Limnol. Oceanogr., 55(5), 2010, 2001–2010

doi:10.4319/lo.2010.55.5.2001

Revisiting silicon budgets at a tropical continental shelf: Silica standing stocks in sponges surpass those in diatoms

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Abstract

Most of the silicon (Si) in marine coastal systems is thought to recirculate under the biological control of planktonic diatoms. We challenge this view after comparing the biogenic silica (bSi) standing stocks contributed by communities of planktonic diatoms and benthic sponges in five habitats of an extensive continental shelf area of the Mesoamerican Caribbean. In most habitats (outer reefs, patch reefs, sea grass beds, and mangroves), the sponge bSi stocks surpassed those of diatoms. Collectively, bSi in sponge communities was about 88.6% of the total Si pool. Diatoms represented 4.2% and ambient silicate about 7.2%. Consequently, when constructing future regional Si budgets in coastal areas, the Si standing stocks in sponge populations should be empirically examined before deciding that their contribution to the total is negligible. In order to understand Si fluxes in coastal areas where sponges are relevant, we need additional empirical approaches to set the timescale of sponge bSi turnover, which appears to be substantially slower than that of diatom bSi.

Silicate, a dissolved form of silicon (Si), is a major ocean nutrient. It fuels primary production by enhancing growth of diatoms, which require silicate to construct their skeletons of biogenic silica (bSi). Therefore, there is enormous interest in predicting the interplay between silicate and bSi budgets. Ever since the earliest models attempting to establish a general balance for Si in the ocean (Harriss 1966; Burton and Liss 1968; Calvert 1968), biological Si cycling has always been thought to revolve around diatoms. Because diatoms are estimated to consume yearly nearly all the Si available in the upper ocean (about 240×10^{12} Si mol) to build their bSi skeletons, silicon pools are thought to be under their control, with other Si-consuming organisms such as sponges, radiolarians, choanoflagellates, and silicoflagellates playing only a negligible role (Tréguer et al. 1995; Ragueneau et al. 2000; Sarmiento and Gruber 2006). Since diatoms are short lived and, upon death, up to 50% of their frustules dissolve readily as reusable silicate before sinking down to the aphotic ocean, it is thought that the largest Si stock recirculates relatively rapidly in a diatom-driven uptake-dissolution loop, completing 39 uptake-dissolution events in about 400 yr (Nelson et al. 1995; Tréguer et al. 1995). Nevertheless, while such a diatom-driven loop may appropriately represent the Si cycling in open-ocean blue water, it may not realistically reflect the situation on at least some continental shelves, which often are characterized by extended shallow bottoms densely populated by long-lived siliceous (Si-consuming) sponges.

In the few sponge species investigated at a population scale so far, the Si standing stocks were surprisingly large when compared with those available as silicate in the ambient water of the respective habitats (Rützler and Mcintyre 1978; Maldonado et al. 2005). More importantly, upon death, the silica skeletal pieces of sponges (spicules) appear to be far more refractory to dissolution than diatom frustules in both basic solutions and seawater (Hurd 1983; Hurd and Birdwhistell 1983; Maldonado et al. 2005). Such differences in dissolution rates between spicules and frustules cannot be explained only in terms of an assumedly larger surface area of diatom frustules, given that sponge spicules with very different surface areas dissolved equally slowly in experimental conditions (Maldonado et al. 2005). Whatever the reason for a much slower dissolution of sponge bSi, the result is that populations of siliceous sponges on continental margins appear to function as benthic Si traps that retard conversion of bSi into silicate (Maldonado et al. 2005).

At first sight, these peculiarities of the Si route through sponges may be perceived as merely anecdotal, because the contribution of these organisms to the global Si budget in coastal areas is regarded to be negligible when compared with that of diatoms (Tréguer et al. 1995; Ragueneau et al. 2000; Sarmiento and Gruber 2006). However, given that the currently accepted model for the marine Si cycle has emerged in the complete absence of quantitative data for sponges, we have decided to revisit empirically the widespread assumption that the bSi standing stock in sponges is negligible when compared with that of diatoms. The importance of sponges to Si cycling in continental waters has been established by the only study to date comparing sponge and diatom contributions, which proved that, contrary to expectations, sponges largely dominated the Si budgets in some Florida lakes (Conley and Schelske 1993). Therefore, in an attempt to provide empirical data to support the widespread—but never tested—assumption that siliceous sponges are negligible when calculating regional Si budgets in marine coastal areas, we have measured for the first time the relative contributions of sponges, planktonic organisms, and ambient silicate in seawater to the local Si stock of several major habitats of a tropical continental shelf.

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Methods

Habitat charting—The Smithsonian Institution's Carrie Bow Marine Field Station, located at the Belize's continental shelf edge, was used as a logistic base for field work. The Belizean section of the Mesoamerican Barrier Reef is 250 km long and runs north–south parallel to the mainland along the outer edge of a large, shallow carbonate shelf (Fig. 1). Because the shelf's edge is distant from the mainland (> 15 km, on average), its seaward region is by and large unaffected by detrimental anthropogenic disturbances. Continental runoff brings in very limited (episodic) amounts of both dissolved nutrients and suspended materials, such as aluminosilicate-rich terrestrial clays, and has no substantial effect on the predominant calcareous rock and sediments of the outer reef platform. This nearly pristine, nonoligotrophic environment consisted of four major habitats: (1) outer reefs (OR), developed along the external shelf edge, with a fore reef facing the open ocean; (2) patch + back reefs (PR), developed at the leeside of the reef ridge, in the cuts between adjacent barrier-reef cays, or scattered across the lagoon; (3) island mangroves (MG), forming cays on the inner reef platform; and (4) sea grass meadows (SG), spread over the sandy bottom of the lagoon. After the four major habitats were charted (OR, PR, SG, MG), a large bottom area (Fig. 1B) of sandy, poorly vegetated lagoon bottom was left, designated as soft bare bottom (BB). To estimate the bottom area and average water depth at the different habitats, we combined information from local marine charts, satellite orthophotographs available in the public domain http://earth.google.com/, and global positioning system (GPS) and depth-sounder field data obtained during boat trips and dives (Fig. 1). For calculations of area and water volume in mangroves, we measured the length of shoreline populated by red-mangrove trees (*Rhizophora mangle*); we estimated that sponge-bearing stilt roots occupied a 2-m-wide band, and that the characteristic mangrove plankton system extended, on average, over the adjacent 5-m-wide band of water column.

