützler, 1978). Therefore, accurate biomass comparisons must include the measurement of a parameter that excludes variable and ecologically inert 'hard tissues' (spicules, sand), such as ash-free dry weight or organic carbon (Rützler, 1978).

Abundance (Volume)

Sponge abundance can also be calculated as volume (displacement or geometric approximation) to avoid the error caused by measuring only projected area of these often massive organisms. Wulff (1994) estimated the volume of 42 sponge species in a 16 m^2 area while studying fish predation of sponges in San Blas Islands, Panama. Sponge volume per substrate area averaged 2078 cm^3 m^{-2} and four species *Aplysina fulva*, *Iotrochota birotulata*, *Amphimedon rubens*, and *Ircinia* sp. accounted for 80% of total sponge volume. It is apparent that for studies of energetics involving sponges volume or biomass in weight are more realistic measures of sponge abundance than projected area.

Symbiotic Associations with Microorganisms

Diverse microbial endosymbionts have been reported in marine sponges. Some of these microorganisms include zooxanthellae associated with boring sponges (Pang, 1973) and various prokaryotes such as cyanobacteria harbored by a large taxonomic range of tropical and sub-tropical sponges (Rützler, 1990; Vicente, 1990), anaerobic phototrophs (Imhoff and Trupper, 1976), archaeobacteria (Preston et al., 1996), nitrifying bacteria (Corredor et al., 1988; Diaz, 1997; Diaz and Ward, 1997), and methanotrophic bacteria (Vacelet et al., 1995). Sponges carrying photosynthetic endosymbionts represent between 28–58% of the sponge diversity in Caribbean reefs (Wilkinson, 1989; Wilkinson and Chessire, 1990). At Carrie Bow these sponges make up 20–75% of the total sponge diversity and 15–95% of the sponge area coverage (Diaz, Smith and Newberry, in prep.). Despite the abundance of sponges carrying photosynthetic symbionts there is no evidence for 'phototrophism' (P:R ratio >3) among Caribbean sponges (Wilkinson, 1989). In terms of Carbon consumption through filter feeding, Caribbean sponges consume 4–8% of the average reef primary productivity (7 g m^{-2} d^{-1}; Kinsey, 1983), approximately 10 times the consumption of sponges in the Great Barrier Reef (Wilkinson and Chessire, 1990).

A less-studied association of Caribbean reef sponges with microbes is an indirectly proven association with nitrifying bacteria (Corredor et al., 1988; Diaz and Ward, 1997). High accumulation of dissolved inorganic nitrogen (nitrate or nitrite) has been detected in incubation experiments with three Caribbean sponges. Environmental nitrification rates of the sponge *P.? zeai* (5.8–10.9 mmol m^{-2} d^{-1}) extrapolated from incubation data (550–1030 nmol g^{-1} h^{-1} of nitrate) and biomass estimates (440 g m^{-2}) on the fore reef on the Barrier Reef off Carrie Bow Cay, Belize, surpasses the highest benthic nitrification rates reported previously (unconsolidated reef sediments: 1.68 mmol m^{-2} d^{-1}; Capone et al., 1992).

Space Competition

Various encrusting sponges have been found to overgrow corals and other sessile taxa in the Atlantic (Vicente, 1978; Suchanek et al., 1983; Aerts and van Soest, 1997). *Chondrilla nucula* was the principal aggressor on the fore reef of Cayo Enrique (Puerto Rico) with 67–80% success of overgrowth when encountering other sessile reef organisms (Vicente, 1978). This species has also been reported as a frequent aggressor in other Caribbean localities such as St. Croix (Suchanek et al., 1983) and Belize (Rützler, unpubl.). Recent studies in the Colombian Caribbean seem to show that overgrowth of corals by sponges is dependent on sponge species composition and coral cover rather than on the characteristics of the corals (Aerts and van Soest, 1997). The sponge species that overgrew corals most frequently were the thick-encrusting *Desmapsamma anchorata*, the ramose *Aplysina cauliformis*, and the vase-shaped *Callyspongia armigera*. Morphological plasticity of sponges, ability to attach to one another without causing harm (Rützler, 1970; Sarà, 1970), and diverse chemistry (Faulkner, 1995) are probably among the most important causes for their capacity to overgrow other organisms and avoid being overpowered by them.

