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Siliceous sponges as a silicon sink: An overlooked aspect of benthopelagic coupling in the marine silicon cycle

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Abstract

Our current understanding of the silicon (Si) cycle in the ocean assumes that diatoms dominate not only the uptake of silicic acid, but also the production and recycling of biogenic silica (BSi), and that other organisms with siliceous skeletons, including sponges, radiolarians, and silicoflagellates, play a negligible role. In this study, we reexamine some aspects of the potential contribution by sponges and present in vitro evidence that BSi in the form of sponge spicules redissolves into silicic acid at far slower rates than those known for diatom frustules. We also show that the retention of Si by siliceous sponges in some sublittoral and bathyal environments is substantial and that sponge populations function as Si sinks. Additionally, by reanalyzing published information on sponge growth and BSi content, we estimate that BSi production rates by sublittoral sponges in Si-poor and Si-rich marine areas fall quite close to values known for diatom assemblages. Therefore, sponges may affect Si cycling dynamics and Si availability for diatoms, particularly in Si-depleted environments. Altogether, our data strongly suggest that the role of sponges in the benthopelagic coupling of the Si cycle is significant.

Silicon (Si), in the form of silicic acid, is a fundamental nutrient for diatoms, silicoflagellates, radiolaria, and many sponges, all of which polymerize it to build skeletons of biogenic silica (BSi). Because the biological use of Si has relevant ecological effects, including control of marine primary productivity (Nelson et al. 1995; Tréguer et al. 1995), indirect control of CO_2 production, and linkage to the carbon cycle (Harrison 2000; Tréguer and Pondaven 2000), it is important to understand the cycling of Si in nature. A widely accepted global model has recently emerged (Tréguer et al. 1995; Ragueneau et al. 2000) from the refinement of earlier ideas (e.g., Burton and Liss 1968; Calvert 1968; Hurd and Birdwhistell 1983). The major assumptions of this model are that (1) the content of silicic acid in the ocean has been constant for the past 10,000 yr; (2) virtually all uptake of silicic acid and production of BSi may be attributed to photoautotrophic diatoms that occur in surface waters (0–200 m deep), with negligible contribution from siliceous sponges, radiolarians, and silicoflagellates; and (3) only 3% of the annual oceanic production of BSi becomes buried in seafloor sediments because BSi in dead skeletons readily redissolves when exposed to seawater that is undersaturated with silicic acid (Tréguer et al. 1995).

Some of the first authors who investigated the modeling of the Si cycle suggested that siliceous sponges play a role in the global balance of Si (e.g., Harriss 1966). However, most current research efforts that examine the global marine Si cycle ignore the contribution of sponges and focus on refining estimates of the rates of dissolution of diatom frustules (e.g., Greenwood et al. 2001; Gallinari et al. 2002; Rickert et al. 2002). Because seawater is highly undersaturated with Si, any siliceous skeleton exposed to seawater will readily redissolve into silicic acid, following a thermodynamically favored reaction. The rapid postmortem dissolution observed for diatom frustules (e.g., Bidle and Azam 1999) clearly fits such a theoretical prediction. However, the theory does not appear to apply to sponges, which have a variety of spicules permanently exposed to seawater, such as those forming ''roots'' for attachment, long stalks that elevate the sponge body for enhanced filter feeding, velvety surfaces that smooth water flow around the body, lacerating walls that deter predators, long palisades that prevent filtering surfaces from clogging, and minute hooks that capture microinvertebrates. Because these exposed spicules confer adaptive advantages to sponges, mechanisms for reducing their dissolution rate may have been favored by natural selection. This raises the possibility that controls on the dissolution of sponge spicules are uniquely different from those of diatoms.

Likewise, the scientific literature on Si-cycle modeling provides no solid empirical or observational support for the

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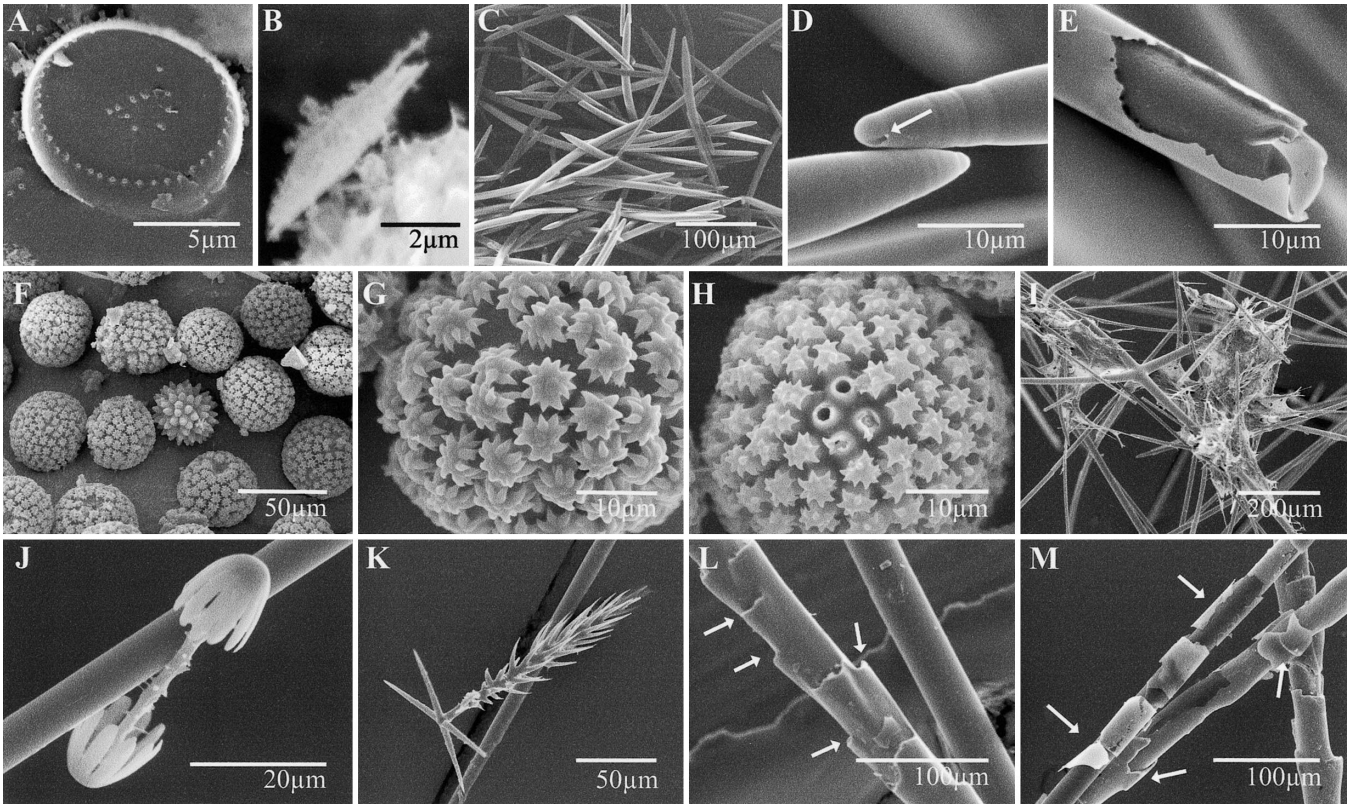

