

## Sponge contribution to the silicon cycle of a diatom-rich shallow bay

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15 **Running title:** Coastal silicon cycle through sponges

16 **Keywords:** silicon, silicifiers, sponges, coastal ocean, benthic-pelagic coupling

17

18 **Abstract**

19 In coastal systems, planktonic and benthic silicifiers compete for the pool of dissolved silicon, a  
20 nutrient required to make their skeletons. The contribution of planktonic diatoms to the cycling of  
21 silicon in coastal systems is often well characterized, while that of benthic silicifiers such as sponges  
22 has rarely been quantified. Herein, silicon fluxes and stocks are quantified for the sponge fauna in the  
23 benthic communities of the Bay of Brest (France). A total of 45 siliceous sponge species living in the  
24 Bay account for a silicon standing stock of 1215 tons, while that of diatoms is only 27 tons. The  
25 silicon reservoir accumulated as sponge skeletons in the superficial sediments of the Bay rises to  
26 1775 tons, while that of diatom skeletons is only 248 tons. These comparatively large stocks of  
27 sponge silicon were estimated to cycle two orders of magnitude slower than the diatom stocks.  
28 Sponge silicon stocks need years to decades to be renewed, while diatom turnover lasts only days.  
29 Although the sponge monitoring over the last 6 years indicates no major changes of the sponge  
30 stocks, our results do not allow to conclude if the silicon sponge budget of the Bay is at steady state,  
31 and potential scenarios are discussed. The findings buttress the idea that sponges and diatoms play  
32 contrasting roles in the marine silicon cycle. The budgets of these silicon major users need to be  
33 integrated and their connections revealed, if we aim to reach a full understanding of the silicon  
34 cycling in coastal ecosystems.

35

## 36 **Introduction**

37       There is great interest in understanding the cycling of silicon (Si) in marine environments because  
38 this nutrient is key to the functioning of marine ecosystems. In coastal oceans, Si is responsible for  
39 sustaining a large proportion of primary productivity and many of the food webs that ultimately  
40 sustain fish and human populations (Kristiansen and Hoell 2002; Ragueneau et al. 2006). Shortage of  
41 Si availability in coastal areas frequently reflects situations of ecosystem disequilibrium and  
42 proliferation of harmful algal blooms (Davidson et al. 2014; Glibert and Burford 2017; Thorel et al.  
43 2017). Thus, a thorough understanding of the cycling of Si in coastal marine environments is critical  
44 for effective ecosystem management.

45       A substantial part of the Si cycling in the marine environment occurs through a variety of micro-  
46 and macro-organisms, the silicifiers, which require Si to build their siliceous skeletons (DeMaster  
47 2003; Tréguer et al. 2021). To date, our understanding of the biogeochemical cycling of Si in the  
48 marine environment is based predominantly on the role of diatoms, microscopic unicellular  
49 eukaryotic algae which are the most abundant silicifiers in the global ocean (Malviya et al. 2016;  
50 Tréguer et al. 2021). Other silicifiers, such as siliceous Rhizaria and sponges, have received less  
51 attention and, consequently, their role is largely dismissed in most budgets of the marine Si cycle. To  
52 quantify the cycle contribution of siliceous sponges is particularly complicated given their benthic  
53 nature and heterogeneous distribution across the depths of the world's oceans. However, there is  
54 growing evidence that sponges are important contributors to the Si cycle in terms of Si standing  
55 stocks and reservoirs (Maldonado et al. 2010, 2019).

56       In the present study, the Bay of Brest (France) was monitored to assess the relative contribution of  
57 siliceous sponges to the Si budget of this emblematic coastal system. This Bay has been the subject  
58 of numerous ecological, biogeochemical, and physical studies and is currently one of the best-studied

59 coastal ecosystems in Europe, in terms of both structure and ecosystem functioning (Le Pape et al.  
60 1996; Del Amo et al. 1997; Chauvaud et al. 2000; Ragueneau et al. 2018). In this ecosystem, diatoms  
61 dominate the annual pelagic primary production (Quéguiner and Tréguer 1984; Del Amo et al. 1997).  
62 Other planktonic silicifiers such as silicoflagellates, polycystines, and phaeodarians are rarely  
63 recorded in the monthly surveys of the planktonic community of the Bay, and when found, they are  
64 low abundant (<https://www.phytobs.fr/>). Silicic acid (dSi) concentrations vary over the year cycle  
65 from below 1  $\mu\text{M}$  in spring and early summer up to 15-20  $\mu\text{M}$  in late autumn and winter. Therefore,  
66 in this ecosystem diatom's activity is limited by dSi principally during spring and early summer  
67 (Ragueneau et al. 2002), but sponges are limited all year round, as these organisms need dSi  
68 concentrations of 100-200  $\mu\text{M}$  to reach their maximum speed of Si consumption ( $K_M = 30\text{-}100 \mu\text{M}$   
69 Si; Reincke and Barthel 1997; Maldonado et al. 2011, 2020; López-Acosta et al. 2016, 2018).

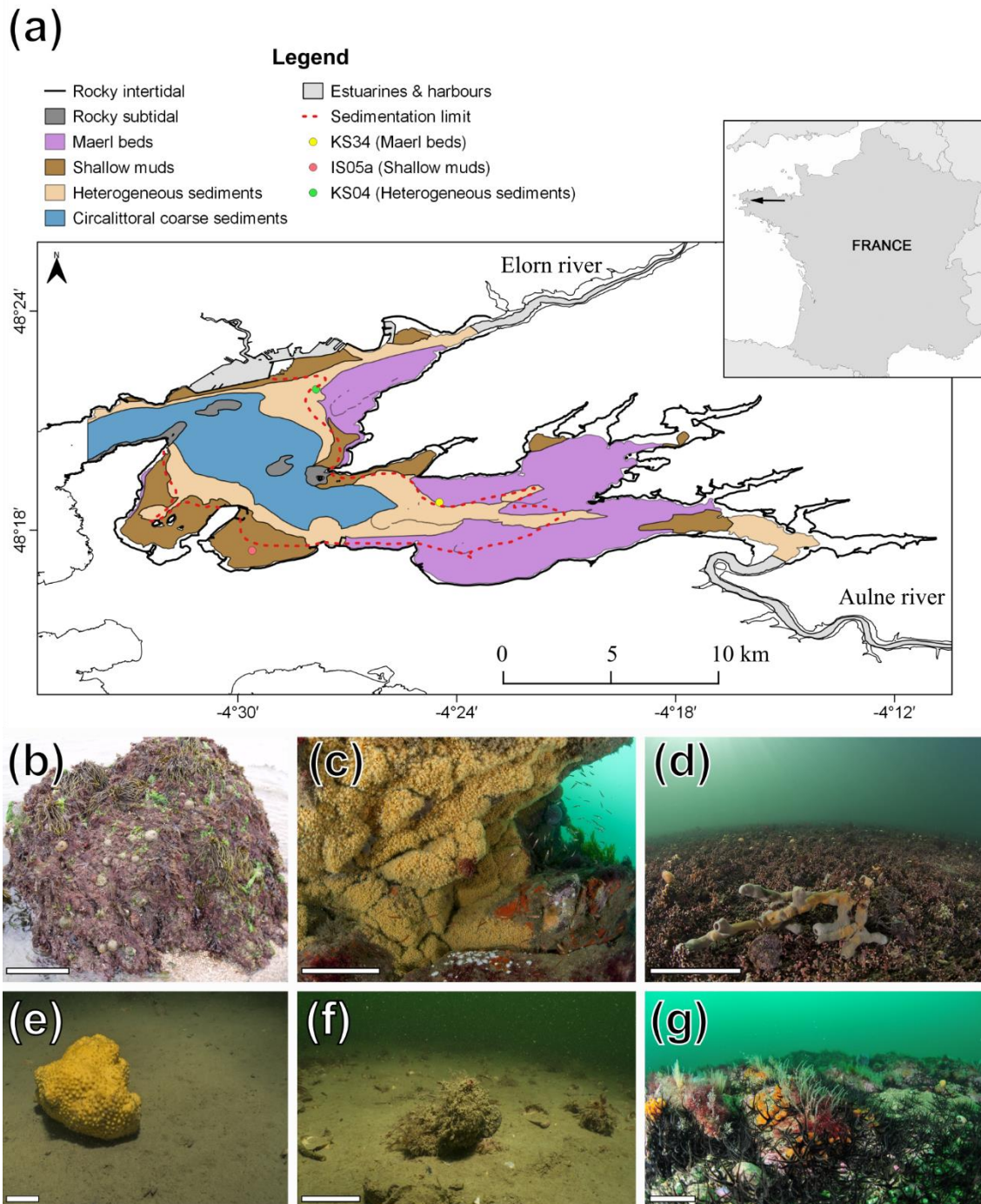
70 In this system, both dredging and diving research activities have identified important populations  
71 of siliceous sponges (Jean 1994; López-Acosta et al. 2018), and a previous study firstly estimated  
72 that the sponge silica production represents ca. 8% of the net annual silica production in the Bay  
73 (López-Acosta et al. 2018). Nevertheless, the large amounts of Si within the sponge bodies (i.e., the  
74 Si standing stock) remain unquantified, as well as the fate of such Si once the sponges die. Herein,  
75 we are estimating these parameters and providing the most complete cycle of Si through sponges for  
76 this coastal ecosystem. The findings are discussed within the regional Si budget of the Bay of Brest  
77 previously published by Ragueneau et al. (2005), which considered only the contribution of  
78 planktonic diatoms.

79

## 80 **Materials**

### 81 **Study area**

82 The Bay of Brest (NW France) is a semi-enclosed marine ecosystem of about 130 km<sup>2</sup> (harbors  
83 and estuaries not included) that is connected to the Atlantic Ocean through a narrow (1.8 km wide)  
84 and deep (45 m) strait. The Bay is a shallow system, with a maximum depth of 40 m and a mean  
85 depth of 8 m. It is a macro-tidal (maximum tidal amplitude = 8 m) system that receives high nutrient  
86 loadings mainly from two small rivers ([Fig. 1a](#)). During all the year cycle, the tidal and wind currents  
87 together with the shallowness of the Bay make nutrient concentration to remain relatively  
88 homogeneous in the water column (Delmas and Tréguer 1985; Salomon and Breton 1991; Le Pape et  
89 al. 1996).