Measurement of seawater silicate and plankton bSi—We measured concentrations of silicate and plankton bSi in the seawater overlaying the benthic habitats. Because both nutrient concentration and plankton abundance vary seasonally, we attempted to capture the two periods that differed most by sampling in both winter (November–December 2005) and summer (July 2006). Water samples for nutrient analysis were collected by diver-operated Niskin bottles from both middle depth and near bottom (i.e., within 0.5 m from bottom or mangrove roots) and pooled for the analyses ($n = 6$, per season and habitat; $n = 4$ per open-water reference values). We also sampled oceanic water at 12 m depth, 5 km seaward of the barrier reef (Fig. 1) over some 400 m bottom depth, which served as a reference for comparison with continental shelf habitats. Water subsamples were transferred to HCl-cleaned, 20-mL polyethylene vials and refrigerated in the dark for 3 d before measuring concentration of molybdate-reactive silicate using a Bran-Luebbe, Transference Automated Analysis Colorimetric System (TrAACS-2000).

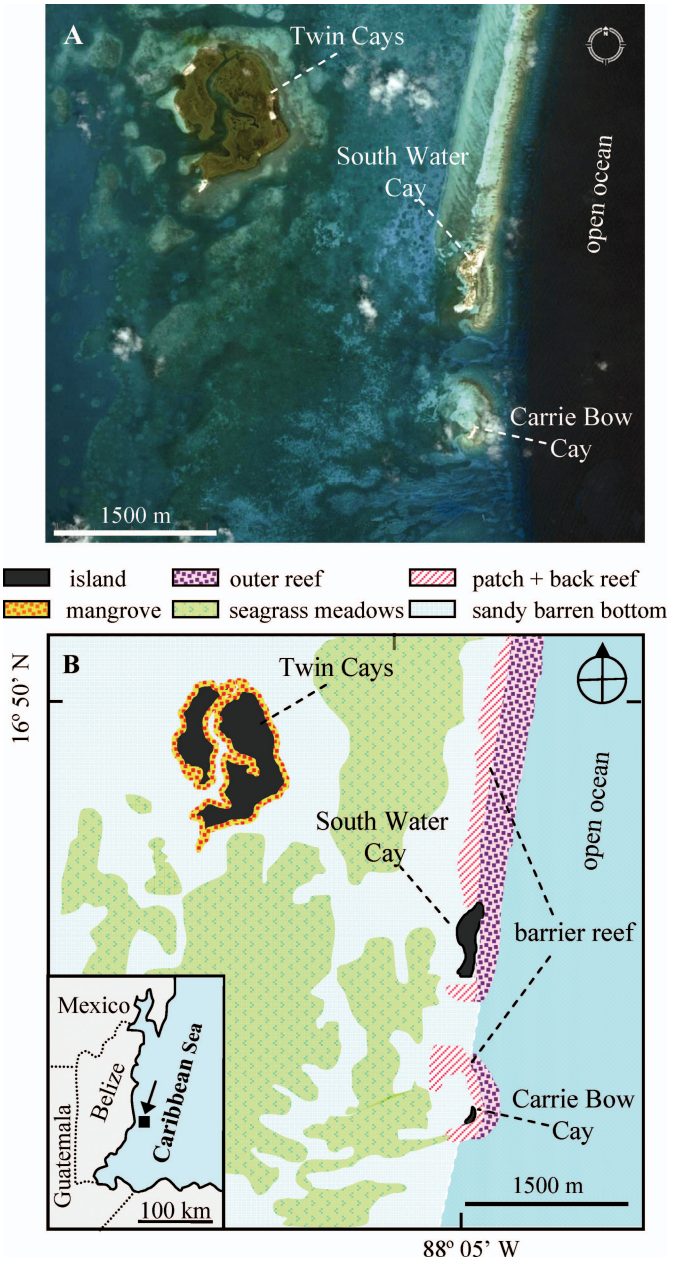

Fig. 1. Surveyed continental shelf area off Belize, Central America. (A) Orthophotograph of the studied shelf area and the adjacent open ocean, which is separated from the lagoon by the reef barrier. (B) Map with inset showing the position of the enlarged study area. Keys point out the location and relative size of the habitats.

Samples for estimating the plankton bSi stock over the benthic habitats were collected at various depths (2–15 m) using diver-operated Niskin bottles both in the morning and in the evening and pooled in the analyses to compensate for the daily variability of plankton occurrence in each habitat ($n_{OR} = 20$; $n_{PR} = 25$; $n_{SG} = 22$; $n_{MG} = 23$). Known volumes of water (1–2 liters, depending on habitat and season) were filtered immediately after collection through polycarbonate membrane filters (4.7 cm in diameter, 0.6-μm pore size) using a vacuum pump. Filters

were dried at 60°C, folded, and stored in the refrigerator for 2 months, then subjected to a double, wet-alkaline digestion to discriminate Si derived from biogenic and lithogenic sources (Ragueneau et al. 2005). After each alkaline digestion of filters, silicate concentrations were determined by autoanalyzer. Aluminum concentrations were determined using a colorimetric method (Grasshoff et al. 1983). Because lithogenic silica (lSi) was undetectable in nearly all our winter samples, the summer samples and the final regional calculations were run without lSi correction.

Values of silicate concentration and planktonic bSi for the BB habitat were estimated as the average of values measured for all other shelf habitats, except the peculiar mangrove environment. When required, silicate concentrations and bSi biomass were converted into Si biomass, according to the ratios of their respective molecular and atomic weights. Differences in rank-transformed data for both silicate concentrations and plankton bSi concentrations were examined as a function of season (winter vs. summer) and habitat (OR, PR, SG, MG) by two-way ANOVAs, followed by subsequent, pairwise Student–Newman–Keuls (SNK) tests to identify groups responsible for significant differences in the main factors. Local Si stocks in silicate and plankton for each of the habitats were calculated from data on bottom area, average water depth, and average Si content per unit volume for each of the sources.

For the taxonomic study of microplankton (radiolarians, choanoflagellates, diatoms, silicoflagellates, dinoflagellates, and coccolithophorids), 100-mL subsamples ($n = 3$) of seawater per habitat and season were collected, fixed in Lugol's iodine solution, and stored in the refrigerator until taxonomic identification using an inverted compound microscope. A detailed account of the composition and abundance of the major phytoplankton groups in the studied habitats will be reported elsewhere (A. Bucci unpubl. data).