Fig. 1. Morphological evidence of skeletal dissolution after 8 months of dissolution in laboratory conditions. (A) The structure of *T. weissflogii* frustules was unrecognizable at (B) the end of the experiment. (C) Most oxeas of *P. ficiformis* experienced no appreciable dissolution, (D) with only very few spicules showing incipient signs of dissolution at their tips (arrow); (E) dissolution was more obvious in those spicules that were mechanically broken prior to or during the experiment. (F, G) Most sterrasters of *G. neptunii* showed no sign of dissolution, (H) with only a very few having the tip of some spines slightly dissolved. (I, J, K, L) Spicules from the body of *S. hawaiicus* experienced no dissolution after 8 months, despite large differences in their size and shape. (L) Nevertheless, the characteristic multilayered structure of some ornaments (arrows) in the large spicules making the stalk (M) demonstrated partial peeling and some dissolution (arrows).

assumption that the use of Si by sponges is negligible. Indeed, the current state of knowledge makes it impossible to formulate even a rough estimate of the global sponge contribution to the marine Si cycle. This lack of information is likely to be one of the main reasons why the dogmatic assumption that sponges are unimportant has automatically been transferred from earlier to more recent models.

The main objective of this study was to revisit the applicability of two basic assumptions inherent to the current understanding of the marine Si cycle, namely that (1) dissolution kinetics obtained from diatom frustules also apply to siliceous skeletons of marine sponges, and (2) the use of Si by marine sponges can be regarded as negligible when compared to that of diatoms.

Materials and methods

BSi dissolution experiments—We examined potential differences in dissolution between diatom and sponge skeletons in short-term and long-term laboratory experiments. Although flow-through dissolution experiments are appropriate to mimic the conditions of dissolution in some particular ocean environments, we opted for the simpler batch design, which allows the investigation of dissolution differences with a minimal variability of experimental conditions.

In a short-term laboratory experiment, we compared the dissolution rates of (1) frustules of the ubiquitous diatom *Thalassiosira weissflogii* (CCAP 1085/r strand; Fig. 1A), cultured in the laboratory under nonlimiting concentrations of silicic acid (100 μmol L^{-1}), according to the Guillard f/2 protocol (e.g., Bayraktaroglu et al. 2003); (2) needlelike spicules (oxeas) of the Mediterranean demosponge *Petrosia ficiformis* (Fig. 1C); and (3) chemically pure silica gel. To prepare the treatments, we cleaned frustules and sponge spicules with 45% hot nitric acid and washed cleaned skeletons in four distilled-water steps alternated with either decantation or gentle centrifugation. Then, we added 250 $\pm$ 18 μg of dried and cleaned frustules, sponge spicules, or silica gel to polypropylene bottles (n = 25 per group), each filled with 125 ml of autoclaved, 0.22-μm filtered Mediterranean surface seawater, which is highly undersaturated with silicic acid (0.2–5 μmol L^{-1}, depending on season). Control bottles (n = 25) contained seawater but no skeletal material. Bottles were incubated at 15°C with 100 rpm of orbital agitation to mimic the erosion experienced by skeletons tumbling on the seafloor. Silicic acid concentration was measured after 2 h,

24 h, and 14 d by triplicate analyses of 9-ml subsamples using a TRAACS-2000 autoanalyzer. BSi dissolution was calculated by assuming that BSi represents about 95% of spicule and frustule dry weight (e.g., Schwab and Shore 1971). To avoid a cumbersome repeated-measure design in the statistical approach, differences in dissolution between silica types were analyzed separately at each time point using a one-way Kruskal–Wallis nonparametric analysis of variance on ranks, after data failed the assumptions for a parametric approach. A posteriori Dunn tests were used to identify the groups responsible for the significant differences ($p < 0.05$) detected by the nonparametric analysis of variance.

In a long-term dissolution experiment, we investigated whether differences in shape (and therefore specific surface area), which are known to influence BSi dissolution kinetics (e.g., Lewin 1961; Hurd and Birdwhistell 1983; Gallinari et al. 2002), could account for the potential differences in dissolution between diatom frustules and sponge spicules. Using the experimental setup described, we compared the dissolution of (1) *T. weissflogii* frustules, (8–10 μm in diameter, 2-μm-high circular hollow boxes; Fig. 1A); (2) oxeas of the demosponge *P. ficiformis* (200–300 μm long, 8–12-μm-thick rods; Fig. 1C); (3) sterrasters of the Caribbean demosponge *Geodia neptunii* (25–40 μm in diameter, solid, aster-like spicules ornamented by curved spines; Fig. 1F,G); and (4) a mixture of spicules from the hexactinellid sponge *Sericolophus hawaiicus* (diverse shapes from 30 μm to several centimeters; Fig. 1I–L). During this experiment, bottles were sampled after 2 h, 24 h, 14 d, and 8 months. For the first 14 d, bottles were maintained at 15°C and provided with agitation; they were then left undisturbed (with no agitation) at 20°C ± 5°C for 7.5 months. Differences in BSi dissolution between skeleton types at each time point were statistically analyzed using the one-way, Kruskal–Wallis analysis of variance on ranks, followed by Dunn's tests, as for the short-term experiment. If the surface area is to explain differences in dissolution, there should be substantial differences not only between diatoms and sponges but also between different spicule shapes. At the end of the 8-month experiments, we recovered the undissolved skeletal fractions by filtering the seawater through 0.22-μm filters. After filters were dried at 60°C for 48 h, they were gold coated for the examination of skeletal dissolution using a Hitachi S-2300 scanning electron microscope.

Si in sponges and ambient water—We investigated the roles of sponges in regional Si cycling in three representative marine environments. For this purpose, we used data from field studies carried out in the Bahamas, in the Western Mediterranean, and in the Hawaiian Archipelago from 1999 to 2003, in which we estimated Si content in a sponge population from a coral reef, a sublittoral rocky bottom of a temperate zone, and a bathyal sandy bottom of a continental slope, respectively. Then, we compared Si values in each local sponge population with those in the ambient water of their respective habitats.