90

91 **Fig. 1. (a)** Map of the Bay of Brest (France), showing the six major habitats defined for this study  
92 according to their depth, substrate type, and sponge fauna. Estuaries and harbors, depicted in grey in  
93 the map, have not been considered in the study. Red dashed line indicates the limit of sedimentation  
94 in the Bay, under which the sedimentation rate is negligible. Circles indicate the geographical

95 location of the examined cores. **(b-g)** General view of the habitats of the Bay: **(b)** rocky intertidal, **(c)**  
96 rocky subtidal, **(d)** maerl beds, **(e)** shallow muds, **(f)** heterogeneous sediments, and **(g)** circalittoral  
97 coarse sediments. Scale bars indicate 10 cm.

98

99 The Bay hosts abundant and diverse benthic communities, developed in a mixture of hard and soft  
100 substrates (Grall and Glémarec 1997). The benthic ecosystem of the Bay consist of six major  
101 habitats, according to depth, nature of substrate, and biota (Hily et al. 1992; Gregoire et al. 2016): 1)  
102 the rocky intertidal coastline that remains emerged during spring low tides; 2) the rocky subtidal  
103 bottoms, down to 20 m depth, that mostly surround the islets of the Bay; 3) the maerl beds, soft  
104 bottoms with dense assemblages of *Lithophyllum* spp. down to 15 m depth; 4) the shallow mud  
105 bottoms down to 10 m depth, mostly in the peripheral zones of the Bay; 5) the heterogeneous  
106 sediments from 5 to 25 m depth which consist of a mix of mud, calcareous detritus, and gravel  
107 bottoms; and 6) the circalittoral coarse sediments, consisting of gravel and pebble bottoms located  
108 mostly in the central, deepest zones (20 to 40 m) of the Bay (Fig. 1a-g). Using QGIS software,  
109 version 3.10.2 (QGIS Development Team 2020), the benthic habitats of the Bay were delimited and  
110 their areas were calculated (Fig. 1a; Table 1). This resulted in the most updated map of the benthic  
111 habitats of the Bay of Brest, which includes the up-to-date information of the bottom communities of  
112 the Bay from the annual monitoring conducted by the Marine Observatory of the European Institute  
113 for Marine Studies (Derrien-Courtél et al. 2019).

114

115 **Table 1. Features of the benthic habitats of the Bay of Brest (France), including bottom area**  
116 **(10<sup>6</sup> m<sup>2</sup>), relative contribution (%), sampled area (m<sup>2</sup>), mean (±SD) depth (m), and richness of**

117 **siliceous species of each habitat and the total Bay.** RI, rocky intertidal; RS, rocky subtidal; MB,  
118 maerl beds; SM, shallow muds; HS, heterogeneous sediments; CS, circalittoral coarse sediments.

Habitat	Bottom area (10 <sup>6</sup> m <sup>2</sup> )	Sampled area (m <sup>2</sup> )	Depth (m)	Si species richness
RI	1.98 (1.5%)	23	0.0 (± 0.0)	4
RS	2.64 (2.0%)	31	12.4 (± 4.0)	31
MB	45.84 (34.4%)	40	5.4 (±1.6)	19
SM	22.19 (16.7%)	17	5.1 (± 3.0)	2
HS	31.79 (23.9%)	36	11.4 (± 3.7)	16
CS	28.69 (21.6%)	23	25.6 (± 4.5)	32
Total	133.13 (100%)	170	9.9 (± 8.1)	45

119

120

## 121 **Silicon standing stock in sponge communities**

122 To estimate the Si standing stock of the sponge communities within the Bay of Brest, quantitative  
123 surveys were conducted across the six benthic habitats. The sampling effort carried out within a  
124 given habitat depended on both its relative surface to the total Bay extension and the relative internal  
125 variation (Eberhardt 1978). Three sampling techniques were used for the different habitats: (1) the  
126 rocky intertidal was sampled by using 23 random quadrats (1×1 m) at low tides; (2) the rocky  
127 subtidal, the maerl beds, the shallow mud, and the heterogeneous sediments above 20 m depth were  
128 sampled by scuba diving using 119 random 1×1 m quadrats; (3) the heterogeneous sediment and  
129 circalittoral coarse sediment located below 20 m depth were sampled using an epibenthic trawl over  
130 small transects (1 m wide × 5–10 m long, trawl length precision = ± 1m; n= 28). Each sponge found  
131 within the quadrats or in the trawls was counted, taxonomically identified to the species level, and  
132 measured for volume and silica content (i.e., biogenic silica, bSi). To determine the sponge volume,  
133 the body shape of each individual was approximated to one or a sum of several geometric figures  
134 (e.g., sphere, cylinder, cone, rectangular plate, etc.) and the linear parameters needed to calculate the  
135 volume (length, width, and/or diameter) were measured in situ using rulers (Maldonado et al. 2010).



136 Counts and volume values in each habitat were normalized to  $\text{m}^2$ . Non-siliceous sponge species were  
137 taxonomically identified but not considered in the calculations.

138 The relationship between the mean siliceous sponge abundance (i.e., number of individuals) and  
139 biomass (i.e., volume) in each habitat was normalized per  $\text{m}^2$  and analyzed by Spearman rank  
140 correlation. Between-habitat differences in the sponge abundance and biomass per  $\text{m}^2$  were examined  
141 by Kruskal-Wallis analysis when data did not meet normality and/or equal variance, following  
142 Shapiro-Wilk and Brown-Forsythe tests, respectively. Post-hoc pairwise multiple comparisons  
143 between groups were conducted using the non-parametric Dunn's test.

144 To estimate sponge silica content in a given sponge volume, a plastic cylinder of known volume  
145 was filled with sponge tissue ( $n = 3$  to  $5$  for each species, depending on availability), applying  
146 minimum compression. Sponge tissue samples were then dried at  $60^\circ\text{C}$  to constant dry weight (g),  
147 and desilicified by immersion in 5% hydrofluoric acid solution for 5 hours, rinsed in distilled water  
148 three times for 5 minutes, and dried again at  $60^\circ\text{C}$  to constant dry weight (Maldonado et al. 2010).  
149 Silica content per unit of sponge volume ( $\text{mg bSi mL}^{-1}$  sponge) was calculated as the difference in  
150 weight before and after desilicification and multiplied by a factor of 0.8. Such a factor was applied to  
151 remove overestimates of the skeletal biogenic silica due to tiny sand grains (lithogenic silica) that  
152 might be embedded into the sponge tissues (Maldonado et al. 2010).

153 Mean skeletal content ( $\text{mg bSi mL}^{-1}$  sponge) of each species was subsequently used to estimate Si  
154 standing stock in the sponge communities per unit of bottom area in the six habitats of the Bay, and  
155 that at the ecosystem level. Between-habitat differences in mean sponge Si standing stock per  $\text{m}^2$   
156 were examined by a Kruskal-Wallis analysis, followed by pairwise Dunn's tests to identify  
157 significant differences between groups. Finally, the relationship between skeletal content and sponge  
158 abundance per  $\text{m}^2$  and that between skeletal content and sponge biomass per  $\text{m}^2$  in the sponge  
159 communities of the Bay were also examined using regression analysis.

160

### 161 **Dissolved silicon consumption by sponge communities**

162 The annual consumption of dSi (and consequently biogenic silica production) by the sponge  
163 communities of the Bay was estimated by using the dSi consumption kinetic models developed  
164 elsewhere (López-Acosta et al. 2016, 2018) for the four dominant sponge species at the Bay  
165 (*Haliclona simulans*, *Hymeniacidon perlevis*, *Tethya citrina*, and *Suberites ficus*). By knowing the  
166 monthly average dSi availability in the bottom waters of the Bay over the last decade (2012-2021;  
167 [Table S1](#)) and the consumption kinetics of each of the four dominant species at the Bay, the average  
168 ( $\pm$ SD) annual dSi consumption rate by these species was estimated. This average was then  
169 extrapolated to the rest of the sponge species in the Bay to estimate dSi consumption by habitat and  
170 for the entire Bay, according to the previously estimated species sponge biomass per habitat (mL  
171 sponge m<sup>-2</sup>) and habitat bottom area (m<sup>2</sup>).

172

### 173 **Sponge biogenic silica in superficial sediments**

174 The amount of sponge Si in the sediments was determined by analyzing superficial sediments  
175 samples (defined herein as the upper-centimeter layer of sediment) from three stations from the  
176 shallow plateaus of the Bay of Brest ([Fig. 1a](#)). In the Bay, there are two major depositional  
177 environments with contrasting features: 1) the shallow terraces or plateaus, up to 10 m depth, where  
178 the fine sediment that regularly arrives through the rivers' discharges is homogeneously deposited,  
179 and 2) the deepest bottoms, up to 40 m depth, where the strong tidal currents prevent the fine  
180 sediment from being deposited on the bottom (Salomon and Breton 1991; Gregoire et al. 2017;  
181 Lambert et al. 2017). The latter are located mainly in the central zone of the Bay and the two paleo-  
182 channels that cross each of the basins of the Bay from the rivers' mouths to the central zone, where

183 they converge (see Figure 1 in Gregoire et al. 2017). This depositional configuration was originated  
184 by the action of successive sea-level low stands and it has been preserved over the last millennia by  
185 the effect of tidal currents in deep-water areas, which keep the inherited shape by preventing the  
186 deposition of the fine sediment supplied by rivers (Gregoire et al. 2016, 2017). As a consequence of  
187 this hydrodynamic regime, the fine sediment does not settle on the deepest areas of the Bay, the  
188 sediments of which mainly consist of coarse particles such as gross fragments of shells and small  
189 pebbles (Gregoire et al. 2016). On the contrary, the fine sediment settles all over the shallow  
190 plateaus, which are less affected by the tidal currents. Hence, the shallow plateaus account for  
191 virtually the total area of sediment deposition in the Bay bottoms (Ehrhold et al. 2016). These  
192 shallow plateaus, which account for about half of the Bay surface, are mainly covered by maerl beds,  
193 shallow muds and partially by heterogeneous sediments (Fig. 1a; Table 2).