*Measurement of sponge b*Si—To estimate the Si content in the sponge communities, we identified taxonomically all sponges found in random sampling quadrats ($n = 409$), measured in vivo the volume of each siliceous individual ($n = 1882$), and calculated Si content from average Si values (mg Si cm^{-3} of living tissue) determined for each species through previous hydrofluoric acid (HF) desilicification. Aspiculate and calcareous sponge species were not considered in those quantifications.

The sponge communities at the OR, PR, SG, and MG habitats were investigated by scuba diving and sampled using random 1-m^2 polyvinylchloride quadrats, with various replication efforts depending on habitat size and heterogeneity of the sponge assemblages ($n_{OR} = 99$; $n_{PR} = 64$; $n_{SG} = 135$; $n_{MG} = 111$). In a conservative approach, the sandy, poorly vegetated lagoon bottom (BB) was assumed to lack sponges, although some siliceous species are known to be adapted to this habitat (Wiedenmayer 1977; Rützler 1997). In mangroves, we accounted for the sponge fauna growing on the stilt roots inside 1-m^2 quadrats established at the water surface because the muddy mangrove bottoms, which often lacked sponges, were not reached by all roots. Safety rules limited the scuba survey on the outer fore reef to a maximum depth of 25 m. The volume (cm^3) of each individual was estimated using a combination of 20 and 50 cm plastic rulers. The body shape was approximated to one or, more often, several geometric figures (spheres, ovals, solid cylinders, hollow cylinders, rectangular plates), and the linear parameters (length, width, diameters) were measured in situ to calculate volumes. To prevent overestimation, we applied a one-fourth reduction to volume values calculated for each individual. To convert measured sponge volumes to bSi content, we filled a plastic measuring cylinder with sponge tissue, applying minimum compression and proportional amounts of both ectosomal and endosomal regions. After drying pieces ($n = 3$ to 6, depending on availability) to constant weight at 60°C, we desilicified by immersion in 5% HF for 5 h, then rinsed in distilled water three times for 2 min to remove all HF, and dried to constant weight again. We calculated bSi content per unit sponge volume as the dry weight difference before and after desilicification. To prevent overestimation of skeletal bSi, we assumed that only 75% of the weight difference contributes to sponge skeleton. Mean weight of bSi content per cubic centimeter sponge volume served as an estimate of total bSi content per species and bottom area in the various habitats. Differences in sponge bSi as a function of habitat (OR, PR, SG, MG) were examined by a Kruskal–Wallis analysis, followed by pairwise Dunn's tests to identify groups responsible for the significant differences in the main factor.

To estimate sponge bSi, we preferred dissolving siliceous spicules by immersion in HF over the alternative approach of removing the organic tissue in boiling nitric acid to weigh the nondissolved residue. This was done for several reasons: (1) Unlike HF, nitric acid treatment requires sample boiling, which in turn requires the use of heavy glass containers, thereby reducing the accuracy of subsequent weighing. (2) Skeletal content tends to be overestimated when nitric acid is used because it does not eliminate foreign inorganic elements that sponges typically incorporate in their tissue or skeletal organic fibers (sand grains, skeletal remains, etc.). (3) Boiling in nitric acid also produces salts that mask skeletal content unless samples are rinsed in distilled water, a tedious process that risks removing sponge spicules. (4) Heating of glass containers usually causes changes in both container volume and mass, introducing an uncontrolled factor in the weighing process. (5) With HF at room temperature and low concentration, the main concern is that all spicules have been dissolved during the treatment. If spicules had not all been dissolved in some tissue samples, the results would have led us to underestimate the sponge skeletal mass, which in turn would have merely made our estimates of sponge Si content more conservative.

Results

We surveyed a 21.7-km^2 continental shelf area located about 15.5 km from the nearest mainland and including three small islands (Fig. 1). Our estimates of bottom

extension (m^2) and water-column volume (m^3) for each of the habitats (Fig. 1; Table 1) revealed that sandy unvegetated bottoms (BB) and sea grass meadows (SG) were the best represented habitats in terms of both area (51.5% and 43.5%, respectively) and water volume (49.6% and 42.3%, respectively), with only minor contributions (< 8%, collectively) by the remaining habitats (i.e., outer reef, patch reef, and mangroves).

Silicate at the shelf averaged 3.6 ± 0.6 $\mu g\ L^{-1}$ (mean ± SD, $n = 56$), with detectable differences between seasons and habitats (Fig. 2A). Planktonic bSi content averaged 113.9 ± 99.7 $\mu g\ L^{-1}$ ($n = 91$), again with differences between seasons and habitats (Fig. 2B). The taxonomic study of plankton samples ($n = 30$; 100 mL each) revealed a total of 210 species, with members of only two siliceous groups (silicoflagellates and diatoms) and no choanoflagellate or radiolarian. Silicoflagellates of a single species appeared in three samples, for a total of only five cells. Diatoms consisted of 103 species totaling 14,153 cells, which accounted for 71.5% ± 11.6% of all microphytoplankton cells in winter and 87.5% ± 20.5% in summer. The species *Thalassionema nitzschoides* and *Thalassionema frauenfeldii* and several *Chaetoceros* spp. dominated in both winter and summer.

The quadrat survey ($n = 409$) of the sponge communities at the habitats revealed 67 siliceous species (Table 2) averaging 4.6 individuals m^{-2}, a biomass of 2.6 ± 14.3 liters of living tissue m^{-2}, and a mean bSi content of 0.3 ± 2.7 kg m^{-2}. There were large between-habitat differences in both sponge biomass and bSi (Fig. 3). The skeletal content of siliceous sponges of our tropical assemblage accounted for 15–25% of dry weight in some species, up to 50–65% in others, averaging 53.4 ± 6.1 bSi mg per liter of living tissue (Table 2). In mangroves, the overabundant, midsize "fire sponge," *Tedania ignis* (Fig. 4A) made the largest bSi contribution (0.1 ± 0.8 kg m^{-2}), while *Iotrochota arenosa*, a new species discovered during our survey, was the major bSi contributor (1×10^{-3} kg m^{-2}) in sea grass beds (Fig. 4B). In reef habitats, the large and well-silicified "giant barrel sponge" *Xestospongia muta* (Fig 4F) and the congeneric *Xestospongia rosariensis* respectively averaged 0.5 ± 3.2 and 0.1 ± 0.9 kg bSi m^{-2} and were major bSi contributors, with large individuals of the former species containing up to 28 kg bSi each.