For the reef habitat, we surveyed about 2,500 m^2 of a dense Caribbean population of the thickly encrusting demosponge *Chondrilla nucula,* which is able to overgrow living corals and to rapidly expand in affected reef areas of Bahamian reefs. In the study area (Lee Stocking Island, Exuma Sound, Bahamas), this sponge occupies a wide range of shallow habitats from reef crests to inter-reef seagrass beds. We estimated sponge coverage from 2,500-cm^2 random photographic quadrats ($n = 62$), subsequently analyzed with National Institutes of Health Imagetool software. Sponge coverage was then converted to Si content by collecting 2.7-cm-diameter samples ($n = 25$) comprising the entire sponge thickness (2–4 mm) and examining dry weight differences before and after desilicification with 5% hydrofluoric acid for 12 h (Bavastrello et al. 1993). We failed to obtain direct measurements of silicic acid concentration for this Bahamian reef because an extreme customs alert in the Miami airport following the events of 11 September 2001 prevented the transport of biological samples on international flights. Thus, we have used data available in the literature (Tréguer et al. 1995) to interpret and discuss our findings.

For the sublittoral temperate system, we investigated a large population of the encrusting demosponge *Crambe crambe,* a dominant species in most sublittoral hard-bottom communities of the northernmost Mediterranean coast of Spain. Over about 250 km of coastline in the study area, the bottom (between 0- and 20-m depth) consists mostly of rocky vertical walls and large stone blocks, with a minimal occurrence of soft bottoms arising from interspersed beaches and coves. In June–July 2002 and 2003, we estimated the coverage of *C. crambe* in these 5–20-m-deep rocky bottoms by analyzing 1-m^2 random quadrats ($n = 100$). Quadrats were subdivided into 25 subquadrats of 20 × 20 cm, and sponge coverage was estimated in situ by measuring subquadrat occupancy with a resolution of up to one fourth of a subquadrat. Sponge coverage was then converted into Si content by examining differences in dry weight of 2.7-cm-diameter samples of sponge tissue ($n = 25$) comprising the entire sponge thickness (1–3 mm) before and after desilicification with hydrofluoric acid. We also estimated silicic acid content in ambient surface water (0–55 m deep) from this area of the Catalan sea by sampling ($n = 755$) with 2-liter Niskin bottles during summer and winter cruises and analyzing refrigerated samples 24 h later using a TRAACS-2000 autoanalyzer. Results are presented as averages per 10-m depth intervals ($n = 3$–50 samples per depth level).

The bathyal environment was investigated using the Pisces-V manned submersible (University of Hawaii). On the westward slope of the Mauna Loa Volcano (Hawaii) in November 2001, we studied a dense bathyal population of the stalked hexactinellid sponge *S. hawaiicus,* which forms a continuous band between 350- and 450-m depth over a distance of 30.1 km. We estimated sponge numerical abundance (individuals m^{-2}) from videotransects recorded using a Hi-8 video camera externally mounted on the submersible. Videotapes were randomly subsampled by stopping the video player ($n = 50$) and counting the number of sponge individuals per approximate square meter of bottom, as seen on the video screen. For the calibration of bottom area on the video screen, we videotaped previously marked 1-m^2 quadrats on the seafloor, which also provided direct counts of sponge abundance. Using the submersible manipulator arm, we collected a total of seven large and six small (<25 cm

in height) sponges to determine their Si content. The Si content of the sponge stalks, which are structures made of bare spicules, was calculated from the weights of the stalks after manually removing the epibionts, eliminating the interspicule sediment by sonication, rinsing in distilled water, and drying at 60°C until constant weight was achieved. The Si content in the remaining body portions was estimated as the dry-weight difference of small tissue pieces before and after desilicification with hydrofluoric acid ($n = 39$). We examined the natural ambient distribution of silicic acid in relation to the *S. hawaiicus* bed by collecting seawater samples every 20 m between 0- and 750-m depth ($n = 1$–3 per depth level) using a set of Niskin bottles mounted on the Pisces-V submersible. Samples were refrigerated for 4 d until analysis with a TRACCS 2000 autoanalyzer. To ascertain the situation of the sponge bed relative to the bathymetric position of the permanent deep-sea thermocline (10°C), we recorded seawater temperatures between 0- and 700-m depth with an externally mounted temperature sensor connected to the submersible CTD logger.

BSi production by sponges—We estimated the potential role of sponges in BSi production indirectly by reanalyzing published data derived from long-term monitoring studies of sponge growth and population dynamics in both a sublittoral Mediterranean community characterized by slightly silicified sponges and a sublittoral Antarctic community characterized by heavily silicified sponges. In the first case, we reanalyzed data on the growth of 1- to 2-yr-old *C. crambe* individuals, averaging about 80 mm² in area, which were monitored for 2 yr by Turon et al. (1998) in the same Mediterranean rocky bottoms (5–20-m depth) where we sampled *C. crambe* for Si content. We combined both information types to estimate BSi production. For the Antarctic populations, we estimated BSi production by reanalyzing information on sponge growth and ash weight : wet weight ratios provided by Dayton et al. (1974) and Dayton (1979) during a 10-yr monitoring of a sponge-dominated community (30–60 m deep) at McMurdo Sound (Ross Sea, Antarctica).

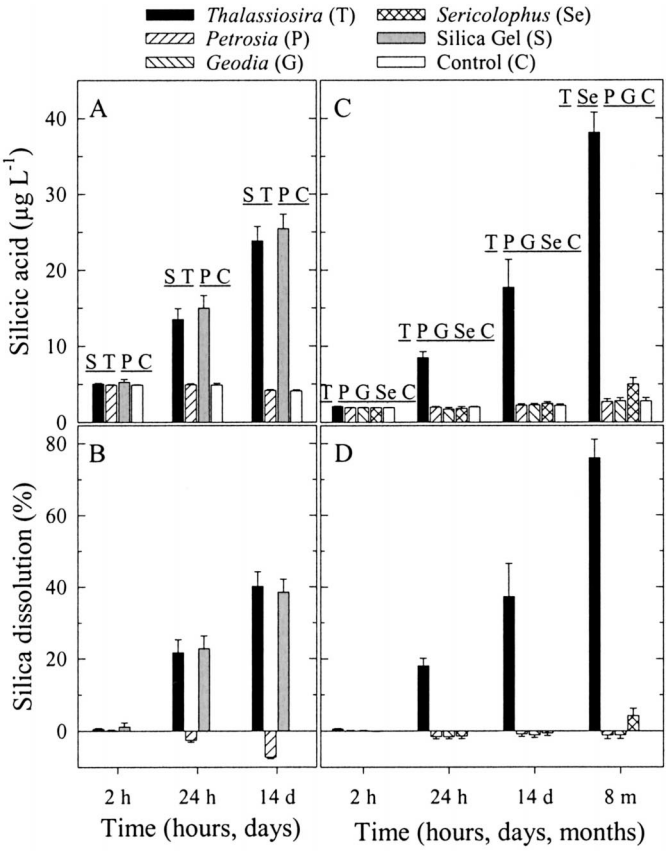

Fig. 2. (A, C) Mean (±SD) silicic acid concentration and (B, D) BSi dissolution in the experimental bottles during the 14-d and 8-month dissolution experiments, respectively. Initial silicic acid concentration for all treatment corresponds to that in the control treatment after 2 h. Note that some adsorption of silicic acid on the wall of culturing bottles caused slightly negative dissolution values in some treatments over time. Letters summarize the results of a posteriori pairwise comparisons for the groups (*see* graph legend) involved in the analyses of between-group differences in silicic acid that follow a significant Kruskal–Wallis analysis of variance at each time. Groups of underlined letters indicate nonsignificant differences between pairs of means according to Dunn's tests ($p > 0.05$).