194 To estimate the amount of sponge silica in the superficial sediments of the Bay, one core was  
195 sampled at each benthic habitat represented at the shallow plateaus: core SRQ3-KS34 from maerl  
196 beds, core SRQ1-IS05 from shallow muds, and core SRQ3-KS04 from heterogeneous sediments  
197 (Fig. 1a, Table 2). Present-day sedimentation rates were estimated from radiocarbon dating of  
198 superficial sediment in the cores (Gregoire et al. 2017; Ehrhold et al. 2021). The bottoms of the  
199 deepest areas of the Bay, on which sedimentation rates are negligible (Ehrhold et al. 2016), were  
200 interpreted as null contributors to the sponge silica accumulation in the Bay (see below).

201

202 **Table 2. Summary of core features including core label, coordinates, depth (m), average ( $\pm$ SD)**  
203 **sedimentation rate ( $\text{cm y}^{-1}$ ), the benthic habitat compartment they represent, and the extension**  
204 **of the benthic habitat over the sedimentation limit of the Bay ( $\text{km}^2$ ). Present-day sedimentation**

205 rates for the superficial sediments of each core were estimated from  $^{14}\text{C}$  radiocarbon dating in  
206 Gregoire et al. (2017) and Ehrhold et al. (2021).

Core label	Coordinates		Depth (m)	Sedimentation rate ( $\text{cm y}^{-1}$ )	Benthic habitat compartment	Compartment extension ( $\text{km}^{-2}$ )
	Latitude	Longitude				
SRQ3-KS34	48° 18.760' N	4° 24.474' W	10	0.037 ( $\pm$ 0.003)	Maerl beds (MB)	40.06
SRQ1-IS05a	48° 17.441' N	4° 29.609' W	7	0.090 ( $\pm$ 0.002)	Shallow muds (SM)	17.21
SRQ3-KS04	48° 21.858' N	4° 27.857' W	7	0.077 ( $\pm$ 0.001)	Heterogeneous sediments (HS)	9.18

207  
208

209 To quantify the sponge silica in the superficial sediment layer, one to three sediment subsamples  
210 of 10 mg each were collected from the upper 1-cm layer of each core and subsequently processed by  
211 light microscopy, following the methodology described in Maldonado et al. (2019). Briefly, sediment  
212 subsamples were transferred to test tubes, boiled in 37% hydrochloric acid to remove calcareous  
213 materials, then in 69% nitric acid to complete digestion of organic matter, rinsed in distilled water,  
214 and sonicated for 15 minutes to minimize sediment aggregates. The sediment suspension was then  
215 pipetted out and dropped on a microscope glass slide to measure the volume of each skeletal piece. A  
216 total of 230 smear slides in which 48320 spicules, either entire or fragmented, were examined  
217 through contrast-phase compound microscopes. Using digital cameras and morphometric software  
218 (ToupView, ToupTek Photonics), the volume of each spicule or spicule's fragment was estimated by  
219 approximating its shape to one or the sum of several geometric figures (Maldonado et al. 2019).  
220 Measured volumes of sponge silica were subsequently converted into Si mass, using the average  
221 density of  $2.12 \text{ g mL}^{-1}$  for sponge silica (Sandford 2003).

222 To determine the reservoir of sponge silica in the superficial sediment of the Bay, the obtained  
223 mass of sponge silica per gram of sediment in each core was extrapolated to the area of each benthic  
224 habitat over the sedimentation limit, delimited with a red dashed line in [Figure 1](#) from the

225 sedimentological data published in Ehrhold et al. (2016). It means that the sponge silica mass per  
226 gram of sediment from core SRQ3-KS34 was extrapolated to 40.06 km<sup>2</sup>, that of core SRQ1-IS05 to  
227 17.21 km<sup>2</sup>, and that of core SRQ3-KS04 to 9.18 km<sup>2</sup> (Table 2). Sponge Si deposition rate was  
228 estimated from the amount of sponge Si determined in the superficial sediments of each core and the  
229 sedimentation rate (Table 2). Sponge Si burial rate, i.e., the amount of sponge silica that is ultimately  
230 preserved in the sediments, was estimated from the rate of sponge Si deposited annually in the  
231 superficial sediments and the average percentage estimated for sponge Si preservation in sediments  
232 of marine continental shelves (i.e., 52.7 ± 29.8%; Maldonado et al., 2019). The contribution of  
233 sponges to the Si benthic efflux from the sediments of the Bay was calculated as the difference  
234 between the sponge Si deposition and burial rates.

235

### 236 **Sponge silica budget in a coastal ecosystem: the Bay of Brest**

237 The quantified stocks and fluxes of sponge Si were used to build a sponge Si budget for the Bay of  
238 Brest. These results were discussed in the context of previous studies and compared with those  
239 reported in the literature for the community of planktonic diatoms in the Bay.

240

## 241 **Results**

### 242 **General features of the sponge assemblages**

243 The survey of the sponge fauna at the Bay of Brest revealed a total of 53 sponge species, most of  
244 them belonging to the class Demospongiae (n=51), and only 2 species belonging to the class Calcarea  
245 (Table S2). Species from classes Hexactinellida and Homoscleromorpha were not found. Forty-five  
246 (85%) of the 53 identified species had siliceous skeletons. The other 8 were non-siliceous sponge

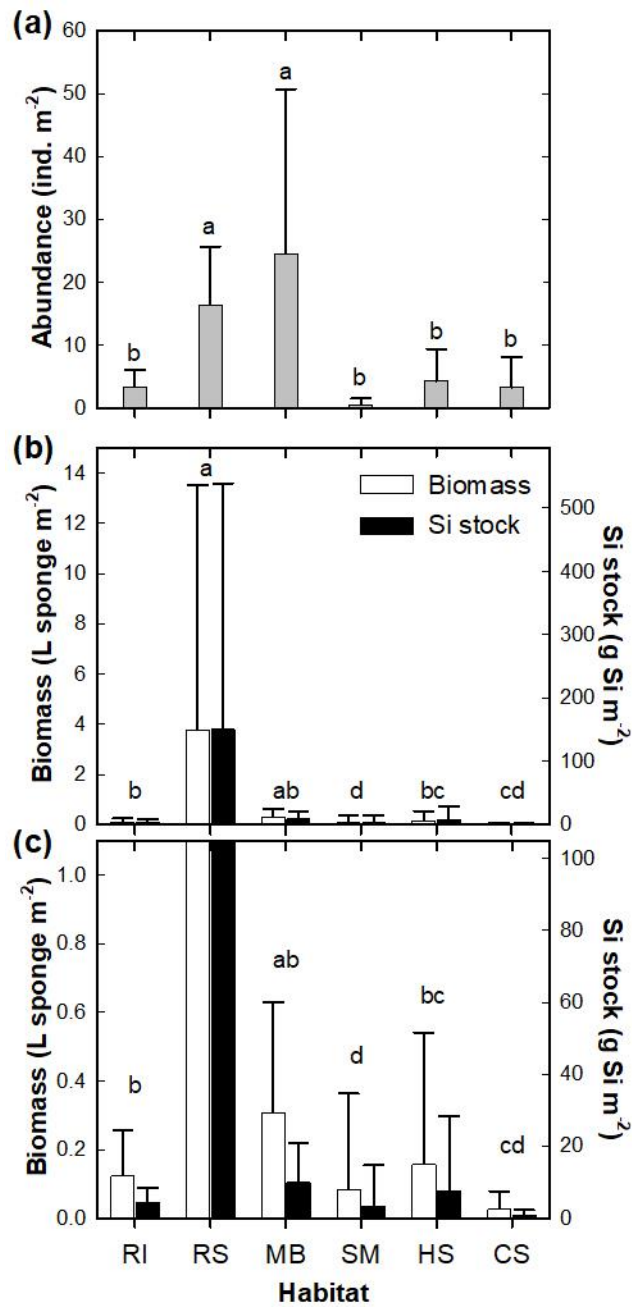
247 species with a skeleton made of either calcium carbonate (n=2) or skeletal protein (n=6). Non-  
248 siliceous sponges were not considered in the following quantifications of sponge abundance and  
249 biomass.

250 Sampling yielded a total of 1807 sponge individuals for which volume was determined (Table 1).  
251 At the Bay level, the siliceous sponge fauna averaged  $11.0 \pm 11.1$  individuals  $m^{-2}$  and a biomass of  
252  $0.31 \pm 0.35$  L of living sponge tissue  $m^{-2}$ . The large variation associated (i.e., standard deviation, SD)  
253 to the sponge abundance and biomass normalized per  $m^2$  is derived from the patchy spatial  
254 distribution of the sponges at both intra- and inter-habitat level. In contrast, the standard error (SE) of  
255 the mean ( $=SD/\sqrt{N}$ ) is low (SE of sponge abundance = 0.85; SE of sponge biomass = 0.03),  
256 indicating that mean values are accurate. A Spearman's correlation involving the six habitats  
257 revealed a strong positive linear relationship between the mean abundance and biomass of siliceous  
258 sponges per  $m^2$  of sampled bottom ( $N = 6$ ,  $\rho = 0.886$ ,  $p = 0.033$ ). This relationship informs that body  
259 size is more or less uniformly distributed across species and specimens of the different habitats.

260 At the habitat level, there were large between-habitat differences in both sponge abundance and  
261 biomass (Fig. 2). The total number of siliceous sponges per  $m^2$  significantly differs between habitats  
262 ( $H= 89.059$ ,  $df= 5$ ,  $p < 0.001$ ). Mean siliceous sponge abundance per  $m^2$  in the benthic communities  
263 of the maerl beds and rocky subtidal habitats ( $24.6 \pm 26.2$  and  $16.4 \pm 9.3$  individuals  $m^{-2}$ ,  
264 respectively) were significantly higher than that in the other habitats (Fig. 2a). Biomass of siliceous  
265 sponges ( $L m^{-2}$ ) also differed significantly between habitats ( $H= 78.324$ ,  $df= 5$ ,  $p < 0.001$ ). A  
266 posteriori pairwise comparison revealed that mean sponge biomass per  $m^2$  at the rocky subtidal  
267 habitat, which showed the highest sponge biomass per sampled bottom ( $3.8 \pm 9.7 L m^{-2}$ ), was  
268 significantly higher than that at the heterogeneous sediments ( $0.16 \pm 0.38 L m^{-2}$ ) and the rocky  
269 intertidal ( $0.12 \pm 0.13 L m^{-2}$ ) habitats. Mean sponge biomass per  $m^2$  at maerl beds ( $0.31 \pm 0.32 L m^{-2}$ ),  
270 which ranked second, did not differ significantly from that at the rocky subtidal, either at the

271 heterogeneous sediments and rocky intertidal habitat. Mean sponge biomass per m<sup>2</sup> at shallow muds  
272 and circalittoral coarse sediments were similar to each other and significantly lower than those at the  
273 rest of habitats in the Bay (Fig. 2b-c).