By integrating the average Si content of the three investigated sources (i.e., seawater, plankton, and sponges; Table 1) over the bottom area and water depth of the various habitats, we calculated a regional budget of 290.7 $\times 10^3$ kg Si, averaging 13.4 $\times 10^3$ kg km^{-2}. Contrary to what might be expected, diatoms did not dominate this Si stock (Table 1). Mangrove habitat, which occupied only 0.2% of the shelf area, contributed 1.5 $\times 10^3$ kg (0.5%) to the regional pool. This bSi derived largely (98.4%) from the skeletons of the 12 sponge species identified from red-mangrove stilt roots (Table 2; Fig. 4A); the diatom community (67 species) accounted for only 0.4%; and silicate in seawater for 1.1% (Table 1). Sea grass beds covered nearly half (43.6%) of the shelf area but contributed only 12.2% (35.6 $\times 10^3$ kg) to the regional Si pool. The sponge fauna of this habitat consisted of 23

Table 1. Summary of dimensions and Si contribution of the various ecological compartments studied on the Belizean shelf. Data are bottom area, average depth, and estimated water volume over the habitats, as well as mean Si content (mg) in dissolved silicate and plankton organisms per liter seawater, mean Si content (mg) in sponge skeleton per square meter of habitat bottom, and total Si content (kg) in each source studied (i.e., dissolved in seawater, plankton organisms, and sponge populations). OR, outer reefs; PR, patch reefs + back reefs; SG, sea grass beds; MG, mangroves; BB, sandy, poorly vegetated lagoon bottom without noticeable sponges.

Habitat	Bottom area (10^5 m^2)	Mean depth (m)	Water volume (10^6 m^3)	Mean dissolved Si (mg L^{-1})	Mean plankton Si (mg L^{-1})	Mean sponge Si (mg m^{-2})	Total dissolved Si (10^3 kg)	Total plankton Si (10^3 kg)	Total sponge Si (10^3 kg)	Total Si (10^3 kg)
OR	6.45	20.00	12.90	0.101	0.060	303,679.757	1.302	0.770	195.938	198.010
PR	4.89	10.00	4.89	0.094	0.044	78,146.254	0.459	0.214	38.246	38.919
SG	94.53	10.00	94.53	0.091	0.056	2,306.816	8.571	5.259	21.806	35.635
MG	0.43	3.00	0.13	0.129	0.056	86,260.087	0.017	0.007	1.485	1.509
BB	110.72	10.00	110.72	0.097	0.053	0.000	10.756	5.870	0.000	16.627
Total	217.02	10.28	223.17				21.105	12.120	257.475	290.700

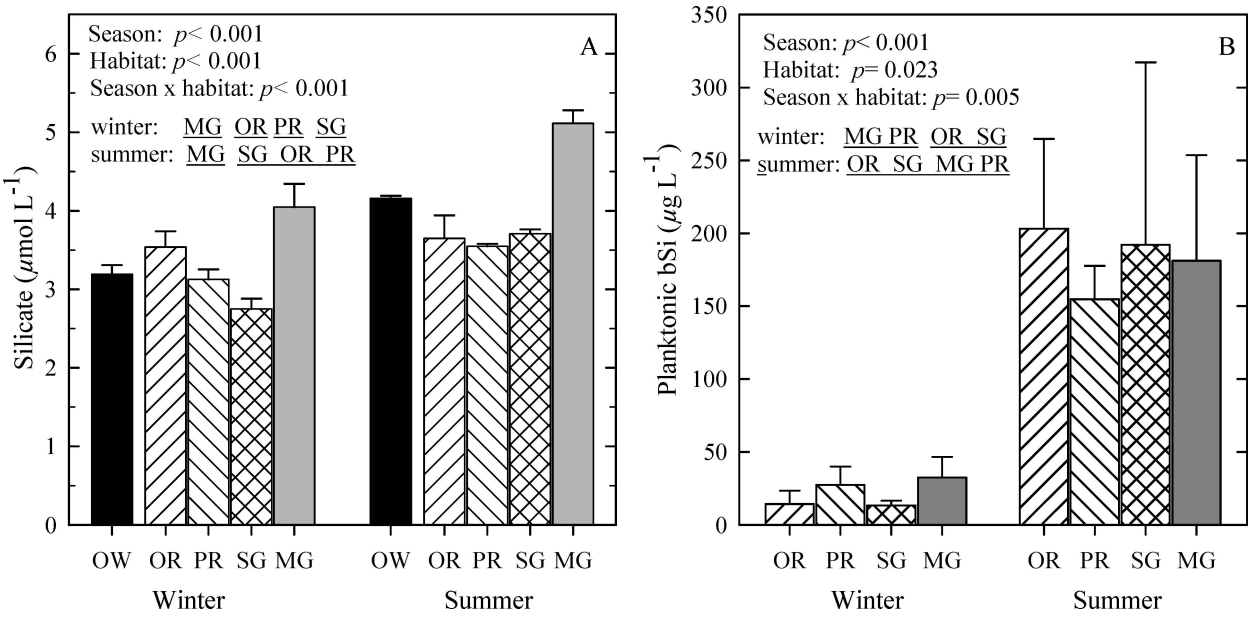

Fig. 2. Summary of concentrations (mean ± SD) of (A) ambient seawater silicate and (B) planktonic bSi and their respective two-way ANOVAs showing differences in rank-transformed data as a function of season (winter vs. summer) and habitat (OR, outer reefs; PR, patch + back reefs; SG, sea grass beds; MG, mangroves). (A) There was a significant "season effect" ($p < 0.001$) on silicate, with slightly higher concentrations in summer (4.00 ± 0.56 μmol L^{-1}) than in winter (3.37 ± 0.74). This seasonal trend was also seen in reference samples of surface oceanic water (OW). Significant between-habitat differences ($p < 0.001$), as well as a significant season–habitat interaction ($p < 0.001$), indicate that between-habitat differences depend on season. Habitat keys (near top of graph and ordered in decreasing magnitude) summarize the results of pairwise SNK tests, with keys sharing underline being not significantly different from each other. Mangroves showed significantly higher concentration in both seasons ($p < 0.05$), and differences among the remaining habitats (OR, PR, SG) were evident only during winter ($p < 0.05$). (B) Mean planktonic bSi was about eight times higher in summer (182.382 ± 79.307 μg L^{-1}) than in winter (22.795 ± 13.358 μg L^{-1}); the ANOVA revealed that significant between-habitat differences ($p = 0.023$) depended on season. ($p = 0.005$). "A posteriori" SNK tests indicated that small between-habitat differences were detectable only in winter.