Sponges and the Reef Framework

At least 19 sponge species (14 clionids, and five oceanapiids) make up the excavating sponges in the Caribbean (Rützler, 1971, 1974; Pang, 1973). Boring sponges of the genus *Cliona* are often the most abundant and destructive of the bioeroding infauna (Fig. 1B) (Holmes, 1997). In shallow waters of Jamaican reefs, it was found that boring sponges that produce deep excavations *(Aka* spp.) are most frequently present in massive coral heads, while those that make superficial excavations and carry 'zooxanthellae' favor flattened coral colonies exposed to the ambient light. The silt-sized chips produced by the bioerosion of these sponges contribute to the sediments of reefs and the excavations affect the structural integrity of coral colonies (Rützler, 1975; Holmes, 1997). While high levels of boring sponge activity may result in net decrease of reef accretion, non-burrowing demosponges are found to increase the rates of carbonate accretion on coral reefs (Wulff and Buss, 1979). Non-burrowing sponges are found to bind coral colonies, in shallow and deep reef areas, reinforcing the reef frame and decreasing considerably the loss of coral colonies due to disengagement by wave action, fish predation, and other forces (Wulff and Buss, 1979). Preliminary experiments show that sponges could indeed be used in reef restoration by stabilizing coral rubble (Wulff, 1984).

Sponges and the Water Column

Much less understood but no less important is our knowledge about the relations of sponges with the water column and its processes. Well-known is the place of sponges as filter feeders *par excellence* (Vacelet and Boury-Esnault, 1995). Large amounts of water are pumped daily and potentially 'modified' by circulation through the sponge body (Reiswig, 1971). Important recent discoveries demonstrate the role of sponges in the productivity and nutrient fluxes in their surrounding water. Two Caribbean sponges, *Ircinia strobilina* and *Ircinia felix*, were found to be a net sink for prokaryotes (heterotrophic bacteria, *Synechococcus* and *Prochlorococcus* spp.), and a net source for nano- and pico-eukaryotes (Pile, 1997). Furthermore, it has been shown that reef sponges exude bioactive metabolites (Thomson, 1985) that may impact plankton and nearby benthic organisms and net release of dissolved inorganic nitrogen by reef and mangrove sponges has also been demonstrated (Diaz and Ward, 1997; Pile, 1997). It is evident that Caribbean sponges play an important role in the fate of particulate organic matter (POC, PON), and that they are also a source of dissolved inorganic nitrogen (DIN) (Fig. 2). Less clear is their role as sink or source of dissolved organic matter (DOM) and detritus, as indicated in Figure 2 by question marks. The large biomass of sponges on coral reefs, their high water filtering rates, and their associations with microbes of yet unknown diversity strongly suggest an important role in the balance and dynamics of carbon and nutrients in the water column.

Discussion and Conclusions

The information compiled in this study demonstrates that sponges are among the most prominent Caribbean coral reef groups in open reef habitats and the most diverse and abundant component in sub-rubble reef communities. Therefore, any assessment or monitoring effort of a coral reef must include a characterization of its sponge diversity as well as its species composition and biomass. Regarding sponge diversity, we must encourage