274



275

276 **Fig. 2. Summary of (a) average ( $\pm$ SD) abundance (individuals  $m^{-2}$ ), (b-c) biomass (L sponge  $m^{-2}$ ;  
277  $^2$ ; white bars), and silicon (Si) standing stock (g Si  $m^{-2}$ ; black bars) in the siliceous sponge fauna  
278 of the habitats of the Bay of Brest (France). Significant between-habitat differences of (a)  
279 abundance and (b) biomass and Si stock of the sponge fauna are indicated with different letters  
280 according to the results of Kruskal-Wallis analysis and the a posteriori pairwise Dunn's tests. (c) This  
281 graph makes visible the contribution of the habitats with sponge biomass and Si standing stock  
282 records lower than 1 L sponge  $m^{-2}$  and 100 g Si  $m^{-2}$ . Habitats abbreviations are RI for rocky  
283 intertidal, RS for rocky subtidal, MB for maerl beds, SM for shallow muds, HS for heterogeneous  
284 sediments, and CS for circalittoral coarse sediments.**

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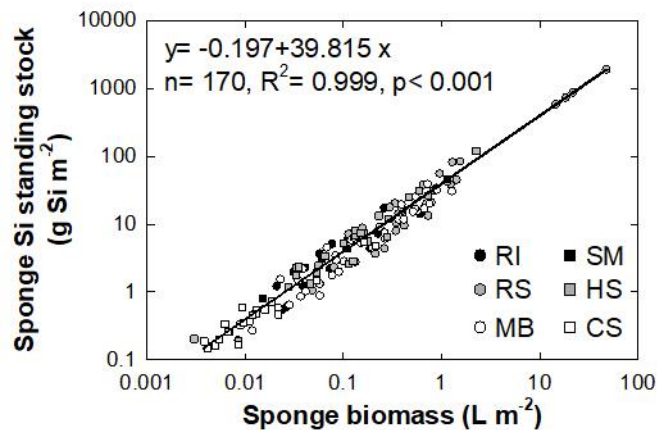
## 286 **Silicon standing stock in the sponge communities**

287 The importance of the siliceous skeleton content per mass unit of sponge tissue varied largely  
288 between sponge species (Table 3). It ranged from  $29.8 \pm 2.9$  to  $145.6 \pm 14.2$  mg bSi per mL of living  
289 sponge tissue (Table 3), accounting for 19.6% to 63.5% of the specific dry weight (DW). The  
290 average skeletal content estimated for the siliceous sponge fauna of the Bay of Brest was  $59.6 \pm 27.1$   
291 mg bSi  $mL^{-1}$  ( $45.8 \pm 10.6\%$  bSi/DW). From these figures, it is estimated that the Si standing stock in  
292 the sponge fauna of the Bay of Brest is  $12.3 \pm 14.1$  g Si  $m^{-2}$ . Nevertheless, there are large between-  
293 habitat differences in the sponge Si standing stock per  $m^2$  (Fig. 2b-c). The highest mean Si standing  
294 stock occurred in the rocky subtidal habitat ( $151.1 \pm 387.6$  g Si  $m^{-2}$ ). At this habitat, large specimens  
295 of *Cliona celata* were common (mean abundance=  $0.5 \pm 0.7$  individual  $m^{-2}$ , mean biomass=  $7.4 \pm$   
296  $13.5$  L individual $^{-1}$ ). The large specimens of this species, which is moderately silicified ( $85.6 \pm 7.2$   
297 mg bSi  $mL^{-1}$ ; Table 3), are responsible for the 89.2% of the total biomass and Si standing stock of the  
298 rocky subtidal habitat. The maerl beds ranked second in Si standing stock, with an average of  $10.0 \pm$



299 10.7 g Si m<sup>-2</sup> (Fig. 2b-c). In this habitat there is large abundance of sponges (24.6 ± 26.2 individuals  
300 m<sup>-2</sup>) with body size ranging from small to medium (mean biomass= 12.4 ± 37.1 mL individual<sup>-1</sup>).  
301 Four of the 19 siliceous sponge species identified at this habitat accounted for 84% of the total  
302 sponge Si standing stock (*Haliclona simulans*, *Hymeniacidon perlevis*, *Tethya citrina*, and *Suberites*  
303 *ficus*). A Kruskal-Wallis analysis confirmed that the between-habitat differences in sponge Si  
304 standing stock per m<sup>2</sup> are statistically significant (H = 71.701, df = 5, p<0.001). The pairwise  
305 comparison of mean Si standing stock revealed the same pattern of between-habitat differences than  
306 that obtained in the pairwise comparison of mean sponge biomass (Fig. 2b-c). Further analysis  
307 indicated a significant linear relationship (n= 170, R<sup>2</sup>= 0.999, p<0.0001) between sponge biomass  
308 and Si standing stock per m<sup>2</sup> across habitats (Fig. 3).

309



311 **Fig. 3. Relationship between silicon (Si) standing stock (g Si m<sup>-2</sup>) and biomass (L m<sup>-2</sup>) of**  
312 **siliceous sponges per m<sup>2</sup> of sampled bottom at the Bay of Brest (France).** Symbols represent the  
313 location of the data (i.e., habitat; abbreviations mean: RI, rocky intertidal; RS, rocky subtidal; MB,  
314 maerl beds; SM, shallow muds; HS, heterogeneous sediments; CS, circalittoral coarse sediments).  
315 Sponge Si stock and biomass are shown in logarithmic scale.

316

317 By integrating the average Si content of the sponges across the bottom area of each habitat, a total  
318 Si standing stock of  $1215 \pm 1876 \times 10^3$  kg Si ( $43.3 \pm 66.8 \times 10^6$  mol Si) in the sponge communities of  
319 the Bay of Brest was estimated. The small-scale patchiness in the spatial distribution of the sponges  
320 within a habitat causes some sampling quadrats to contain many sponges while others contain very  
321 few or none. This effect, when propagated for the calculation of the global mean of the Bay, results in  
322 a large SD value. In addition, about 90% of the stock is accumulated in the sponge fauna of three  
323 habitats, which—in order of contribution—are the maerl beds, the rocky subtidal, and the  
324 heterogeneous sediments.

325

### 326 **Dissolved silicon consumption by sponge communities**

327 The average monthly concentrations of dSi at the bottom waters of the Bay ranged from 2 to 13  
328  $\mu\text{M}$  (Table S1). At these nutrient concentrations, the most abundant species at the Bay (*H. perlevis*,  
329  $68.6 \pm 85.1$  mL  $\text{m}^{-2}$ ) consumed  $7.2 \pm 8.9$  mmol Si  $\text{m}^{-2} \text{y}^{-1}$ . Interestingly, the species *T. citrina* and *S.*  
330 *ficus*, which show comparatively lower biomass records in the Bay ( $24.5 \pm 34.1$  and  $7.7 \pm 13.3$  mL  
331  $\text{m}^{-2}$ , respectively), had similar rates of Si consumption ( $7.5 \pm 10.5$  and  $7.1 \pm 21.0$  mmol Si  $\text{m}^{-2} \text{y}^{-1}$ ,  
332 respectively). This is because their affinity for dSi is higher (affinity coefficient,  $V_{\text{max}}/K_{\text{M}} = 6.9 \times 10^{-3}$   
333 and  $4.4 \times 10^{-3}$   $\mu\text{mol Si h}^{-1} \text{sponge-mL}^{-1} \text{Si-}\mu\text{M}^{-1}$  for *T. citrina* and *S. ficus*, respectively, compared to  
334  $2.1 \times 10^{-3}$   $\mu\text{mol Si h}^{-1} \text{sponge-mL}^{-1} \text{Si-}\mu\text{M}^{-1}$  for *H. perlevis*).

335 Not surprisingly, most of the sponge Si consumption of the Bay occur in the rocky subtidal habitat  
336 and maerl beds, where sponges are very abundant and they show moderate to large biomass records  
337 (Fig. 2). The rocky subtidal habitat, which represents only 2.0% of the Bay bottom but hosts about  
338 30% of the total sponge biomass in the Bay, shows an annual sponge Si consumption rate of  $74.2 \pm$

339  $141.4 \times 10^3 \text{ kg Si y}^{-1}$  ( $2.6 \pm 5.0 \times 10^6 \text{ mol Si y}^{-1}$ ). The maerl beds, in which *H. perlevis*, *T. citrina*, and  
340 *S. ficus* are abundant in both terms of number of individuals and biomass, shows an annual Si  
341 consumption rate of  $73.6 \pm 112.7 \times 10^3 \text{ kg Si y}^{-1}$  ( $2.6 \pm 4.0 \times 10^6 \text{ mol Si y}^{-1}$ ). Collectively, the  
342 assemblage of siliceous sponges in the Bay is estimated to consume annually  $200.8 \pm 372.1 \times 10^3 \text{ kg}$   
343  $\text{Si y}^{-1}$  ( $7.2 \pm 13.2 \times 10^6 \text{ mol Si y}^{-1}$ ).

344

### 345 **Sponge bSi in sediments**

346 The superficial sediments (i.e., the upper 1-cm layer) of cores SRQ3-KS34, SRQ1-IS05a, and  
347 SRQ3-KS04, contained respectively a total of 1.07 ( $\pm 0.05$ ), 1.30, and 0.32 million spicules or spicule  
348 fragments per g of sediment, with an average spicule content of 0.89 ( $\pm 0.51$ ) million spicules  $\text{g}^{-1}$   
349 sediment for the set of studied cores (Table 4). In all cores, most spicules (98.3-99.1%) were  
350 recognized as megascleres, either entire or fragmented. The microscopic study of the superficial  
351 sediment in the cores showed only small between-area differences in the mass of sponge bSi, which  
352 ranged from 0.799 to 2.505  $\text{mg Si g}^{-1}$  sediment (Table 4). The average content of sponge bSi in the  
353 sediments of the Bay of Brest was 1.565 ( $\pm 0.866$ )  $\text{mg Si g}^{-1}$  sediment.

