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Biodeposition by an invasive suspension feeder impacts the biogeochemical cycle of Si in a coastal ecosystem (Bay of Brest, France)

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Abstract. Biodeposition is a process that strongly affects physical, chemical and biological properties near the sediment–water interface, and mollusks have been shown to influence the cycling of many biogenic elements. In the Bay of Brest ecosystem, the invasive benthic suspension feeder *Crepidula fornicata* has been proliferating for 50 years, and its influence on phytoplankton dynamics at a seasonal scale, via its role on a coastal silicate pump, has been suggested by Chauvaud et al. (2000) [Chauvaud L., Jean F., Ragueneau O. and Thouzeau G. 2000. Mar. Ecol. Prog. Ser. 200: 35–48] and tested by Ragueneau et al. (2002a) [Ragueneau O., Chauvaud L., Leynaert A., Thouzeau G., Paulet Y.-M., Bonnet S., Lorrain A., Grall J., Corvaisier R., Le Hir M., Jean F. and Clavier J. (2002a). Limnol. Oceanogr. 47(6): 1849–1854]. In the present manuscript, we explore further, at an annual scale, the role of biodeposition in the Si cycle of the Bay of Brest. We show that annual biodeposition Si can represent up to 84% of river silicic acid inputs. We also show that preservation of biogenic silica in *C. fornicata* mats is very good (27%), leading to an annual retention of Si of 23% of river inputs. We suggest that this high retention is essentially controlled by the biodeposition mechanism, which is directly under the control of the proliferation of the exotic suspension feeder. We conclude that this mechanism might be very important in controlling the Si retention along the land–ocean continuum and should be tested in the many areas of the coastal ocean submitted to the proliferation of such exotic species that modify sedimentation of biogenic matter.

Introduction

Si and coastal food webs

The nutrient silicic acid (DSi) plays a major role in the functioning of ecosystems in many regions of the coastal ocean (review in Ragueneau et al. submitted). The reason is linked to the importance of diatoms in marine food webs, and to anthropogenic influences on watersheds and on rivers. Diatoms are microscopic algae that have a specific requirement for DSi, to build their frustule. They form the basis of the classical and economically desirable food chain which leads to secondary consumers (suspension feeders, copepods and ultimately fish) (Cushing 1989). When growing under nutrient replete conditions, they consume DSi and dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in a Si:N:P ratio of 16:15:1 (Brzezinski 1985). When DSi is missing, diatoms become replaced by other phytoplankton groups that do not have any requirement for this nutrient, such as dinoflagellates (Officer and Ryther 1980). Smayda (1990) has documented a wide variety of coastal ecosystems where increasing frequency and magnitude of harmful algal blooms have been associated to decreasing Si:N and Si:P ratios, with important consequences for pelagic and benthic food webs. Fluxes of N and P have increased globally by a factor of 2 (Meybeck, 1998), decreasing the Si:N and Si:P ratios. Decreasing Si:N and Si:P ratios also occur because more Si is being retained along the aquatic continuum from land to ocean, because of eutrophication (Schelske and Stoermer 1971; Conley et al, 1993) and river manipulation (Van Bennekom and Salomons 1981; Humborg et al. 1997, 2000).

The biodeposition mechanism

Biodeposition in beds of suspension-feeding mollusks results from the active filter feeding by a mollusk, which leads to non-digested material being excreted to the sediment surface as feces and pseudo-feces (Norkko et al. 2001). Mollusks, therefore, strongly affect physical, chemical and biological properties near the sediment–water interface (review in Graf and Rosenberg 1997). In particular, these processes typically result in local deposition rates that exceed that of passive physical sedimentation (Dame 1993; Dobson and Mackie 1998) and create an enrichment of sediments in C and N (Kautsky and Evans 1987). Beyond their role on sediment properties, mollusks strongly influence the cycling of several biogenic elements such as carbon (Doering et al. 1986), nitrogen (Dame et al. 1991), phosphorus (Asmus et al. 1995), sulfur (Hansen et al. 1996) and inorganic carbon (Chauvaud et al. 2003). Because of the intensity of benthic–pelagic coupling in coastal waters, they play an essential role in the functioning of coastal ecosystems in general (Alpine and Cloern 1992; Dame 1996; Wildish and Kristmanson 1997).