Results

BSi dissolution experiments—Under the laboratory conditions of the short-term experiment, the dissolution of both frustules and silica gel relative to controls and sponge spicules was statistically detectable after just 2 h, and differences became dramatic after 24 h (Fig. 2A,B). After 14 d, both diatom frustules and silica gel had similarly dissolved by about 38%, while there was no detectable dissolution of sponge spicules.

In the long-term experiment, after the first 14 d, the dissolution of diatoms but not spicules was detected (Fig. 2C,D). After 8 months, frustules had dissolved by about 75%, while all three types of sponge spicules resisted dissolution (Fig. 2C,D). Sterrasters and oxeas of demosponges, which have very different shapes, showed no detectable dissolution, and hexactinellid spicules dissolved by only 5%. Note that some adsorption of silicic acid on the wall of culturing bottles caused slightly negative dissolution values in some treatments.

Electron microscopic analysis of spicules detected little evidence of physical dissolution after 8 months (Fig. 1D,E,H), while all diatom frustules were unrecognizable due to severe dissolution (Fig. 1H). Therefore, surface area alone cannot account for the drastic differences in dissolution dynamics between frustules and spicules. Most oxeas of *P. ficiformis* did not undergo appreciable dissolution (Fig. 1C), with only a very few spicules showing incipient signs of dissolution at their tips (Fig. 1D, arrow); dissolution was more obvious in those spicules that were mechanically broken prior to or during the experiment (Fig. 1E). Most sterrasters of *G. neptunii* showed no sign of dissolution (Fig. 1F,G), with only a very few having the tip of some spines slightly dissolved. The small difference found between hexactinellid and demosponge spicules was due to some dissolution of the peripheral growth layers of the largest hexactinellid spicules (Fig. 1L,M); the smallest hexactinellid spicules were virtually intact after 8 months (Fig. 1J,K).

Si in sponges and ambient water—Coverage by *C. nucula* in a reef and the adjacent seagrass in which the population develops averaged 44.66% ± 10.33% of the available substratum (Fig. 3A,C). This high coverage indicates that the sponge may locally monopolize the available hard substrata if conditions are optimal for its growth, as appears to be the case in affected reef areas. The BSi content of this encrusting sponge is estimated at 15.1 ± 4 mg cm^{-2} of sponge cover (17.9% ± 1.9% of dry weight), which means that the local population of *C. nucula* alone retains about 67.4 g BSi m^{-2} of the bottom area. Because the concentration of silicic acid in surface Caribbean waters averages <5 μmol L^{-1} (e.g., Tréguer et al. 1995), the content of Si per square meter of bottom retained by the studied population of *C. nucula* alone represents at least that contained in 6.2×10^6 liters of reef water and is about 200 times that available in an overlying 30-m water column.

Our estimates of Si content in a Mediterranean sublittoral population of *C. crambe* show that Si retention in this temperate benthic environment is also far from negligible. This sponge covers about 12.5% ± 13.3% of rocky substratum in the 5–20-m-deep sublittoral clift (Fig. 3D,E), which amounts to 5.4 ± 5.7 g BSi m^{-2} or 81 kg BSi per linear km of rocky clift. Since the concentration of silicic acid in surface water of this Mediterranean area averages 1.39 ± 0.60 μmol L^{-1} (Fig. 4A) and *C. crambe* contains 4.3 ± 3.6 mg Si cm^{-2} of sponge cover (about 15% of dry weight), it can be deduced that the population of this sponge alone retains an amount of Si m^{-2} of rocky bottom that is equivalent to that contained in about 5.9×10^6 liters of coastal seawater and about 298 times that available in a 1-m^2 × 20-m-deep water column.

Unlike the encrusting demosponges studied, the hexactinellid sponge *S. hawaiicus* consists of a cuplike body (up to 20 cm in diameter) anchored to the soft bottom by a flexible stalk (up to 35 cm in height and 1.9 cm in diameter) made of bare spicules exposed directly to seawater (Fig. 3F). The maximum sponge density in central areas of the population band is 10–14 individuals m^{-2} and 0–2 individuals m^{-2} near the edges of the band, with the overall density averaging 2.3 individuals m^{-2} (Fig. 3G). As in the sublittoral populations studied, our estimates indicate that the amount of Si contained in this bathyal population is not negligible. Mid-size and large individuals contain about 13.1 ± 6.7 g BSi, and small individuals contain about 2.8 ± 1.2 g BSi. We estimate from these quantities that this population sequesters at least 27 g BSi m^{-2} and about 2.7 tons per linear km of sponge band. Moreover, this is a very conservative estimate of total BSi content trapped in the sponge bed, because it does not consider the abundant isolated spicules scattered on the bottom and the numerous stalks that protrude from the bottom long after the sponges die (Fig. 3G,H, arrows). An individual stalk spicule alone may be up to 40 cm in length and 600 μm in diameter and contains on average 20.6 ± 8.7 mg BSi ($n = 25$). From these quantities, it can be inferred that just the living population of *S. hawaiicus* (stalks and spicules scattered on the bottom are not included) contains 12.620 g Si m^{-2} on average. Water samples taken on the shelf and slope suggest that the concentration of silicic acid in the ambient water in which the sponge population occurs ranges from 35 μmol L^{-1} in its upper bathymetric limit to 70 μmol L^{-1} in its lower limit (Fig. 4B), averaging 50.570 ± 14.850 μmol L^{-1} across the sponge bed. This means that the sponges retain an amount of Si m^{-2} of bottom that is equivalent to that contained in 2.6×10^6 liters of ambient water from their habitat. Such an amount of Si also represents several times that contained in the entire 400-m-high water column above the sponge bed. Because the sponge population occurs below the 10°C permanent deep-sea thermocline (Fig. 4B), seasonal processes are unlikely to modify the concentration of silicic acid in the ambient water substantially. However, we found that silicic acid concentration does not increase uniformly with depth but, rather, decreases above and below the sponge band (Fig. 4B). Therefore, we cannot discard the idea that Si uptake and retention by this bathyal population may somehow be affecting the vertical distribution of silicic acid.