354

355 **Table 4. Summary of the results obtained during the microscopic examination of the superficial**  
356 **sediments of the Bay of Brest.** Average ( $\pm$ SD, when available) spicule counts (in millions per gram  
357 of sediment), contribution (%) of megascleres (spicules longer than 100  $\mu\text{m}$ ) and microscleres  
358 (spicules shorter than 100  $\mu\text{m}$ ), and mass of sponge silica per gram of sediment for each core are  
359 indicated, as well as for the set of study cores.

Core label	Benthic habitat	N spicules (N x 10 <sup>6</sup> g <sup>-1</sup> sed.)	Spicule-type contribution (%)		Sponge Si in superficial sed. (mg Si g <sup>-1</sup> sed.)
			Megascleres	Microscleres	
SRQ3-KS34	Maerl beds (MB)	1.07 (± 0.05)	99.1 (± 0.3)	0.9 (± 0.3)	1.391 (± 0.241)
SRQ1-IS05a	Shallow muds (SM)	1.30	99.0	1.0	2.505
SRQ3-KS04	Heterogeneous sediments (HS)	0.32	98.3	1.7	0.799
AVERAGE (±SD)		0.89 (± 0.51)	98.8 (± 0.4)	1.2 (± 0.4)	1.565 (± 0.866)

360

361

362 Sponge Si deposition rates in the studied areas ranged from 9.4 to 64.4 x 10<sup>3</sup> kg Si y<sup>-1</sup>, depending  
 363 on the habitat (Table 5). When deposition rates were extrapolated to the total extension of the shallow  
 364 plateaus (i.e., 66.45 km<sup>2</sup>), it resulted in a mean deposition rate of 108.7 ± 9.1 x 10<sup>3</sup> kg Si y<sup>-1</sup> (3.9 ±  
 365 0.3 x 10<sup>6</sup> mol Si y<sup>-1</sup>). The sponge Si burial rate was then calculated from the deposition rate and the  
 366 average preservation rate of sponge silica determined by Maldonado et al. (2019) for continental-  
 367 shelf sediments. This approach yielded an average burial rate of sponge silica in the sediments of the  
 368 shallow plateaus of 57.3 ± 18.2 x 10<sup>3</sup> kg Si y<sup>-1</sup> (2.0 ± 0.6 x 10<sup>6</sup> mol Si y<sup>-1</sup>). The differences between  
 369 deposition and burial rate is, in the long run, the sponge contribution to the benthic Si efflux from  
 370 sediments, which was estimated to be 51.4 ± 17.7 x 10<sup>3</sup> kg Si y<sup>-1</sup> (1.8 ± 0.6 x 10<sup>6</sup> mol Si y<sup>-1</sup>) for the  
 371 shallow plateaus of the Bay (Table 5).

372

373 **Table 5. Sponge silicon (Si) stock in the superficial sediments of each depositional environment**  
 374 **of the Bay of Brest, along with the deposition, burial and benthic flux rate of sponge Si.** Area  
 375 (km<sup>2</sup>) to which the sponge Si data were extrapolated is indicated. These areas do not correspond to  
 376 the total habitat extension but to the habitat area that is above the sedimentation limit of the Bay  
 377 (indicated with a red dashed line in Fig. 1a) for cores representing the shallow depositional plateaus.

Core label	Benthic habitat	Area km <sup>2</sup>	Sponge Si STOCK	Sponge Si FLUXES		
			reservoir 10 <sup>3</sup> kg Si	deposition rate 10 <sup>3</sup> kg Si y <sup>-1</sup>	burial rate 10 <sup>3</sup> kg Si y <sup>-1</sup>	benthic flux 10 <sup>3</sup> kg Si y <sup>-1</sup>
SRQ3-KS34	Maerl beds (MB)	40.06	937.93	34.91	18.39	16.52
SRQ1-IS05a	Shallow muds (SM)	17.21	715.41	64.39	33.92	30.47
SRQ3-KS04	Heterogeneous sediments (HS)	9.18	121.70	9.38	4.94	4.44
378 TOTAL		66.45	1775.04	108.68	57.25	51.43

379

380 According to the depositional environments of the Bay, the deep sediments were not considered in  
 381 the calculations of the total sponge Si reservoir and sediment fluxes rates (see Methods). This is also  
 382 supported by the sponge spatial distribution at the Bay, which shows that in the deepest areas  
 383 sponges are particularly low abundant ( $3.2 \pm 4.9$  ind. m<sup>-2</sup>) and their contribution to the Si standing  
 384 stock is significantly low ( $0.8 \pm 1.4$  g Si m<sup>-2</sup>; Fig. 2). By extrapolating the sponge silica content  
 385 determined in the superficial sediments of the Bay (Table 5), a total sponge silica reservoir in the  
 386 superficial (upper centimeter) sediment layer of the Bay of Brest of  $1775 \pm 162 \times 10^3$  kg Si ( $63.2 \pm$   
 387  $5.8 \times 10^6$  mol Si) was estimated.

388

## 389 Discussion

### 390 Sponge fauna within the Bay of Brest

391 The survey of the sponge fauna of the Bay of Brest revealed that sponges are ubiquitous and widely  
 392 present in most of the habitats (17-36 spp. per habitat; Table 1, Fig. 2, Table S2). Only two habitats,  
 393 the shallow muds and the rocky intertidal, showed low sponge species richness ( $\leq 4$  species per habitat;  
 394 Table 1, Table S2). These two habitats, the former characterized by muddy bottoms and scanty hard

395 substratum and the latter by periodic air exposures during low tides, hosted only a handful of species  
396 able to deal with those harsh conditions (Table S2).

397 The taxonomic composition and spatial distribution of the sponge fauna significantly differed  
398 between habitats (Table 1, Fig. 2). Spatial heterogeneity has been widely reported for sponge  
399 distributions across all oceans, with a variety of biological and physical reasons behind it (Hooper  
400 2019). Among the habitats of the Bay, the rocky subtidal is the one with the highest sponge biomass  
401 per unit area ( $3.8 \pm 9.7 \text{ L m}^{-2}$ ; Fig. 2b), reaching values similar to those reported in some emblematic  
402 sponge aggregations in tropical and polar latitudes (Maldonado et al. 2017 and references therein).  
403 According to their extension, the maerl beds, which accounted for about one third of the total surface  
404 of the Bay (Table 1), hosted most of the sponge individuals and biomass of the Bay — $79 \pm 46\%$  of the  
405 total number of sponges ( $1416 \pm 1474$  million of individuals) and about  $44 \pm 23\%$  of the total sponge  
406 volume ( $31.9 \pm 47.0 \times 10^6 \text{ L}$ ) estimated at the Bay of Brest. Thus, the maerl beds of the Bay serve as  
407 substrate to highly diverse and abundant sponge fauna, which along with other benthic organisms,  
408 make these bottoms real sponge and biodiversity hotspots, similar to what has been reported for maerl  
409 beds from other ocean regions (Sciberras et al. 2009; Ávila and Riosmena-Rodriguez 2011; Neill et al.  
410 2015).

411

## 412 **Biogenic silica stock as sponge skeletons**

413 Our results indicate that a substantial amount of the biogenic silica stock of the Bay of Brest is in  
414 the form of sponge silica, in both the living sponge fauna and the sediments of the Bay (Fig. 4). In  
415 the sponge communities, the Si standing stock within the skeleton of the sponges totaled  $1215 \pm 1876$   
416  $\times 10^3 \text{ kg}$  of Si. The siliceous skeleton accounted for 19.6-63.5% of the sponge dry weight, depending  
417 on the species (average value =  $45.8 \pm 10.6\% \text{ bSi/DW} = 59.6 \pm 27.1 \text{ mg bSi mL}^{-1}$ ; Table 3). Similar

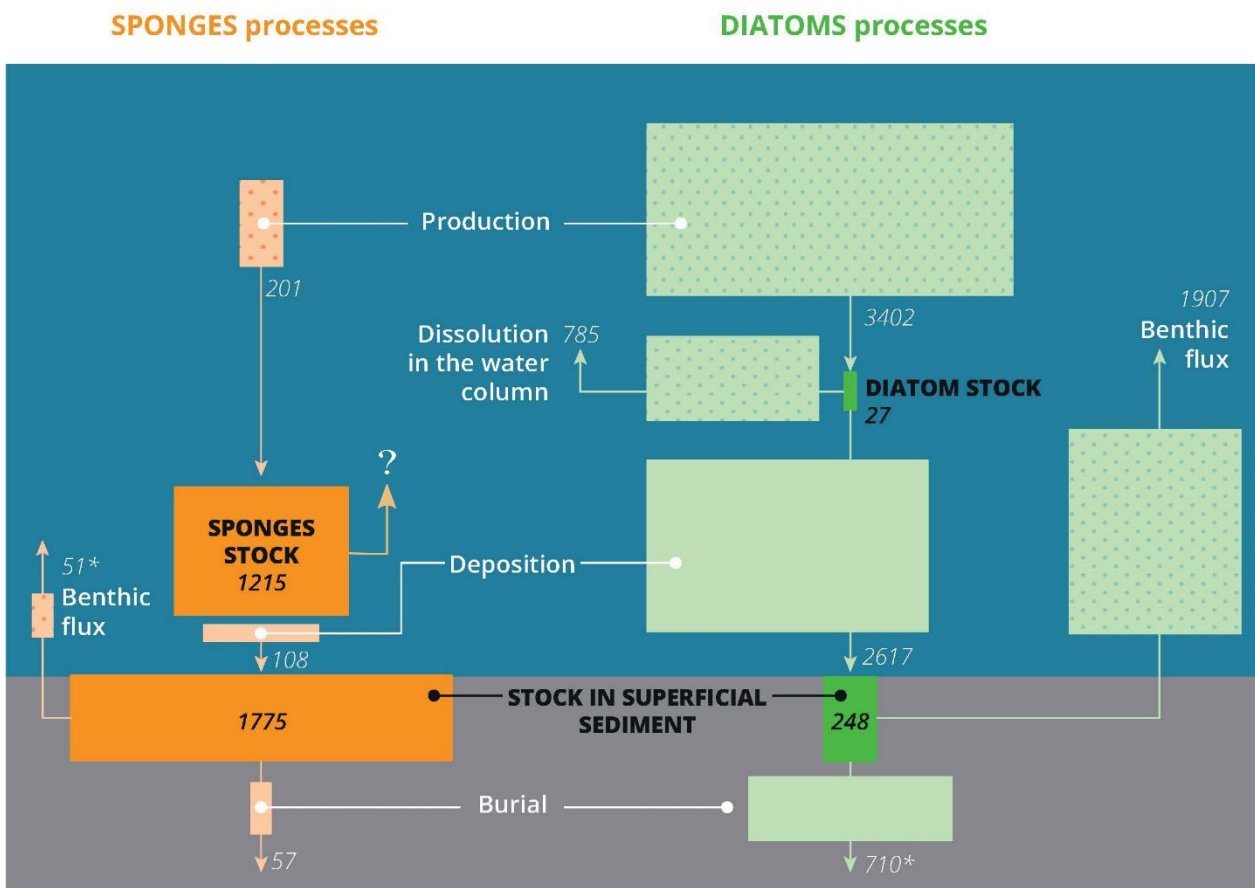
418 bSi content and between-species variability was also reported in a sponge-rich community of the  
419 Belizean Mesoamerican Barrier Reef ( $53.4 \pm 6.1$  mg bSi mL<sup>-1</sup>; Maldonado et al. 2010).