Biodeposition and Si cycling: ecological implications

Recently, Chauvaud et al. (2000) have proposed that benthic suspension feeders also impact the Si cycle, with potentially important ecological implications. Their hypothesis was based on the study of the impact on the functioning of the Bay of Brest ecosystem, of the proliferation of *Crepidula fornicata* (gastropod), a benthic suspension feeder that invaded the bay in the early 1950's. The mechanism involves increased activity of suspension feeders during early spring (filtration and subsequent production of enormous quantities of biodeposits, in the form of faeces and pseudo-faeces), which leads to temporary retention of biogenic silica (BSi) in the sediments of the Bay. This retention limits the export of Si out of that Bay, in a sort of coastal 'silicate pump' (Del Amo et al. 1997a) that works opposite to the oceanic silicate pump described by Dugdale et al. (1995) and Dugdale and Wilkerson (1998). Subsequent BSi dissolution during late spring and summer, enhanced by increasing temperature and elevated bacterial activity in the upper slipper limpet layer, would provide the necessary DSi required by diatoms to maintain their dominance throughout the productive period (Chauvaud et al. 2000).

Ragueneau et al. (2002a) have successfully tested this working hypothesis during the year 2000, demonstrating the direct effect of *C. fornicata* on DSi benthic fluxes and discussing the ecological implications of this invasion, in terms of phytoplankton dynamics. In the present paper, the biogeochemical implications of this proliferation are explored.

Biodeposition and Si cycling: biogeochemical implications

Diatoms are taken up by benthic suspension feeders in the process of feeding with regeneration of DSi from the biodeposits in the sediments (Asmus et al. 1990). Only very few investigations of mollusks and mollusk beds as sources and sinks of silicon exist in the literature (Asmus 1986; Doering et al. 1987; Dame et al. 1991; Prins and Small 1994) where high rates of DSi release are observed from sediments probably occurring through the silicate pump mechanism described above for the Bay of Brest (Chauvaud et al. 2000). Benthic filter feeders produce such high quantities of biodeposits that the subsequent dissolution of BSi allows for high rates of benthic DSi fluxes, with important ecological implications in terms of diatom dominance throughout the productive period (Ragueneau et al. 2002a). However, due to the importance of biodeposition, even if only a small fraction of the BSi embedded in mollusk feces and pseudo-feces gets preserved, the accumulation of BSi may represent an important flux, which needs to be quantified.

Biodeposition is increasing in many ecosystems throughout the world, following the invasion of benthic suspension feeders, be it either accidental (ballast water) or for aquaculture purposes (e.g. Mack et al. 2000). It is our hypothesis, that increasing biodeposition may lead to enhanced retention of the element Si along the land–ocean continuum. Herein, we will demonstrate that Si retention in the Bay of Brest is mostly driven by the biodeposition mechanism and that this process needs to be tested in other ecosystems where the proliferation of invasive species has already led to drastic changes in sedimentation.

Materials and methods

Study area

The study was conducted in the Bay of Brest ecosystem, a shallow (mean depth is ca. 8 m) semi-enclosed, macrotidal, coastal bay of 180 km^2, related to the adjacent Atlantic Ocean through a small strait of 1.8 km wide and 50 m deep (Figure 1). The Bay is fed mostly by two rivers, namely the Aulne and Elorn, which bring 80% of the total freshwater. The Bay of Brest is a productive area, with an annual C primary production estimated at 12.3 mol C m^{-2} yr^{-1} (Del Amo et al. 1997b). The productive period typically extends from early April to late September (Del Amo et al. 1997b; Ragueneau et al. 2002a).

Quantification of Si fluxes through the Bay

Si fluxes through the Bay of Brest ecosystem are described in Figure 2. Most of the external inputs of DSi occur from the two rivers (R), the Aulne and Elorn, with negligible inputs from the adjacent Iroise Sea (Ragueneau et al. 1994). Production of biogenic silica (P) is sustained by these river inputs and internal recycling, in the water column and at the sediment–water interface (BF). Note that water column dissolution has been measured by Beucher et al. (2004) at the SOMLIT station (Figure 1). Our results will be compared to these estimates based on the use of the ^{30}Si isotope technique described in Corvaisier et al. (in press). The biogenic silica produced, that is neither recycled in the water column