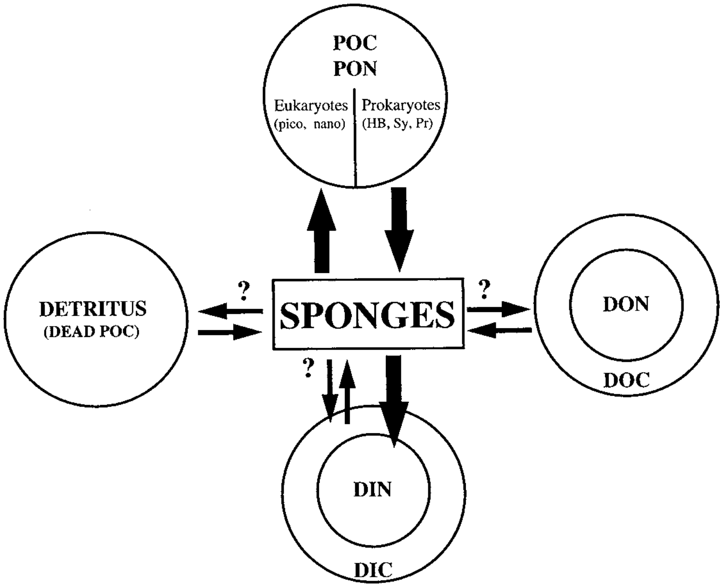

Figure 2. Schematic representation of the relationships of sponges with the water column. Four major compartments in the water column are distinguished: Particulate organic carbon (POC) and nitrogen (PON), dissolved organic carbon (DOC) and nitrogen (DON), dissolved inorganic carbon (DIC) and nitrogen (DIN), detritus. Well-known relations that have been established are represented by thick arrows. Some Caribbean sponges have been found to be net sink for prokaryotes (heterotrophic bacteria, *Synechoccocus*, and *Prochlorococcus* spp.) and net source for eukaryotes (nano- and pico-eukaryotes). The net release of dissolved inorganic nitrogen (DIN) has been measured for various reef sponges. Other detected or expected, but not assessed, relations with other components of the water column (dissolved organic nitrogen, detritus, etc.) are represented with smaller arrows and question marks.

use and standardize tools for estimating species richness on reefs. The lack of a comprehensive knowledge of sponge diversity on Caribbean coral reefs is due to shortage of suitable literature, low number of Porifera specialists, and difficulties encountered by non-specialists in identifying sponge species. Generating field-oriented, taxonomically sound classification guides and training non-specialists who are involved in assessment and monitoring programs (e.g., CARICOMP, Rapid Assessment surveys) would improve this situation. Publication of useful field guides (e.g., Rützler 1986, Humann, 1992) is expensive because of the high cost of important color images but may become affordable soon by using electronic means of distribution. Another problem is the need to verify field identifications by examining microscope preparations (Rützler, 1978), which is cumbersome for non-specialist field workers but could be encouraged in special workshops.

Diversity data of sponges and other reef epibenthos reported from several Caribbean localities are quite variable (Table 1). Standardization of methods could make this information more comparable. The 'species-specific' functionality of sponges on coral reefs argues for the need to study the composition of sponge communities in order to allow predictions regarding reef health, successional changes, and success of restoration. For example, burrowing sponges decrease reef stability, while non-burrowing ones may increase accretion and several species play an important role in reef space exploitation through direct competition and epizoism.

Measuring area coverage may reflect how sponges impact reef-substrate space in comparison with other sessile benthos groups. However, the large variation of shape and volume with species, growth form, and age makes volume or weight estimates a more realistic measure of sponge abundance. These more tedious and time-consuming methods might be selected for special surveys where assessing and monitoring biomass is important. For example, quantitative studies of sponge predation, infauna, productivity, or nitrification require knowledge of biomass or standing crop.

Although sponges are traditionally considered to be simple and efficient consumers, they acquire metabolic diversity through their associations with microbes, many of them endosymbionts. The study of the physiology and ecology of these associations is also necessary to grasp the role of sponges in coral reefs, particularly in view of different bioactive metabolites that may be produced by host and symbiont (Faulkner et al., 1998). Basic aspects of sponge biology and ecology, such as systematics, abundance, growth, reproduction, means of dispersal, and physiological tolerance should be a priority when attempting to preserve and protect coral reefs. However, the participation of sponges in nutrient and carbon fluxes, in connecting benthic and pelagic reef compartments, and as hosts of diverse microbial associations should not be ignored because it contributes substantially to the healthy function of coral reefs.

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