420 To date, only few studies have measured the amount of Si trapped in sponge communities of  
421 shallow-water ecosystems. The sponge Si standing stock per m<sup>2</sup> in the Bay of Brest ( $12.3 \pm 14.1$  g Si  
422 m<sup>-2</sup>) is about 5 times higher than that found in the sublittoral population of the encrusting  
423 demosponge *Crambe crambe* at the Catalan coast of the NW Mediterranean ( $2.5 \pm 2.7$  g Si m<sup>-2</sup>;  
424 Maldonado et al. 2005) and, interestingly, similar to that measured in the sublittoral sponge-rich  
425 assemblages of the Belize section of the Mesoamerican Barrier Reef ( $12.0$  g Si m<sup>-2</sup>; Maldonado et al.  
426 2010). The sponge Si standing stock of the Bay of Brest is also similar to that found at bathyal depths  
427 at the westward slope of the Mauna Loa Volcano of Hawaii ( $12.6$  g Si m<sup>-2</sup>; Maldonado et al. 2005),  
428 where a dense monospecific population of the highly-silicified hexactinellid *Sericolophus hawaiiicus*  
429 occurs. Higher records of Si sponge stocks have only been reported from 1) the monospecific sponge  
430 ground of the hexactinellid *Vazella pourtalessii* at the Nova Scotian continental shelf, Canada ( $43.8 \pm$   
431  $74.6$  g Si m<sup>-2</sup>; Maldonado et al. 2021), 2) the continental margins of Antarctica ( $178$  g Si m<sup>-2</sup>; Gutt et  
432 al. 2013), where heavily silicified demosponges and hexactinellids co-occur, and 3) the singular  
433 epibathyal reefs of the hexactinellid *Aphrocallistes vastus* in British Columbia (Canada), where high  
434 densities of heavily silicified individuals grow on exposed skeletons of dead sponges, leading to  
435 outstanding accumulations of sponge silica in the form of siliceous reefs ( $4238 \pm 924$  g Si m<sup>-2</sup>; Chu et  
436 al. 2011). Altogether, these results support the idea that sponge communities are transient Si sinks  
437 (Maldonado et al. 2005, 2010) and suggest that relevant standing stocks of sponge silica are likely to  
438 occur not only in deep-sea and polar latitudes but also in shallow-water ecosystems from temperate  
439 latitudes, in which diverse and abundant sponge populations may easily develop (Van Soest et al.  
440 2012; Maldonado et al. 2017).

441 The amount of sponge silica accumulated in only the superficial (upper centimeter) sediment layer  
442 of the Bay of Brest ( $1775 \pm 162 \times 10^3$  kg Si; Fig. 4) falls in the same order of magnitude than that  
443 accumulated in the living sponge fauna of the Bay ( $1215 \pm 1876 \times 10^3$  kg; Fig. 4). The Si stock in the  
444 superficial sediments is in the form of siliceous spicules that reach the sediments after sponge death  
445 (Chou et al. 2012; Lukowiak et al. 2013; Maldonado et al. 2019), the abundance of which appears to  
446 be proportional to the silica standing stock in the sponge communities living nearby (Bavestrello et  
447 al. 1996; Lukowiak et al. 2013). The amounts of sponge silica deposited on the superficial sediments  
448 of the Bay of Brest ( $0.799 - 2.505$  mg Si  $g^{-1}$  sediment; Table 4) are among the highest determined in  
449 superficial sediments of continental margins from different oceans and seas ( $0.014 - 2.572$  mg Si  $g^{-1}$   
450 sediment; Sañé et al. 2013; Maldonado et al. 2019). For instance, the amount of sponge silica  
451 determined in the superficial sediments of the shallow muds ( $2.505$  mg Si  $g^{-1}$  sediment, core SRQ1-  
452 IS05a; Table 4) is nearly identical to that determined in the superficial sediments of the slope of the  
453 Bransfield Strait in Antarctica ( $2.572 \pm 0.861$  mg Si  $g^{-1}$  sediment; Maldonado et al. 2019), where  
454 dense sponge aggregations occur (Ríos and Cristobo 2014; Kersken et al. 2016; Gutt et al. 2019).  
455 Combining the cores examined in this study ( $1.565 \pm 0.241$  mg Si  $g^{-1}$  sediment), the sediments of the  
456 Bay had about 60% more sponge silica than the average estimated for the sediments of continental  
457 margins in the global ocean ( $0.924 \pm 0.854$  mg Si  $g^{-1}$  sediment; Maldonado et al., 2019), indicating  
458 that sediments from areas where sponges abound become an important reservoir of biogenic silica.

459





460

461 **Fig. 4. Scheme summarizing the silicon stocks and fluxes through the sponge and planktonic**  
 462 **diatom communities of the Bay of Brest (France).** Stocks and fluxes of silicon (Si) mediated by  
 463 sponges are in orange, and those mediated by diatoms are in green. Stocks of biogenic silica are  
 464 indicated in tons of Si. Fluxes of silicic acid, with a dotted pattern, and those of biogenic silica,  
 465 lacking the dotted pattern, are indicated in tons of Si per year. The size of the boxes representing both  
 466 stocks and fluxes is proportional to their rate. Fluxes of Si through diatoms are from Ragueneau et al.  
 467 (2005), stock of biogenic silica in planktonic diatoms has been calculated from Beucher et al. (2004),  
 468 and reservoir of diatom silica in superficial sediments are from Song and Ragueneau (2007); more  
 469 details about calculations in the main text. Asterisks (\*) refer to fluxes derived indirectly.

470

## 471 **Silicon cycling through the sponge assemblage**

472 The siliceous skeletons produced by the sponges as part of their annual growth are progressively  
473 accumulated within the sponge body for the lifespan, which is thought to range from years to decades  
474 or centuries in shallow-water sponge species from temperate latitudes (McMurray et al. 2008;  
475 Teixidó et al. 2011; McGrath et al. 2018). When a sponge dies or part of its body is removed or  
476 damaged by either natural or anthropogenic processes, the siliceous spicules within the sponge tissue  
477 are freed and end deposited on the superficial sediments (Chou et al. 2012; Lukowiak et al. 2013;  
478 Maldonado et al. 2019). In the Bay of Brest, the deposition of sponge silica was estimated to be  $108$   
479  $\pm 9 \times 10^3 \text{ kg Si y}^{-1}$  (Fig. 4). Such rate is about twice smaller than the rate at which sponges produce  
480 silica in the Bay ( $201 \pm 372 \times 10^3 \text{ kg Si y}^{-1}$ ; Fig. 4). That would mean that the sponge fauna of the  
481 Bay of Brest would be increasing at a rate of  $92 \pm 241 \times 10^3 \text{ kg Si y}^{-1}$  ( $3.3 \pm 8.6 \times 10^6 \text{ mol Si y}^{-1}$ ),  
482 which would double the sponge Si standing stock (i.e., the sponge population) in about 13 years. In  
483 contrast, the sponge fauna survey of the Bay over the last 6 years and the long-term survey conducted  
484 in the area by the Marine Observatory of the IUEM since 1997 do not indicate that the sponge  
485 populations of the Bay are increasing at such high rate, rather the abundance and biomass of the  
486 sponge assemblages appear to be relatively constant in the long run (J. Grall, pers. comm.). Other  
487 reasons may also contribute to the imbalance between the annual silica production and deposition  
488 rates. First, the sponge mortality rate is unlikely to be constant every year. Indeed, a longer time  
489 frame (of at least a decade) is likely needed to capture the Si cycling dynamics in the sponge  
490 populations (McMurray et al. 2015; Bell et al. 2017). Second, there might be some partial rapid ( $<1\text{y}$ )  
491 dissolution of the spicules upon sponge death. Although sponge silica is more resistant to dissolution  
492 than that of others silicifiers (Rützler and Macintyre 1978; Erez et al. 1982; Maldonado et al. 2005,  
493 2019), the most labile fraction of the sponge silica might be dissolved before the spicules being  
494 accumulated in the sediments. This would be in agreement with a recent study (Ng et al. 2020) that

495 has measured through  $\delta^{30}\text{Si}$  that the remineralization of silica from demosponges —the same Class  
496 of sponges as those occurring in the Bay of Brest— may be locally significant in superficial  
497 sediments where sponges abound. In the study, Ng and co-authors determined that the benthic Si  
498 effluxes from bottoms with sponges were from 2 to 10 times higher than those from sediments  
499 without sponges. Finally, it cannot be excluded that part of the sponge silica deposited on the Bay  
500 bottoms is exported out of the Bay during the monthly strong tidal currents during spring tides or  
501 during extreme storms events, the force of which has been suggested to partially transport the  
502 deposited sediments of the Bay (Beudin 2014). Further research is necessary to resolve which of  
503 these processes, or if a combination of them, could explain the imbalance between the annual sponge  
504 silica production and deposition rates at the Bay.