species, typically small individuals scattered at low density (Table 2; Fig. 4B,C). Yet it provided 61.2% of the local Si stock, while the diatom community (59 species) and seawater silicate accounted for 14.8% and 24%, respectively (Table 1). Patch + back reefs occupied only 2.2% of the studied shelf but contributed 38.9 × 10^3 kg (13.3%) to the regional Si pool (Table 1). Again, most of the Si in these reef habitats (98.2%) was provided by the 22 identified sponge species, which occurred at relatively high density (Table 2; Fig. 4D). The 56-species diatom community (0.6%) and seawater silicate (1.2%) made only minute contributions. The importance of sponges was even higher on outer reefs (Table 2; Fig. 4E,F). This habitat represented only 2.9% of the studied shelf area but contributed 198 × 10^3 kg Si to the regional Si pool (Table 1), by far the largest level (68.1%) for all the habitats. About 98.9% of that Si came from the 40 identified sponge species, whereas diatoms (42 species) and seawater silicate collectively contributed only 1.1%. After charting the four major habitats (OR, PR, SG, MG), we examined the large (51%) soft-bottom, barren area (BB). Despite its size, the BB habitat contributed only a modest 5.6% (i.e., 16.6 × 10^3 kg Si) to the regional Si pool (Table 1). In the absence of sponges, the Si stock on BB came largely from silicate in ambient water (64.6%) and diatoms (35.4%).

Altogether, about 88.6% of the Si budget on the coastal shelf derived from the skeleton of living sponges, about 7.2% from silicate in the local water column, and only 4.2% from the frustules of planktonic diatoms (Table 1).

Discussion

Our research has shown, contrary to expectations, that sponges comprise the largest standing stock of bSi in this regional pool, being clearly dominant in four out of the five sublittoral systems investigated. Such a sponge dominance cannot be attributed to impoverished environments in terms of either nutrients or phytoplankton. Both silicate and plankton bSi concentrations fell within the range of values measured for other nonoligotrophic, subtropical, and temperate coastal zones lacking large river plumes (Ragueneau et al. 2005) and were notably higher than those typically recorded from offshore subtropical systems (Brzezinski and Kosman 1996; Sarmiento and Gruber 2006). The portion of the Mesoamerican shelf we studied was relatively shallow, favoring a low contribution of diatoms to the regional budget. Nevertheless, according to the measured bSi concentrations (Table 1), the shelf depth would have to average 220 m before the plankton bSi could approach the level of sponge bSi in the regional pool. Therefore, sponges would still play a relevant role in this coastal system, even if it was a very deep continental shelf with homogeneous diatom production through the entire water column.

Table 2. Summary of sponge bSi contents per species. Mean bSi (mg) content per cubic centimeter of living sponge tissue and mean (± SD) bSi stock per square meter in each habitat. OR, outer reefs; PR, patch + back reefs; SG, sea grass beds; MG, mangroves.

		OR		PR		SG		MG	
Sponge species	bSi mean	mean	SD	mean	SD	mean	SD	mean	SD
Agelas clathrodes	32.44	155.64	861.20	77.54	442.44	0.00	0.00	0.00	0.00
Agelas conifera	71.88	14186.31	32289.05	3052.67	20608.11	0.00	0.00	0.00	0.00
Agelas dispar	68.87	0.00	0.00	0.00	0.00	134.87	1567.04	0.00	0.00
Agelas sceptrum	74.89	1945.84	10566.71	1403.86	11319.68	0.00	0.00	0.00	0.00
Agelas wiendermayeri	39.04	1656.42	11103.13	2.23	12.84	0.00	0.00	0.00	0.00
Amphimedon compressa	76.12	368.82	1871.71	0.00	0.00	1748.63	14175.59	0.00	0.00
Amphimedon erina	82.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Biemna caribea	34.78	0.00	0.00	0.00	0.00	0.00	0.00	268.86	1421.91
Biemna sp.	32.68	0.00	0.00	19.15	154.41	0.00	0.00	0.00	0.00
Callyspongia fallax	19.37	7.11	70.75	0.00	0.00	0.00	0.00	0.00	0.00
Callyspongia plicifera	17.18	620.80	2555.41	0.00	0.00	0.00	0.00	0.00	0.00
Callyspongia ramosa	28.12	0.00	0.00	53.41	328.21	0.00	0.00	0.00	0.00
Callyspongia sp.	30.52	143.19	1394.23	0.00	0.00	0.00	0.00	0.00	0.00
Callyspongia vaginalis	29.78	345.49	1855.05	1352.28	5168.84	0.00	0.00	0.00	0.00
Calyx podatypa	40.74	0.00	0.00	0.00	0.00	208.07	1268.02	0.00	0.00
Chalinula molibta	27.16	0.00	0.00	0.00	0.00	0.00	0.00	1475.10	7680.84
Chondrilla nucula	35.76	5.70	49.51	0.00	0.00	1.49	13.02	0.00	0.00
Cinachyrella apion	46.97	926.46	8778.63	389.11	3137.47	0.00	0.00	0.00	0.00
Clathria venosa	37.92	0.00	0.00	0.00	0.00	51.76	591.60	0.00	0.00
Cliona caribbaea	21.22	5.46	41.62	1625.58	4175.42	0.00	0.00	0.00	0.00
Cliona delitrix	21.22	12.18	94.26	0.00	0.00	0.00	0.00	0.00	0.00
Cliona varians	81.20	320.66	1603.99	63.18	329.87	874.31	7087.80	0.00	0.00
Cryptotethya cripta	51.44	844.48	8402.92	575.12	3490.99	339.04	3939.34	0.00	0.00
Desmapsamma anchorata	48.75	0.00	0.00	0.00	0.00	372.51	1166.04	0.00	0.00
Ectyoplasia ferox	45.70	1345.55	9063.72	0.00	0.00	0.00	0.00	0.00	0.00
Geodia neptunii	94.05	46658.25	254851.20	23568.15	190035.70	0.00	0.00	0.00	0.00
Halichondria magniconulosa	30.71	0.00	0.00	0.00	0.00	0.00	0.00	5493.02	27960.93
Haliclona curacaoensis	38.88	0.00	0.00	0.00	0.00	0.03	0.36	0.00	0.00
Haliclona implexiformis	50.77	0.00	0.00	0.00	0.00	5.85	44.03	6233.98	31749.94
Haliclona manglaris	27.38	0.00	0.00	0.00	0.00	0.00	0.00	264.52	1344.17
Haliclona sp.1	38.20	0.00	0.00	0.00	0.00	1.84	10.28	0.00	0.00
Haliclona sp.2	33.12	0.00	0.00	0.00	0.00	30.66	283.16	0.00	0.00
Haliclona sp.3	37.17	0.00	0.00	0.00	0.00	0.00	0.00	89.72	547.48
Haliclona sp.4	38.20	6.50	40.96	0.00	0.00	0.00	0.00	0.00	0.00
Haliclona sp.5	31.83	0.00	0.00	0.00	0.00	2.32	26.91	0.00	0.00
Haliclona tubifera	35.71	0.00	0.00	0.00	0.00	0.00	0.00	4.28	28.32
Holopsamma helwigi	48.83	0.00	0.00	2524.90	6205.53	0.00	0.00	0.00	0.00
Hymeniacidon sp.	67.57	24.56	204.42	0.00	0.00	0.00	0.00	0.00	0.00
Iotrochota arenosa	61.93	0.00	0.00	0.00	0.00	1092.82	2570.13	0.00	0.00
Iotrochota birotulata	45.71	188.57	1541.27	5446.54	5106.06	24.38	131.31	0.00	0.00
Lissodendoryx isodictyalis	45.57	0.00	0.00	0.00	0.00	0.00	0.00	9337.10	47713.79
Lissodendoryx colombiensis	41.77	230.18	2290.42	0.00	0.00	0.00	0.00	0.00	0.00
Monanchora barbadensis	59.42	25.28	109.98	17.69	55.65	0.00	0.00	0.00	0.00
Monanchora cf. *arbuscula*	48.81	0.00	0.00	0.00	0.00	39.11	111.52	0.00	0.00
Mycale cf. *americana*	20.00	0.00	0.00	0.00	0.00	0.17	1.96	0.00	0.00
Mycale laevis	53.10	74.08	493.12	134.22	430.24	0.00	0.00	0.00	0.00
Mycale laxissima	43.66	64.15	638.33	123.28	707.47	0.00	0.00	809.27	4733.88
Mycale microsigmatosa	28.79	0.44	4.38	0.00	0.00	0.00	0.00	607.17	3225.54
Niphates digitalis	33.35	1824.70	7051.73	663.44	4323.96	113.77	1301.44	0.00	0.00
Niphates erecta	75.06	589.23	1686.22	2219.09	8952.80	380.30	1051.37	0.00	0.00
Petrosia pellasarca	56.18	1048.05	8244.79	0.00	0.00	0.00	0.00	0.00	0.00
Petrosia sp.	63.67	0.00	0.00	0.00	0.00	14.23	143.93	0.00	0.00
Petrosia weinbergi	63.67	3395.64	32151.50	0.00	0.00	0.00	0.00	0.00	0.00
Plakinastrella onkodes	186.67	1305.40	5214.70	0.00	0.00	0.00	0.00	0.00	0.00
Plakortis angulispiculatus	149.38	133.74	1330.78	0.00	0.00	0.00	0.00	0.00	0.00
Plakortis halichondroides	84.62	885.07	5978.32	0.00	0.00	0.00	0.00	0.00	0.00
Pseudoaxinella lunaecharta	80.65	13.58	104.58	0.00	0.00	0.00	0.00	0.00	0.00
Scopalina ruetzleri	48.02	166.28	468.84	643.30	1366.77	0.00	0.00	160.87	897.90
Siphonodyction coralliphagum	63.67	147.03	959.63	0.00	0.00	0.00	0.00	0.00	0.00
Tedania ignis	46.16	0.00	0.00	0.00	0.00	196.13	993.26	178252.66	884052.09