BSi production by sponges—According to the data of Turon et al. (1998), the size of 1- to 2-yr-old *C. crambe* individuals increased from about 80 mm^2 up to 200 mm^2 in 2 yr, which shows a yearly growth rate of 0.75 on average. Although *C. crambe* may occasionally grow >100,000 mm^2 in the studied area (pers. comm.), a size-frequency analysis by Turon et al. (1998) indicates that about 80% of the individuals occurring in these Western Mediterranean communities are <3,000 mm^2. We have estimated in previous sections of this study that *C. crambe* covers 12% of the available vertical and subvertical rocky surfaces in the area studied by Turon et al. (1998), which means that about 9.6% (=12.5 × 0.8) of the substrate is occupied by individuals <3,000 mm^2. By assuming that all individuals <3,000 mm^2 have a similar, constant growth rate (i.e., 0.75), 720 cm^2 ($=0.96 \times 10^4 \times 0.75$) of new sponge cover m^{-2} yr^{-1} is expected. Since *C. crambe* averages 4.3 mg Si cm^{-2} of sponge area, it can be deduced that this sponge consumes yearly about 3.096 g Si m^{-2} of rocky bottom. This estimate of Si demand is very conservative, since it excludes not only all conspecific sponges >3,000 mm^2 (which are about 20% of the population), but also all the remaining siliceous sponges in the community.

Estimates of BSi production by heavily silicified sponges were also obtained from a 10-yr investigation on an Antarctic sublittoral sponge community (Dayton et al. 1974; Dayton 1979). These data showed that the demosponge *Homaxinella balfouriensis* was a rare species in 1968, as only eight individuals were found in a 30,000-m^2 area selected for the long-term monitoring. However, the sponge population grew to an average of 7–8 kg wet weight of sponge per square meter in 1975, and in 1977, it became between 4 and 10 times denser than it was in 1975, depending on quadrat. Because ash weight in this species (assumed all to be BSi) represents 6.7% of its wet weight (Dayton et al. 1974), we deduce that BSi production between 1968 and 1975 by just this sponge was about 234.46 g Si m^{-2} yr^{-1} in the studied area.

Discussion

BSi dissolution—Our results show marked differences in dissolution properties between diatom and sponge skeletons

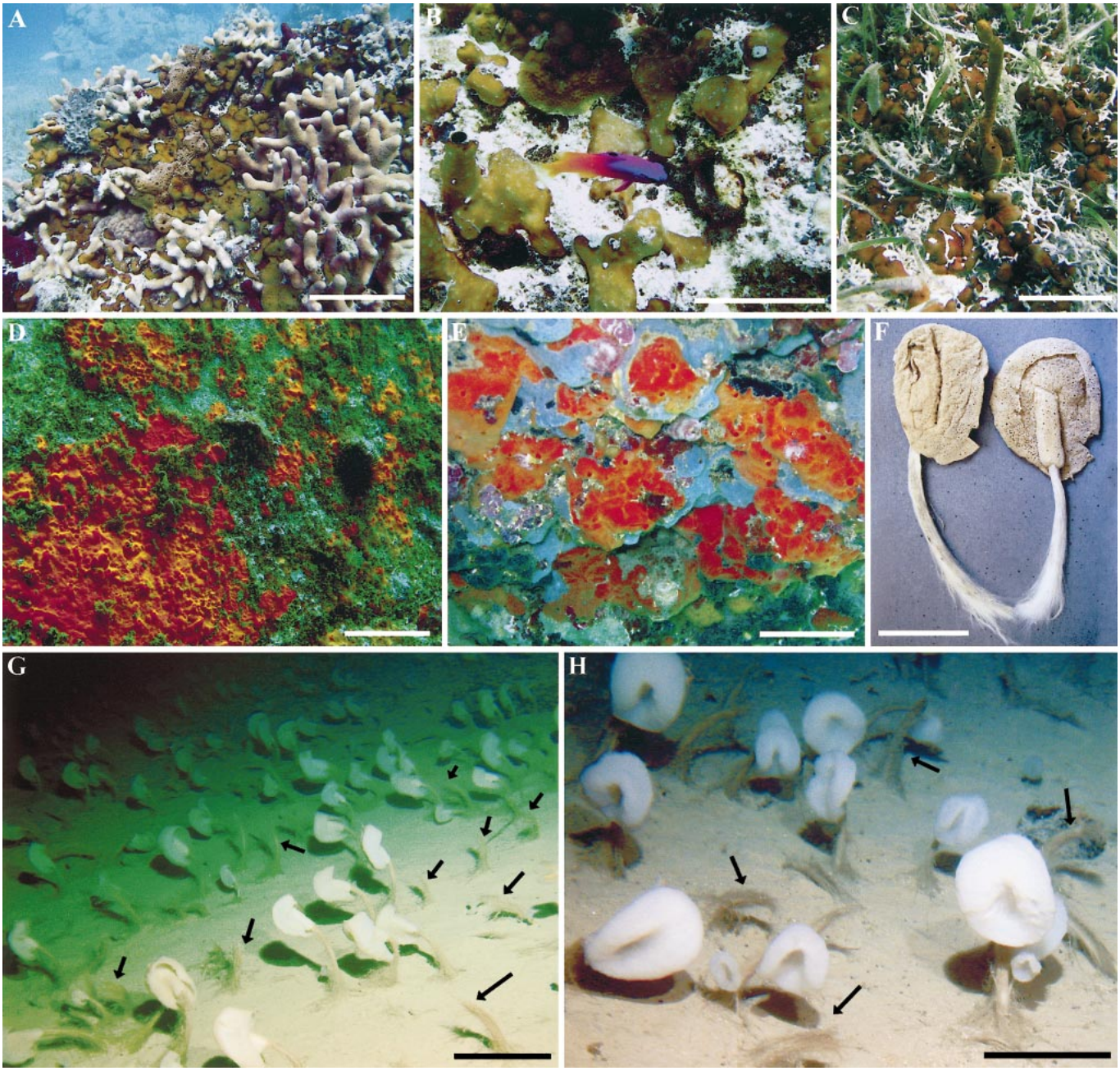

Fig. 3. Sponge abundance in different habitats. (A, B) Abundance of *C. nucula* (in brown) in various Caribbean reef habitats and (C) a *Thalassia* bed. (D) Abundance of *C. crambe* (in red) in Western Mediterranean sublittoral rocky communities at well-lit macroalga-dominated habitats and (E) shaded, filter-feeder dominated habitats. (F) Dried individuals of *S. hawaiicus* showing the exhalant (left) and the inhalant (right) side of the main stalked body, respectively. (G, H) Abundance of *S. hawaiicus* at bathyal depths, forming a dense population with appreciable recruitment and mortality, as shown by the presence of young individuals and persistent stalks that remain after sponge death (black arrows). Scale bars are as follows: A = 20 cm; B = 10 cm; C, D, E = 15 cm; G = 35 cm; H = 20 cm.

in abiotic seawater. Such differences are consistent with a previous study by Katamani (1971), which reported drastic dissolution differences between diatom frustules and an unidentified sponge spicule in distilled water and different salt solutions. These differential dissolution dynamics also agree with the marked resistance to digestion in 1% Na_2CO_3 of spicule-rich sediments relative to diatom-rich sediments, as reported for Florida lake sediments (Conley and Schelske 1993).