505 Through deposition, the sponge silica accumulates in the sediments of the Bay and is finally  
506 buried at an average rate of  $0.06\text{ cm y}^{-1}$  (Gregoire et al. 2017; Ehrhold et al. 2021). Within the first  
507 centimeters of marine sediments, biogenic silica —no matter its origin— dissolves progressively  
508 until the interstitial water becomes saturated in dSi, an asymptotic condition in which biogenic silica  
509 dissolution typically ceases (Rickert et al. 2002; Sarmiento and Gruber 2006; Khalil et al. 2007). In  
510 the sediments of the Bay of Brest, the interstitial water reaches dSi asymptote at 10-15 cm burial  
511 depth (Raimonet et al. 2013), meaning that below that threshold, the amount of sponge silica buried  
512 annually ( $57 \pm 18 \times 10^3\text{ kg Si y}^{-1}$ ; Fig. 4) is preserved definitively in the sediments of the Bay. The  
513 difference between the sponge silica deposited on superficial sediments and that buried definitively in  
514 the sediments ( $51 \pm 18 \times 10^3\text{ kg Si y}^{-1}$ ; Fig. 4) is assumed to be dissolved as interstitial dSi during the  
515 early steps of burial. Such amount of dSi contributes to the saturation of interstitial water and  
516 ultimately feeds the dSi benthic efflux from the sediments of the Bay toward the water column, a  
517 recycling process that helps to sustain the populations of planktonic diatoms during the productive  
518 season in the Bay (Chauvaud et al. 2000; Ragueneau et al. 2002). Further investigation on the

519 processes involved in the dissolution of sponge silica during the early steps of burial would help to  
520 quantify more accurately at which level the sponge Si contributes to the benthic dSi efflux.

521

## 522 **Sponge vs. diatom Si cycle at the Bay of Brest**

523 The biogeochemical cycling of Si in the Bay of Brest through planktonic diatoms is well studied  
524 (e.g., Delmas and Tréguer, 1983; Del Amo et al., 1997; Chauvaud et al., 2000; Beucher et al., 2004)  
525 and summarized in Ragueneau et al. (2005). This budget was based on diatom Si flux rates and did  
526 not consider the sponge Si flux rates, nor the biogenic silica stocks of sponges and diatoms in the  
527 living communities and sediments.

528 To compare the contribution of diatoms and sponges to the Si budget of the Bay, the standing  
529 stocks and Si reservoirs in the form of diatom silica were determined from the literature. According  
530 to it, the standing stock of diatoms in the water column of the Bay ranges from 0.12 to 1.98  $\mu\text{mol Si}$   
531  $\text{L}^{-1}$  over the year cycle (Beucher et al. 2004). Unlike sponges, diatom cells have an ephemeral life of  
532 only days. Therefore, the silica standing crop of planktonic diatoms is known to change drastically  
533 from week to week and over seasons, depending on nutrient availability and hydrological conditions  
534 (Sarhou et al. 2005; Falkowski and Oliver 2007; Armbrust 2009). If the annual mean of diatom silica  
535 in the Bay ( $0.9 \mu\text{mol Si L}^{-1}$ ; Beucher et al. 2004) is homogeneously extrapolated to the whole volume  
536 of the Bay of Brest ( $1.07 \times 10^{12} \text{ L}$ ), an average diatom silica standing stock of  $27 \times 10^3 \text{ kg Si}$  ( $1.0 \times$   
537  $10^6 \text{ mol Si}$ ) is obtained (Fig. 4). This figure integrates the seasonal variability occurring over the year  
538 cycle in the Bay, which range from a minimal value of  $18 \times 10^3 \text{ kg Si}$  ( $0.6 \times 10^6 \text{ mol Si}$ ) in winter to a  
539 maximum value of  $36 \times 10^3 \text{ kg Si}$  ( $1.3 \times 10^6 \text{ mol Si}$ ) in spring.

540 The fate of diatom silica in superficial sediments is largely influenced by the active filter-feeding  
541 of mollusks in the Bay, which defecate Si-rich feces that facilitate the retention of diatom silica at the  
542 sediment surface (Chauvaud et al. 2000; Ragueneau et al. 2002, 2005). The content of diatom silica  
543 in the superficial sediment of the Bay was determined from the analysis of 86 sediment samples from  
544 43 stations across the Bay, which capture both the intra-annual variability (43 samples were sampled  
545 in winter and 43 in late summer) and the different depositional environments of the Bay (Song and  
546 Ragueneau 2007). It resulted in an average diatom silica reservoir in the superficial sediments of the  
547 Bay of  $248 \times 10^3$  kg Si ( $8.8 \times 10^6$  mol Si; Fig. 4).

548 When the Si stocks and fluxes of sponges are compared with those of planktonic diatoms, there  
549 are marked differences (Fig. 4). The rates at which Si is processed through diatoms are one order of  
550 magnitude higher than those through sponges. On the contrary, diatom Si stocks are between 7 to 45  
551 times smaller than those of sponges (Fig. 4), in agreement with the only study to date comparing Si  
552 standing stocks in sponges and diatoms in a coastal ecosystem (Maldonado et al. 2010). These  
553 differences indicate that sponges and diatoms play their respective roles in the Si budget of the Bay at  
554 different speeds and through different mechanisms. The turnover of the diatom silica standing stock  
555 (i.e., standing stock : production rate) in the Bay is about 3 days, whereas that of sponge silica is  
556 about 6 years, that is, approximately 800 times slower than that of diatom silica. Similarly, the  
557 turnover of diatom silica stock in superficial sediments (i.e., reservoir in sediment : deposition rate) is  
558 about 1 month, whereas that of sponge silica is about 16 years (ca. 170 times that of diatom silica).  
559 This means that the cycling of Si through diatoms is comparatively faster, with Si mainly cycling  
560 through them (repeatedly over a year) rather than being accumulated. In contrast, Si accumulates in  
561 huge amounts in sponges over long periods ( $\geq 10$  y), being slowly processed through them. These  
562 results show that impacts on either the sponge populations or the sediments nearby sponge

563 aggregations could have a long-term impact on the sponge Si cycling dynamics, which will require  
564 decades to be restored.

565

## 566 **Conclusion**

567 In shallow-water ecosystems, planktonic and benthic silicifiers have to share the dSi pool and  
568 compete to incorporate this nutrient, which is critical for the growth of both organisms. Our study  
569 highlights that even in coastal, shallow-water systems with a high primary productivity dominated by  
570 planktonic diatoms —such as the Bay of Brest, sponges may account for a stock of biogenic silica as  
571 large as 89-98%. This stock cycles slowly compared to that of diatoms and accumulates bSi in the  
572 sediments. These results suggest that the Si cycling through sponge communities is substantially  
573 different from that through diatom assemblages. Therefore, the comparison between the roles of these  
574 two groups of silicifiers is not straightforward due to their contrasting biological features (e.g.,  
575 benthic and long living vs planktonic and short living). Yet these two types of silicifiers need to be  
576 quantitatively integrated in future approaches, if we aim to understand in depth the intricacies of the  
577 Si cycle in coastal systems.

578

## 579 **Acknowledgments**

580 The authors thank Erwan Amice, Isabelle Bihannic, and Thierry Le Bec for assistance during  
581 underwater fieldwork and for pictures of Fig. 1b-g. Marta García Puig and Marcos Navas Durán are  
582 thanked for helping with the data management of spicule counting. The authors also thank the staff  
583 maintaining the Lanvéoc database for making public their information on nutrient availability at the

584 bottom waters of the Bay of Brest and Sébastien Hervé for the artwork of Fig. 4. Jill Sutton and Fiz  
585 Fernández are especially thanked for their comments on the manuscript. This research was supported  
586 by two Spanish Ministry grants (CTM2015-67221-R and MICIU: #PID2019-108627RB-I00) to MM,  
587 the French National research program EC2CO (grant 12735 – AO2020) to JG, and the ISblue project,  
588 Interdisciplinary graduate school for the blue planet (ANR-17-EURE-0015), co-funded by a grant  
589 from the French government under the program "Investissements d'Avenir", to MLA. MLA thanks  
590 the Xunta de Galicia for her postdoctoral grant (IN606B-2019/002), which also supported this work.  
591 The authors declare no conflict of interest.

592

### 593 **Author Contributions**

594 MLA and MM conceived and designed the study. MLA conducted the sponge fieldwork, with the  
595 help of JG and AL. MLA, MM, and CS taxonomically identified the sponges. MLA processed the  
596 sponge samples to determine specific silica content. AH sampled the sediment cores and provided  
597 sedimentary data. JG and AH provided the bottom mapping data and MLA developed the benthic  
598 habitat and spicule accumulation layers. MLA, CG, and CS conducted sponge silica determination  
599 under the microscope. MLA analyzed and interpreted the data and drafted the manuscript, with  
600 invaluable inputs made by MM and AL. All authors contributed with comments to the manuscript  
601 and approved the submitted version.

602

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- 811

812 **Table 3. Summary of biogenic silica (bSi) standing stock in the sponge assemblages of the Bay of Brest (France).** Average ( $\pm$ SD) silica  
813 content per unit of volume of living sponge tissue ( $\text{mg bSi mL}^{-1}$ ) of each siliceous sponge species and average ( $\pm$ SD) sponge Si stock per  
814 square meter ( $\text{mg Si m}^{-2}$ ) in each habitat (RI, rocky intertidal; RS, rocky subtidal; MB, maerl beds; SM, shallow mud; HS, heterogeneous  
815 sediments; CS, circalittoral coarse sediments) and for the total ecosystem of the Bay of Brest.