Table 2. Continued.

Sponge species	bSi mean	OR		PR		SG		MG	
		mean	SD	mean	SD	mean	SD	mean	SD
Teichaxinella sp.	42.44	0.00	0.00	13.93	77.09	0.00	0.00	0.00	0.00
Timea sp.	50.93	1.56	15.51	0.00	0.00	0.00	0.00	0.00	0.00
Xestospongia carbonaria	71.83	65.58	652.51	0.00	0.00	356.23	1459.15	0.00	0.00
Xestospongia cf. *rosariensis*	63.67	325.67	3174.44	0.00	0.00	0.00	0.00	0.00	0.00
Xestospongia muta	148.36	576443.99	3025200.87	123215.14	993513.54	0.00	0.00	0.00	0.00
Xestospongia proxima	40.84	524.98	5223.78	0.00	0.00	0.00	0.00	0.00	0.00
Xestospongia subtriangularis	91.08	0.00	0.00	0.00	0.00	356.69	2707.12	0.00	0.00
Total averages	53.40	649683.62	3019174.35	167183.82	999253.67	4935.13	9695.21	184542.32	306672.01

The dominance of the sponge bSi standing stock emerged even when our approach tended to underestimate the local bSi stocks. First, we assumed that only three-quarters of the weight decrease measured after desilicification of sponge tissues in HF was attributable to skeletal bSi, the rest was attributable to either tissue attrition or digestion of siliceous sand grains embedded in the sponge tissue. Nevertheless, our histological sections showed no obvious cell damage accounting for tissue attrition. Additionally, the absence of lithogenic Si in our filter digestions indicated that sand grains are overwhelmingly of calcareous nature in this carbonated continental shelf, so that it is unlikely that any acid digestion of siliceous grains embedded in the sponge body would have significantly biased our estimates of skeletal bSi. Likewise, to avoid overestimation of sponge volumes, we used only three-quarters of the measured values. Following these combined corrections, we used only 56.2% of the skeletal Si measured in the final calculations. In addition, we assumed that no sponges occurred on the extensive sandy lagoon bottom (BB habitat), although some siliceous species are known to have adapted to this environment (Wiedenmayer 1977; Rützler 1997).