The reason for the differences in the dissolution dynamics remains unclear. Katamani (1971) reported infrared absorption near 940 cm^{-1} by diatom frustules, an absorption peak that is missing in sponge spicules. This peak indicates either water molecules trapped in the interstitial voids of the BSi

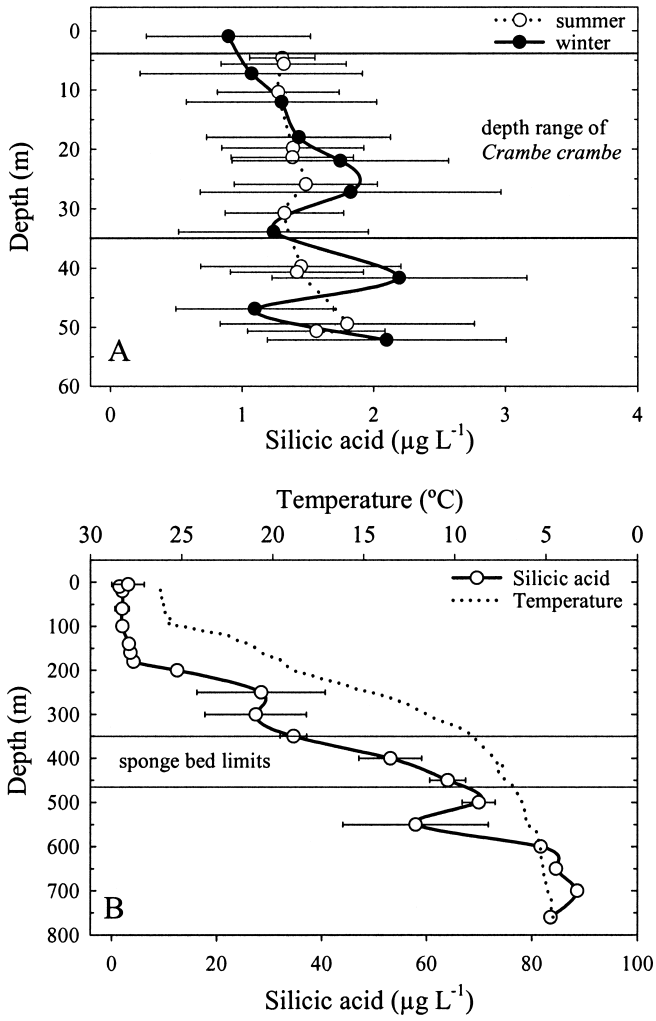

Fig. 4. Bathymetric relationships of silicic acid concentration and sponge populations at sublittoral and bathyal depths. (A) Silicic acid (mean ± SD) profiles in the upper 55 m of the Catalan Sea (Western Mediterranean) where *C. crambe* occurs. Data are from 577 summer and winter samples and averaged by 5-m-depth intervals (n = 3–50). (B) Bathymetric profiles of silicic acid (mean ± SD; n = 1–3) and temperature along the shelf and slope in the area (19°38′N, 156°2′W) where the population of *S. hawaiicus* occurs off the Big Island of Hawaii. Note decreases in silicic acid about 100 m above and below the sponge bed.

polymeric network or hydroxyl groups in various states of association. Nevertheless, such minor differences, even if favoring dissolution of frustules relative to spicules, are insufficient to explain the drastic differences found (Katamani 1971). Substantial incorporation of fourfold-coordinated Al into the BSi polymer during biosilicification by sponges, which is known to drastically reduce the BSi dissolution rate when it is incorporated in trace amounts from the sediment (e.g., Lewin 1961; Dixit et al. 2001), could be responsible for the very different dissolution kinetics (Maldonado et al. unpubl. data).

Whatever the reasons are for the observed resistance to BSi dissolution in sponges, this attribute may have important implications for Si cycling. According to the diatom-based model, the overall residence time of Si in the world ocean is estimated at 15,000 yr, and the residence time relative to total biological uptake in surface waters is about 400 yr, which means that an Si atom passes through the biological uptake and dissolution cycle about 39 times before being removed to the seafloor (Tréguer et al. 1995). However, this is unlikely to hold for siliceous sponges, not only because spicules resist dissolution but also because individual sponges usually live from years to decades or even centuries (e.g., Sarà and Vacelet 1973; Ayling 1983; Pansini and Pronzato 1990; Maldonado et al. pers. comm.). Recently, Leys and Lauzon (1998) estimated that the shallow-water hexactinellid *Rhabdocalyptus dawsoni* can attain an age of at least 220 yr. Therefore, our data indicate that sponge skeletons function as an important Si sink that drastically delays BSi recycling.

Si retention by sponges—Each of the two studied sublittoral populations retains a level of Si that is about 200–300 times that available in the water column above the sponge bottoms. Therefore, the use of Si by sponges on rocky areas of continental shelves is unlikely to be negligible. The local population of *C. nucula* showed a mean coverage as high as 44.6% of the available substratum, which would translate to about 67.4 tons BSi km^{-2} of habitat. It is obvious that such a high *C. nucula* density cannot be realistically extrapolated over very large areas of the reef system. However, many other sponge species, some with a much higher Si content than *C. nucula,* may occur over vast reef areas where *C. nucula* is rare or does not occur. A recent review of the global occurrence of sponges in Caribbean reefs showed a coverage by sponges of up to 24% on hard substrata in light-exposed, open-reef habitats and up to 54% in cryptic subrubble habitats (Diaz and Rützler 2001). Therefore, it appears that the amount of Si retained by living sponges in reef systems, although not easily measurable, is certainly nonnegligible and far higher than that available in the water column. This raises the possibility that sponges rather than diatoms control Si cycling in reefs, an idea previously suggested by Rützler and MacIntyre (1978) after finding that the amount of BSi trapped by living sponges in Belize reefs ranges from 0.1 to 100 g m^{-2} and that sponge spicules are the main component of particulate silica in reef sediments.