Sponge species	BSi content		Sponge contribution to the BSi standing stock ( $\text{mg Si m}^{-2}$ )											
	( $\text{mg BSi mL}^{-1}$ )		RI		RS		MB		SM		HS		CS	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Amphilectus fucorum</i>	36.13	4.79			222.88	655.79	27.59	124.16			3.17	13.25	5.31	25.44
<i>Antho inconstans</i>	33.27	4.25			101.84	567.05								
<i>Biemna variantia</i>	45.38	4.86			4.79	26.67								
<i>Bubaris vermiculata</i>	96.21	11.21											6.77	24.33
<i>Chalinula cf. limbata</i>	43.92	6.96			31.79	177.00								
<i>Ciocalypta penicillus</i>	103.61	0.39			374.14	1,456.86								
<i>Clathria strepsitoxa</i>	29.78	2.89			194.81	519.89					0.77	4.64	0.76	2.39
<i>Cliona celata</i>	85.58	7.24			134,576.89	389,757.49			2,961.26	11,145.37	1.11	6.67	64.09	134.54
<i>Cliona lobata</i>	78.15	5.94											102.10	122.41
<i>Halichondria bowerbanki</i>	58.33	1.83			7.92	32.41	116.13	724.07					0.28	0.96
<i>Halichondria panicea</i>	55.40	11.30	134.18	337.69	60.07	197.04	268.83	677.52			1.56	4.75	3.97	14.96
<i>Halichondria sp.</i>	71.38	0.77			434.84	949.91	73.18	336.72						
<i>Haliclona angulata</i>	39.55	6.92											25.17	69.19
<i>Haliclona cinerea</i>	37.79	4.50			17.10	95.19	6.91	18.02			1.16	6.94	1.48	3.37
<i>Haliclona fibulata</i>	53.64	6.23											132.65	386.64
<i>Haliclona fistulosa</i>	52.52	21.55			24.29	135.26	18.65	116.43					11.64	55.80
<i>Haliclona rosea</i>	32.94	5.41			13.16	45.12	116.88	253.13			20.32	115.42	1.97	6.53
<i>Haliclona simulans</i>	74.95	16.47			554.65	1,613.25	613.86	1,374.11			152.11	411.44	57.56	150.02
<i>Hemimycale columella</i>	49.41	7.03			621.31	1,625.25	37.82	165.58			8.66	51.97	1.10	5.27

<i>Hymedesmia cf. occulta</i>	35.99	6.52										0.88	3.20	
<i>Hymedesmia coriacea</i>	32.58	6.30			0.49	2.74	5.81	27.81				0.65	3.11	
<i>Hymedesmia jecusculum</i>	36.29	5.67			21.73	86.53								
<i>Hymedesmia lenta</i>	30.47	5.05)			7.75	43.17						7.48	27.56	
<i>Hymeniacion perlevis</i>	48.88	6.18	1,975.23	2,898.50	794.85	1,854.75	3,968.75	5,403.69		596.50	1,273.29	54.60	248.94	
<i>Iophon hyndmani</i>	42.56	3.16										5.36	16.97	
<i>Iophon nigricans</i>	43.77	2.11										200.99	905.76	
<i>Mycale contarenii</i>	62.69	7.71			86.50	222.88	20.88	91.83		117.22	594.43			
<i>Mycale macilenta</i>	52.87	5.32			795.91	2,050.78	0.14	0.88		16.91	69.90	3.19	8.36	
<i>Myxilla fimbriata</i>	50.77	4.34			128.62	340.78						0.39	1.86	
<i>Myxilla rosacea</i>	42.64	4.02										0.15	0.73	
<i>Pachymatisma johnstonia</i>	116.70	22.01			3,918.18	15,445.96								
<i>Paratimea constellata</i>	66.94	4.07										0.44	1.83	
<i>Phorbas fictitius</i>	93.20	5.22			420.82	2,061.94	497.65	1,419.77						
<i>Phorbas plumosus</i>	40.95	15.92			122.27	649.18	52.54	160.68						
<i>Polymastia boletiformis</i>	58.91	11.51			58.63	326.44						0.29	1.38	
<i>Polymastia penicillus</i>	71.41	7.84	1.27	6.09	230.17	1,258.52						0.10	0.46	
<i>Protosuberites cf. denhartogi</i>	57.84	4.85			77.23	287.25				0.56	3.38			
<i>Raspailia ramosa</i>	56.76	5.60										1.69	8.12	
<i>Spanioplion armaturum</i>	32.48	3.26			463.15	920.96						0.24	0.96	
<i>Stelligera stuposa</i>	44.70	3.04			76.69	238.29				0.58	3.48	0.74	3.48	
<i>Suberites ficus</i>	114.77	12.45					995.23	6,105.84	582.80	1,801.65	4,972.06	20,926.78		
<i>Suberites massa</i>	96.02	4.70					0.25	1.60						
<i>Tedania anhelans</i>	34.90	6.42					105.64	493.25				122.48	266.90	
<i>Tethya citrina</i>	145.57	14.17	2,166.28	3,780.43	5,623.00	15,889.11	3,103.96	5,192.50		1,743.08	3,022.67	76.76	150.91	
<i>Timea crassa</i>	93.89	4.14								101.31	449.00	161.92	608.25	
<b>Total</b>	<b>59.61</b>	<b>27.07</b>	<b>4,283.08</b>	<b>4,191.32</b>	<b>151,079.97</b>	<b>387,576.21</b>	<b>10,035.84</b>	<b>10,742.40</b>	<b>3,544.06</b>	<b>11,126.45</b>	<b>7,737.09</b>	<b>20,560.60</b>	<b>794.06</b>	<b>1,392.12</b>

## *Supplemental Information*

**Supplementary Table 1. Average concentration ( $\pm$ SD) of dissolved silicon ( $\mu\text{mol Si L}^{-1}$ ) at the bottom waters of the Bay of Brest.** Data come from the Lanvéoc long-term survey series (48.295777° N, 4.454758° W), which sampled bottom water with a 1L syringe manually by scientific divers just over seabed every two weeks at high tide. Data integrated dissolved silicon concentrations from the last decade (2012-2021).

<b>Month</b>	<b>Dissolved Si concentration</b>	
	<b>AVRG</b>	<b>SD</b>
<b>Jan</b>	11.03	2.79
<b>Feb</b>	13.28	5.68
<b>Mar</b>	8.89	5.77
<b>Apr</b>	2.44	2.20
<b>May</b>	3.60	4.25
<b>Jun</b>	2.44	1.22
<b>Jul</b>	2.10	0.93
<b>Aug</b>	2.83	0.55
<b>Sep</b>	4.85	2.20
<b>Oct</b>	8.35	5.08
<b>Nov</b>	8.57	2.46
<b>Dec</b>	10.13	2.36

**Supplementary Table 2.** List of the sponge species of the Bay of Brest (France). Presence at each habitat is indicated. RI, rocky intertidal; RS, rocky subtidal; MB, maerl beds; SM, shallow mud; HS, heterogeneous sediments; CS, circalittoral coarse sediments.

	Habitat					
	RI	RS	MB	SM	HS	CS
Class DEMOSPONGIAE						
Subclass HETEROSCLEROMORPHA						
Order AXINELLIDA						
Family RASPAILIIDAE						
<i>Raspailia ramosa</i>						X
Family STELLIGERIDAE						
<i>Paratimea constellata</i>						X
<i>Stelligera stuposa</i>		X			X	X
Order BIEMNIDA						
Family BIEMNIDAE						
<i>Biemna variantia</i>		X				
Order BUBARIDA						
Family BUBARIDAE						
<i>Bubaris vermiculata</i>						X
Order CLIONAIDA						
Family CLIONAIDAE						
<i>Cliona celata</i>		X		X	X	X
<i>Cliona lobata</i>						X
Order HAPLOSCLERIDA						
Family CHALINIDAE						
<i>Chalinula cf. limbata</i>		X				
<i>Haliclona angulata</i>						X
<i>Haliclona cinerea</i>		X	X		X	X
<i>Haliclona fibulata</i>						X
<i>Haliclona fistulosa</i>		X	X			X
<i>Haliclona rosea</i>		X	X		X	X
<i>Haliclona simulans</i>		X	X		X	X
Order POECILOSCLERIDA						
Family ACARNIDAE						
<i>Iophon hyndmani</i>						X
<i>Iophon nigricans</i>						X
Family ESPERIOPSISIDAE						
<i>Amphilectus fucorum</i>		X	X		X	X

**Table S2.** (Continued)

	Habitat					
	RI	RS	MB	SM	HS	CS
Family HYMEDESMIIDAE						
<i>Hemimycale columella</i>		X	X		X	X
<i>Hymedesmia cf. occulta</i>						X
<i>Hymedesmia coriacea</i>		X	X			X
<i>Hymedesmia jecusculum</i>		X				
<i>Hymedesmia lenta</i>		X				X
<i>Phorbas fictitius</i>		X	X			
<i>Phorbas plumosus</i>		X	X			
<i>Spanioplion armaturum</i>		X				X
Family MICROCIONIDAE						
<i>Antho inconstans</i>		X				
<i>Clathria strepsitoxa</i>		X			X	X
Family MYCALIDAE						
<i>Mycale contarenii</i>		X	X		X	
<i>Mycale macilenta</i>		X	X		X	X
Family MYXILLIDAE						
<i>Myxilla fimbriata</i>		X				X
<i>Myxilla rosacea</i>						X
Family TEDANIIDAE						
<i>Tedania anhelans</i>			X			X
Order POLYMASTIIDA						
Family POLYMASTIIDAE						
<i>Polymastia boletiformis</i>			X			X
<i>Polymastia penicillus</i>	X	X				X
Order SUBERITIDA						
Family HALICHONDRIIDAE						
<i>Ciocalypta penicillus</i>			X			
<i>Halichondria bowerbanki</i>			X	X		X
<i>Halichondria panicea</i>	X	X	X		X	X
<i>Halichondria sp.</i>			X	X		
<i>Hymeniacidon perlevis</i>	X	X	X		X	X
Family SUBERITIDAE						
<i>Protosuberites cf. denhartogi</i>		X			X	
<i>Suberites ficus</i>			X	X	X	
<i>Suberites massa</i>			X			

**Table S2.** (Continued)

	Habitat					
	RI	RS	MB	SM	HS	CS
Order TETHYIDA						
Family TETHYIDAE						
<i>Tethya citrina</i>	X	X	X		X	X
Family TIMEIDAE						
<i>Timea crassa</i>					X	X
Order TETRACTINELLIDA						
Family GEODIIDAE						
<i>Pachymatisma johnstonia</i>			X			
Subclass KERATOSA						
Order DENDROCERATIDA						
Family DARWINELLIDAE						
<i>Aplysilla rosea</i>			X	X	X	
<i>Aplysilla sulfurea</i>			X	X		
Order DICTYOCERATIDA						
Family DYSIDEIDAE						
<i>Dysidea fragilis</i>			X	X		
Family THORECTIDAE						
<i>Hyrrios</i> sp.				X		
Order DENDROCERATIDA						
Family DICTYODENDRILLIDAE						
<i>Spongionella</i> cf. <i>pulchella</i>			X			
Subclass VERONGIMORPHA						
Order CHONDRILLIDA						
Family HALISARCIDAE						
<i>Halisarca dujardinii</i>						X
Class CALCAREA						
Subclass CALCARONEA						
Order LEUCOSOLENIDA						
Family SYCETTIDAE						
<i>Sycon ciliatum</i>			X	X		
Subclass CALCINEA						
Order CLATHRINIDA						
Family CLATHRINIDAE						
<i>Clathrina</i> cf. <i>coriacea</i>				X		