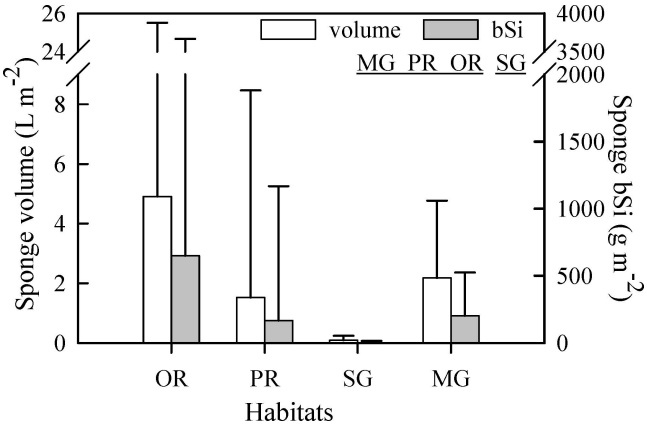

Fig. 3. Summary for data (mean ± SD) of volume and bSi content per area unit in the sponge communities of the habitats. A Kruskal–Wallis analysis of bSi content indicated significant between-habitat differences ($H = 45.457$; $df = 3$; $p < 0.001$). "A posteriori" Dunn's pairwise tests (codes as explained in the legend of Fig. 2A) revealed that mean bSi content per square meter in the sponge community of sea grass beds (SG) was significantly lower ($p < 0.05$) than that in the three remaining habitats (OR, outer reefs; PR, patch + back reefs; MG, mangroves), which did not differ in bSi content. Note that bSi values per unit area were closely correlated with sponge volume but unrelated to species richness in the habitats.

Since the sponge populations of most continental shelves remain uninvestigated in terms of quantification of individual density, individual volumes, and individual Si content, it is difficult to decide whether the average Si standing stock in the Belizean sponges per bottom-area unit is higher or smaller than those on other shelves. The investigated tropical area is rich in sponges; however, many of these tropical sponges are known to either lack silica skeletons (i.e., they are corneous sponges) or to have only slightly silicified skeletons. For instance, the siliceous sponges of our tropical assemblage averaged 53.40 ± 6.14 bSi mg per liter of living tissue, a skeletal content that accounted for 15–25% of dry weight in some species, up to 50–65% in others. These were modest values compared with those for sponge species growing in deeper habitats and at higher latitudes, which typically average 75–95% bSi of dry weight (Dayton et al. 1974; Barthel 1995; Maldonado et al. 2005). Indeed, the abundance of heavily skeletonized sponges is known to increase with increasing latitude and depth (Vacelet 1988; Bavestrello et al. 1993; Barthel 1995), which suggests that the average of sponge Si standing crops on deeper temperate and subpolar continental shelves and slopes could be larger than in our tropical area. In addition, the Si standing crop uncovered in these tropical sponge communities cannot be considered an exception related to a unique shelf environment that favors a high density of sponges. Most of the investigated shelf area consisted of a sandy bottom (94.5%) with little or no sponge cover (Fig. 1; Table 1). A previous assessment of the Si standing stock along a 250-km Mediterranean rocky coast revealed that only one encrusting sponge (*Crambe crambe*) held per square meter of bottom Si, equivalent to 289 times that of the 20-m overlying water column (Maldonado et al. 2005). Even though the Mediterranean sublittoral is not particularly rich in sponges, such a "sponge : ambient silicate" Si ratio is about an order of magnitude higher than that measured for the Belize shelf (≈ 12). Therefore, although there is no certainty whether the estimated bSi standing crop for the Belizean continental shelf is larger or smaller than the average for temperate shelves, it is expected to be close to the value in other tropical shelves, and it may even be an underestimate of the