Control of Si cycling by sponges may also be the normal situation in many sublittoral rocky-bottom systems at temperate latitudes, which are usually characterized by a high abundance of siliceous sponges and an Si-depleted water column. The studied population of *C. crambe,* unlike the small but dense population of *C. nucula,* extends over a vast portion of coastline (approx. 250 km). Therefore, our estimates that *C. crambe* alone retains per square meter about 298 times the Si available in a 1-m^2 × 20-m-deep water column and about 81 kg BSi per linear km of sublittoral clift can be reliably extrapolated to a large coastal area. It is important to remember that not only does this sponge retain a large amount of unreactive BSi, but also that the retention is for its entire lifetime, which may last from years to decades (Turón et al. 1998; Maldonado et al. unpubl. data). Therefore, although spicule production in Western Mediterranean populations of *C. crambe* is chronically limited by silicic acid because of its more efficient uptake by diatoms

(Maldonado et al. 1999), *C. crambe* may reciprocally affect the growth of local diatom populations by immobilizing a large amount of Si that otherwise would recycle rapidly and be available for diatoms. Although *C. crambe* is the most abundant sponge by far on the rocky bottom studied, the remaining pool of siliceous sponges also contributes to the role of sublittoral sponges as a relevant Si sink.

Below the mixed layer of the ocean, where diatoms do not proliferate, the production and retention of BSi by sponges may also have a nonnegligible role. We have shown that Si retention by the dense bathyal population of *S. hawaiicus* is substantial. Moreover, our data provide a very conservative estimate of total BSi content trapped in the sponge bed, since the abundant spicules resting on the seafloor long after the sponges die were not considered. More importantly, the population of *S. hawaiicus* is not an isolated case of sponge abundance at bathyal depths. Recent surveys of 9-km abyssal transects at a depth of 4,100 m off the California coast have shown occurrence of 2,418 heavily silicified hexactinellid stalks at densities of 0.18–0.33 m^{-2} (Beaulieu 2001). Dense populations of heavily silicified demosponges and hexactinellids are known from continental slopes of several North Atlantic locations (e.g., Rice et al. 1990; Barthel et al. 1996; Maldonado and Young 1996), and many of these populations are reported to have persistent spicule skeletons after the sponges die (Bett and Rice 1992; Barthel and Tendal 1993). Siliceous spicules are also extremely abundant in both Arctic and Antarctic bottoms at diverse depths, where they form mats up to 2 m thick (Koltun 1968; Dayton et al. 1974; Van Wagoner et al. 1989), thus having profound effects on the structure of benthic communities (Könnecker 1989; Barthel 1992; Barthel and Gutt 1992). Of particular interest to illustrate the issue of BSi production and retention by sponge spicules below the photic layer is the recent discovery of seven living reefs of hexactinellids at bathyal depths (154–240 m) in the Hecate Strait and the Strait of Georgia in British Columbia (Conway et al. 2001; Krautter et al. 2001). These reefs, similar to ones that were common 200 million yr ago, are built by dictyonine hexactinellids, the skeletons of which consist of a rigid, three-dimensional network of fused siliceous spicules that remains long after the sponges have died and serves as a substratum for subsequent sponge generations. The abundance of living hexactinellids can reach 240 individuals in 10 m^2 (Leys et al. 2004). Because the explored reefs are up to 19 m high and extend from 2 to 10 km^2 (Conway et al. 2001; Krautter et al. 2001; Leys et al. 2004), it can easily be deduced that they function as huge Si traps.

The local evidence discussed herein opens the suspicion that the effects of the Si retention by sponges at the global scale may be more important than thought, even if a numerical amount cannot be provided because of insufficient knowledge of global patterns of sponge BSi content and biomass distribution in the ocean. For instance, although the diatom-based marine Si cycle postulates that 32–39% of the total burial of BSi is concentrated along continental margins (Ragueneau et al. 2000), the impressive sponge populations reported in the literature from the continental shelves and upper slopes strongly suggest that the global burial values are underestimated.

Si uptake and BSi production by sponges—Si uptake rates are well described for a large variety of diatom species and even entire diatom assemblages (*see* Ragueneau et al. 2000), but very little is known about Si uptake rates by sponges. Likewise, the BSi annual gross production in the world ocean due to diatoms that concentrate in the upper ocean is reliably estimated to average 670×10^{13} g Si (Nelson et al. 1995; Tréguer et al. 1995). However, there is not even a rough estimate of the amount due to siliceous sponges.

Uptake data are available for only two sublittoral temperate demosponges under laboratory conditions (Frøhlich and Barthel 1997; Reincke and Barthel 1997; Maldonado et al. 1999). Si uptake in the sublittoral encrusting sponge *C. crambe* was shown to be chronically limited by low silicic acid concentration in ambient water, with uptake increasing with increasing silicic acid concentration in seawater. More importantly, this sponge appears to form a complete spicule skeleton only at ambient concentrations of 100 μmol L^{-1} silicic acid (Maldonado et al. 1999), a value about 60 times higher than the average of the natural concentration over the year (*see* Fig. 4A). A similar Si limitation was shown for the Baltic Sea populations of the thickly encrusting to submassive demosponge *Halichondria panicea.* This sponge, which, in the study area, was the most abundant animal and can account for >15% of benthic biomass, has silicic acid uptake kinetics similar to Michaelis–Menten kinetics. Uptake increases nearly linearly within the 0–30 μmol L^{-1} silicic acid range (Frøhlich and Barthel 1997), which is the natural concentration range in the water column at the sponge habitat, but the half-saturation and saturation stages are achieved only at 40 and 160 μmol L^{-1} silicic acid, respectively (Reincke and Barthel 1997).

Because in both studied sponges significant uptake rates occur only at silicic acid concentrations higher than those naturally occurring in the sponge habitat, it is clear that the populations are chronically limited by Si availability. In contrast, temperate and tropical diatoms reach half-saturation stage at silicic acid concentrations ranging from 0.5 to 5 μmol L^{-1} and at saturation around 10 μmol L^{-1} (Paasche 1973; Ragueneau et al. 2000), which are values that are far more likely to occur naturally in the surface waters of modern oceans than those required by sponges. As suggested by Maldonado et al. (1999), the strong difference in uptake kinetics between sponges and diatoms may indicate that the sponge uptake system evolved in a silicic acid–rich ocean well before the expansion of diatoms during the Cretaceous and the subsequent silicic acid exhaustion by rapid diatom uptake in the photic zone. How these sponges survive in shallow waters of modern oceans characterized by silicic acid concentrations consistently below their half-saturation remains enigmatic. It is obvious that some species, such as *C. crambe,* have developed systems to modulate the silicification level of its skeleton in response to available levels of silicic acid in ambient water, omitting the formation of the most Si-consuming spicules in conditions of low silicic acid availability (Maldonado et al. 1999). It is also possible that sponges, which mostly feed on bacteria but can ingest small and mid-size phytoplankton, use the frustules of ingested diatoms as an Si source. The latter hypothesis is supported by two facts: (1) demosponges appear capable of ac-

tively dissolving BSi into silicic acid using silicase, a BSi catabolic enzyme (Schröder et al. 2003); and (2) *H. panicea* individuals fed with artificial microspheres and chrysophycean microalgae produced abundant fecal pellets containing indigestible materials, such as microspheres and cellulose-walls, while sponges fed with the armored diatom *Phaeodactylum tricornotum* neither formed fecal pellets nor egested isolated diatom skeletons (Wolfrath and Barthel 1989).