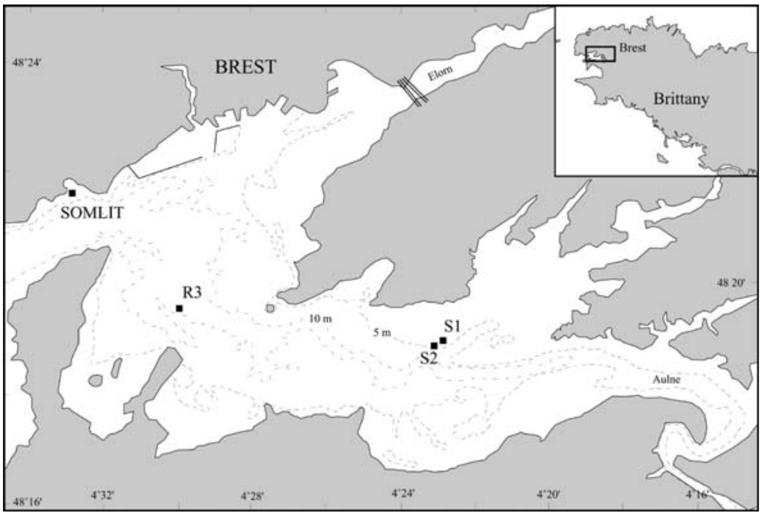

Figure 1. Position of the study sites in the Bay of Brest (northwestern France).

nor exported out of the Bay becomes available for benthic suspension feeders; it is thereafter referred to as net sedimentation (S). Since gastropods control the sedimentation flux and have no known requirement for the element Si, most of the net sedimentation of BSi should be found in the biodeposition flux (B). The fraction of this flux that does not get recycled at the sediment–water interface and within the top centimeters of the sediment column, eventually accumulates in the sediments (A). Finally, the export of Si out of the Bay (E) is calculated by substracting the accumulation flux from the river flux.

In the perspective of building an annual Si cycle in this ecosystem, these fluxes have been quantified during the year 2001, either directly (R, P, BF) or indirectly, from C estimates and the use of appropriate Si:C ratios (S, B) and by difference (A and E):

- River DSi fluxes have been measured on a weekly basis, owing to the ECOFLUX network (Porhel et al. 2001). They consist in the measurement of the DSi concentration at salinity 0 in the Aulne and Elorn rivers, multiplied by the river flows provided by the 'Service Hydrologique Centralisateur' (Nantes).
- Biogenic silica production rates (P) were measured in surface, intermediate and bottom waters at station R3, on a weekly basis between April and late September. Incubations were generally conducted under *in situ*-simulated conditions. About 250 ml samples, in polycarbonate bottle, were spiked with 50,000 dpm (830 Bq) of ^{32}Si tracer (52,000 Bq/μg Si, Los Alamos National Laboratory). At the end of the incubation period (24 h), each sample was gently vacuum-filtered through a 0.6 μm polycarbonate membrane filter (Nuclepore) and rinsed with 10 ml of filtered seawater. The filter was then immediately placed in the bottom of a 20 ml plastic LSC vial. Two milliliters of 2.9 M HF were added to dissolve biogenic silica. The reaction was complete after 30 min and 10 ml of scintillation cocktail (Ultima Gold XR) were then added to each vial. After shaking, samples were counted on a

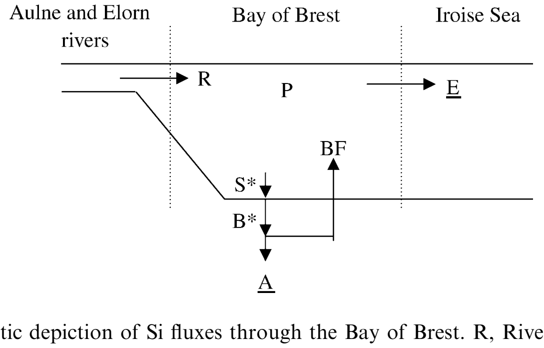

Figure 2. Schematic depiction of Si fluxes through the Bay of Brest. R, River fluxes; P, production; S, net sedimentation; B, biodeposition; BF, benthic fluxes; A, accumulation; E, export out of the Bay. * refers to these fluxes derived indirectly. When underlined, fluxes are determined by difference (see text for details).

Tri-carb 1500 TR instrument (Packard) for 60 min, or when a counting precision of 0.5% was achieved for cpm in each counting window. An equilibrated ^{32}Si solution and ^{32}P standards were used to deconvoluate the energy spectra, as described in Leynaert et al. (1996). For each measurement of BSi production, the corresponding C primary productivity has been measured by means of ^{14}C isotopes.