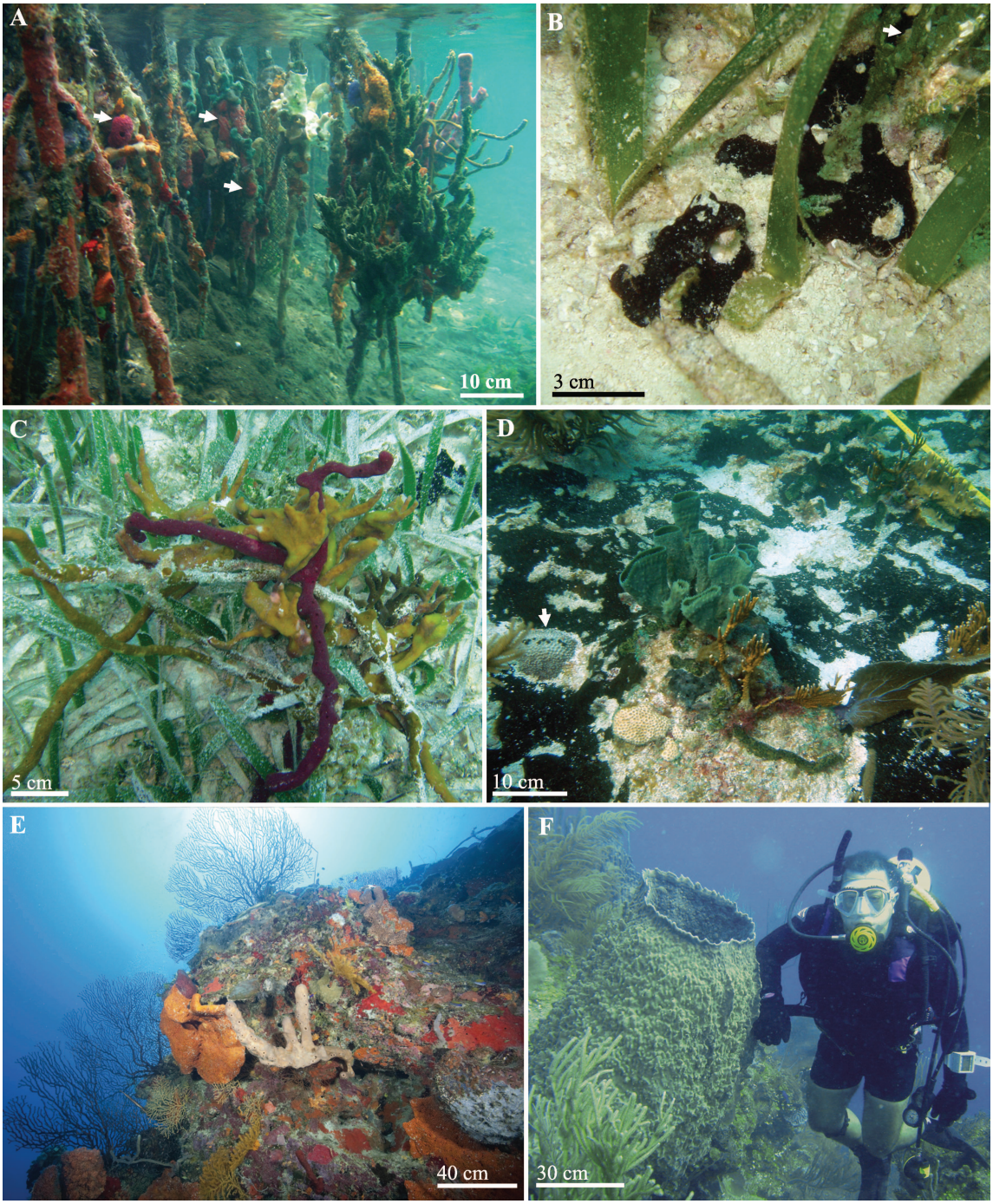

Fig. 4. Views of the studied habitats and sponges that were relevant Si contributors. (A) Permanently submersed red-mangrove roots showing abundance of sponges and other sessile filter feeders. Massive individuals of *T. ignis* (arrows) were major bSi contributors in mangroves. (B) A black sponge species discovered during our survey, *I. arenosa*, was the main bSi contributor in sea grass beds. (C) Branching individuals of *Xestospongia subtriangularis* (brown) and *Amphimedon compressa* (dark red) were also common on the sea grass bottom. (D) Sampling quadrat on a patch reef showing large coral rock area covered by the black encrusting-excavating sponge *Cliona caribbaea*. Note also several individuals of the grayish vase-shaped sponge *Callyspongia vaginalis* and an individual of the nonsiliceous sponge *Ircinia felix* (arrow). (E) General view of the fore reef, showing large gorgonians and high abundance and diversity of sponges. (F) Diver-sized *X. muta* at the fore-reef slope.

situation in high-latitude shelves. However, in coastal upwelling regions and river plumes, diatoms are expected to be favored, and here the relative contribution from sponges may be correspondingly less. Future new studies are required to determine empirically the magnitude of the differences between diatom and sponge bSi standing stocks in a large variety of coastal conditions.

The findings of the current and previous studies (Maldonado et al. 2005) suggest that there are fundamental differences in how sponges and diatoms contribute to the Si cycle of coastal waters. Three important differences have to be acknowledged: (1) most siliceous sponges have long life spans as compared with diatoms, and Si-residence time in sponges is measured in decades, centuries, or millennia, while the life span of diatoms is typically less than a week; (2) the bSi in sponge skeletons is more refractory to dissolution as compared with diatom-bound Si (due to reasons still not clarified); and (3) the Si uptake rate of diatoms saturates at 10 times lower concentrations (10 μmol L^{-1}; Paasche 1973) than that of the only sponge studied so far (*Halichondria panicea*; Reincke and Barthel 1997), indicating that diatoms are more efficient in taking up Si at the low surface concentrations of modern coastal oceans. Therefore, the amount of Si bound in the respective organisms does not necessarily reflect their relative importance for the Si turnover in coastal waters. The very scarce data that are available suggest that sponges are very slow bSi producers. For instance, the demosponge *Tectitethya crypta*, a typical inhabitant of sandy, sparsely vegetated Caribbean lagoon bottoms that reaches up to about 2 liters in size (Reiswig 1974; Rützler and Mcintyre 1978), was estimated to produce 2.5 g bSi per liter of sponge biomass per year. Production for an individual (20 × 30 cm) of the heavily skeletonized deep-sea sponge *Corallistes undulatus* has been estimated at 15 g bSi per year (Ellwood et al. 2007). It has been suggested that the more efficient Si uptake system evolved by diatoms caused a substantial decrease in the availability of silicic acid in surface waters during their evolutionary expansion in the Late Cretaceous (about 100 to 65 million years ago) and during their subsequent Cenozoic diversification (Siever 1991; Maldonado et al. 1999; Lazarus et al. 2009). As a consequence, much older Si-consuming groups with less efficient uptake systems that evolved in ancient, Si-rich oceans, such as sponges (arguably around 630 million year [my] old) and radiolarians (around 530 my old) experienced a drastic decline in the robustness of their silica skeletons (Maldonado et al. 1999; Lazarus et al. 2009). Such a Cretaceous crisis in Si availability has recently been postulated to have acted as an environmental force that selected for independent—but convergent—evolvement of aspiculate sponges from different siliceous lineages (Maldonado 2009). Before the evolutionary expansion of the diatoms, sponges were probably dominant Si users in most habitats on continental shelves and slopes; it should not be surprising that they can still maintain a relevant role at some sites (regional scale) in those systems. Along with the longevity of sponges, the observation that sponge spicules only were dissolved 0% to 5% after 8 months in sterile seawater, while the corresponding dissolution for diatom frustules was 98% (Maldonado et al. 2005), suggests a much slower turnover rate of sponge-bound Si than that estimated for a Si atom in the uptake-dissolution loop driven by diatoms in the photic layer of oceans (about 400 years; Tréguer et al. 1995). A better understanding of the ecology of Si uptake, skeletal secretion, and bSi dissolution in sponges is urgently required to scale the magnitude of Si turnover rates through these organisms on continental shelves and continental slopes. Irrespective of marked differences in rate of production and dissolution of bSi between sponges and diatoms in modern oceans, our data indicate that the standing bSi crop in the sponges of at least some continental shelf areas is significant. Consequently, when constructing future regional Si budgets in coastal areas, the Si standing stocks in local sponge populations should be examined before deciding that their contribution is negligible to the budget of a given region. Altogether, if we are to understand adequately Si fluxes in some coastal regions, we may need a new conceptual Si model, involving three major Si pools: (1) Si in rocks and deep sediment layers that cycles on geological time scales; (2) Si in diatoms that cycles comparatively rapidly and is connected to primary production processes; and (3) Si in sponges that cycles apart from primary production and does so at a much slower (but still undetermined) rate as compared with that of diatoms.

Acknowledgments

We thank Dan Miller, Claudette De Courley, and Michelle Nestlerode for assisting with fieldwork; Zoila Velásquez for help with taxonomy of phytoplankton; Tanya Ruetzler, Jim Taylor, and Martha Richotas for logistic support at the Smithsonian's Marine Field Station at Carrie Bow Cay; Chip Clark for picture 4E; and Venka Macintyre for editorial review. We also thank P. Tréguer for critical review of the manuscript and two anonymous reviewers for their constructive comments. This research benefited from funds provided by a fellowship from the "Formación de Profesorado Universitario" Program (AP2005-5369), a 2005–2006 grant from the Smithsonian's Caribbean Coral Reef Ecosystems Program (CCRE Contribution Number 880), and two grants (MEC-CTM2005-05366/MAR; MCI-BFU2008-00227/BMC) from the Spanish Government.

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Associate editor: Ronnie Nøhr Glud

Received: 18 February 2010
Accepted: 31 May 2010
Amended: 16 June 2010