If most shallow-water sponges are indeed chronically Si limited in their habitats, laboratory estimates of silicic acid uptake by sponges can be of little help in inferring realistically how much Si is used by field sponge populations over long periods under changing levels of ambient silicic acid. Additionally, silicic acid uptake by sponges occurs neither as a continuous process nor at a constant rate, even if the ambient silicic acid concentration were kept constant. Rather, silicic acid uptake is intimately linked to processes governing sponge growth. Both are therefore strongly affected by factors such as seasonality (e.g., Stone 1970; Elvin 1976; Turon et al. 1998), individual age and size (e.g., Dayton et al. 1974; Barthel 1989), incidence of predation and grazing (e.g., Ayling 1983), concentration of bacterial food (Frøhlich and Barthel 1997), and species-specific ''BSi : organic tissue'' ratios. The effects of some of these parameters may be dramatic. For instance, Ayling (1981) observed that some encrusting sponges, which had experimentally been injured to simulate predation, regenerated the lost tissues at rates between 22 and 2,900 times the undisturbed growth rate, depending on species. Therefore, Si uptake and BSi production will be very different in two conspecific populations experiencing different levels of predation or grazing. Similarly, Frøhlich and Barthel (1997) demonstrated that sponges starved for 1 week showed Si uptake rates only 15% as great as those shown by nonstarved sponges. Taken together, this information suggests that estimates of BSi production in the field on a long-term interannual basis rather than extrapolations from short-term laboratory studies of silicic acid uptake provide a more realistic quantification of the use of Si by sponges. Modeling sponge growth and BSi production rates is not easy either, since the information needed for the models is not easily found in the literature. For rocky-bottom communities dominated by the slightly silicified sponge *C. crambe*, we have calculated a yearly production rate of 3.096 g Si m^{-2} of rocky bottom. This estimate is very conservative, since it excludes all conspecific sponges $>3{,}000$ mm^2 (which represent about 20% of the population), as well as all of the remaining siliceous sponges in the community. Therefore, if the entire sponge community were included, we would expect the sponge production rate to be similar to the mean BSi production rate in the upper ocean due to diatoms, which is estimated to be 21 g Si m^{-2} yr^{-1} (Nelson et al. 1995; Regueneau et al. 2000). It is also noteworthy that, according to these calculations, every square meter of rocky bottom in this community demands on average an amount of Si equivalent to that contained in 79.5×10^3 liters of ambient seawater to support the yearly growth of small and mid-size individuals of *C. crambe*. Consequently, each kilometer of a rocky-bottom sponge community (between 10 and 25 m deep) on this 250-km-long rocky coast demands a yearly amount of Si equivalent to that contained in at least 1.193×10^9 liters of coastal seawater. More importantly, such an Si demand to support sponge growth takes place during the warm season (June–October), partially coincidental with maximum Si demand by planktonic diatoms.

The role of heavily silicified sponges, such as many deep-sea and polar species, regarding their use of Si may be of even greater importance. Unfortunately, there is no information available concerning the growth of deep-sea sponges, but some ideas can be extracted from the study of sublittoral Antarctic sponges. Using data in Dayton et al. (1974) and (Dayton 1979), we deduced that BSi production by the demosponge *H. balfouriensis* between 1968 and 1975 occurred at rates of about 234.46 g Si m^{-2} yr^{-1}. Surprisingly, this value is fairly close to the annual BSi production rate of the whole diatom assemblage in the Ross Sea, estimated between 378.14 and 950.46 g Si m^{-2} yr^{-1}, according to mean and maximum production rates, respectively (*see* Ragueneau et al. 2000). More importantly, according to Dayton's data (1979), the BSi production rate by this sponge species in the study area may have doubled these quantities between 1975 and 1977. It should also be kept in mind that many other heavily silicified sponges cooccur in this community. Of particular interest is *Rosella racovitzae*, a heavily silicified hexactinellid that lives under the surface of the dense spicule mat that covers the seafloor. This species made up $>70\%$ of the sponge biomass in the study zone before the population explosion of *H. balfouriensis*. Using data from Dayton et al. (1974) and Dayton (1979) for 32 small individuals, which averaged 623.3 ± 824.2 cm^3 in 1974, we have calculated an average volume increase of $95.6\% \pm 78.8\%$ by 1977. Unfortunately, although such rates of volume increase suggest that the BSi stock in the sponge population doubled over those 3 yr, the structure of the original data does not allow us to translate this quantity into BSi production. In the community, there were also giant hexactinellids, such as *Rosella nuda* and *Scolymastra joubini*, which may be up to 2 m tall, 1.4 m in diameter, and up to 600 kg wet weight, containing up to 50 kg BSi each. Dayton (1979) reported that these two species showed no detectable growth and recruitment in 10 yr. Such a situation could be explained by reproduction being limited to one of few years interspersed by pluriannual periods of no reproductive activity, followed by the rapid growth of initial stages until reaching a relatively large adult stage. If this is the case, as it is also in *H. balfouriensis*, the demand of Si during the population explosion may be very important. In the studied community, there were also species that experienced continuous high recruitment and explosive growth, such as the demosponge *Mycale acerata*, which grows very rapidly after settlement for about 9 yr, achieving a diameter of up to 1.5 m, after which it becomes senescent (Dayton et al. 1974; Dayton 1979). Given that the 30,000-m^2 area monitored in these pioneering studies represents just a tiny parcel of the Antarctic sublittoral shelf covered by dense populations of heavily silicified sponges, it can be postulated that BSi production by the sponge communities on the Antarctic sublittoral shelf is far from being a negligible amount. Rather, it may well be as important as BSi production by diatoms.

The data presented and discussed suggest that siliceous sponges play a nonnegligible role in Si cycling in diverse

marine environments, with substantial contributions to the processes of BSi production and dissolution. This view is also consistent with the suggestion that Si cycling in some Florida lakes, despite diatom abundance, is controlled by the presence of a single freshwater demosponge species (Conley and Schelske 1993).

Our results, though derived from a handful of case studies, stress the need of reassessing the role of sponges in the Si cycling. We still have only an incipient knowledge of global patterns of sponge abundance and Si content in sublittoral and bathyal sponge assemblages, patterns of growth rates and organismal longevity, and patterns of long-term dynamics of in situ spicule dissolution. The situation is even worse where rates of BSi production are concerned. Therefore, an estimation of the global sponge contribution to the Si cycle will still require years of intense research effort. The lack of this knowledge should be kept in mind when revising general models of the marine Si cycle, as sponges are likely to be important contributors to benthopelagic coupling in this cycle.

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