- Benthic fluxes have been measured every 2 months between March and November 2001, at two sites exhibiting contrasted densities of the proliferating benthic suspension feeder *C. fornicata* (Figure 1, S2: 26 ± 5 ind. m^{-2}; S1: 1719 ± 241 ind. m^{-2}; Thouzeau et al. in prep). Fluxes, obtained in mmol Si m^{-2} d^{-1}, were extrapolated to the whole bay by applying the fluxes measured at site S1 to half of the bay surface area and those measured at site S2, to the other half, as *C. fornicata* is now occupying about half of the entire Bay surface area (Ragueneau et al. 2002a). Sediment cores were retrieved manually at 20 m depth using scuba diving; 3 replicates were taken at each site. Following a time zero sampling at sea, cores were then rapidly (within 1–2 h) incubated in the laboratory at the temperature of the bay waters (from 8 °C during winter to 16 °C during summer). The DSi concentration in the water overlying the sediment was monitored every hour during the first 6 h, and then two to three times between 20 and 24 hours following core collection. Homogenization of the overlying water was ensured by pumping water, using a peristaltic pump, 2–3 cm above the sediment water interface and redistributing it near the water surface. The flow rate was adjusted so that one water volume was renewed every hour. Fluxes were then calculated from the linear increase in DSi concentration in the overlying water.
- The BSi net sedimentation has been estimated from the carbon net sedimentation and the use of appropriate Si:C ratios in the phytoplankton. C net sedimentation has been first calculated from a $1 - y$ time series of monthly measurements using sediment traps at three stations in the Bay of Brest (1991); C net sedimentation was then re-estimated using inverse modeling of a mass balance benthic food web (Vézina and Platt 1988; Jean 1994).
- The BSi biodeposition has been estimated from the C biodeposition and the use of a Si:C ratio determined using the experimental set-up described below. The C biodeposition by *C. fornicata* was estimated at the Bay scale by Chauvaud et al. (2000). Theoretically, if sedimentation is biologically controlled by suspension feeder activity, the estimate of BSi biodeposition should approach that of BSi net sedimentation because suspension feeders have no-known requirement for the nutrient DSi. These estimates will thus be compared to check their consistency.
- The BSi accumulation has been estimated using the difference between the BSi biodeposition and the DSi benthic flux ($A = B - BF$). Comparing the DSi accumulation and BSi biodeposition provides a means of studying the conditions of BSi preservation in *C. fornicata* mats.
- The export of Si out of the bay has also been obtained by difference, substracting the accumulation flux from the river input ($E = R - A$).

Si:C ratios in biodeposits

The Si:C ratio in biodeposits depends upon the Si:C ratio in the food (here, assumed to be mostly pelagic diatoms) and the relative retention of Si and C by benthic animals. To estimate the changes in Si:C ratios during transit through the gut of benthic suspension feeders, the following experiment has been performed (Moriceau 2002). Some 40 chains of *C. fornicata*, each containing ca. 10 individuals, have been collected on an intertidal mudflat. They were acclimated for 2 weeks in a thermostated seawater bath. Then, they were starved for 48 h and subsequently fed during 6 h with a solution of the diatom *Chaetoceros calcitrans*. Faeces were collected over a 24 hour period. Figure 3 shows SEM images of the diatoms, before, during and after transit through the gut. BSi and particulate organic carbon (POC) have been measured both on *Chaetoceros* as food, and on the faeces. BSi has been measured according to DeMaster (1981), but using a stronger base (NaOH 0.2 M) to ensure complete dissolution of all the BSi. POC has been measured using a Carlo Erba NC 2500 Element Analyser, following Majeed (1987).

Results

Si fluxes through the Bay of Brest ecosystem

River fluxes

DSi river fluxes exhibited maxima during the winter period, up to 2×10^6 mol Si d^{-1} for the Aulne river and up to 0.3×10^6 mol Si d^{-1} for the Elorn river (Figure 4). River flows measured between January and March 2001 were exceptionally high. From early April, fluxes strongly decreased and almost no DSi was being delivered to the Bay between June and October. Fluxes rose again by early fall. As typically observed in this ecosystem (Ragueneau et al. 1994), the seasonal pattern of nutrient fluxes followed that of precipitation closely.

Distributing these inputs homogeneously over the Bay surface, the river inputs integrated over the 6 months of Winter and Fall 2001 were 0.50 and 0.09 mol Si m^{-2} for the Aulne and Elorn rivers, respectively. During the productive period, these fluxes were reduced to 0.16 and 0.08 mol Si m^{-2}. The annual DSi delivery by rivers was thus 0.83 mol Si m^{-2}, 71% being delivered outside of the productive period.

Production fluxes

^{32}Si weekly measurements at station R3 allowed us to derive a reasonable estimate for the BSi production between April and September, i.e. during the productive period: 0.73 mol Si m^{-2}. The mean daily production of biogenic silica was close to 7.4 mmol Si m^{-2} d^{-1} during spring 2001, becoming twice as low during summer, at a mean value of 3.6 mmol Si m^{-2} d^{-1}. It is interesting

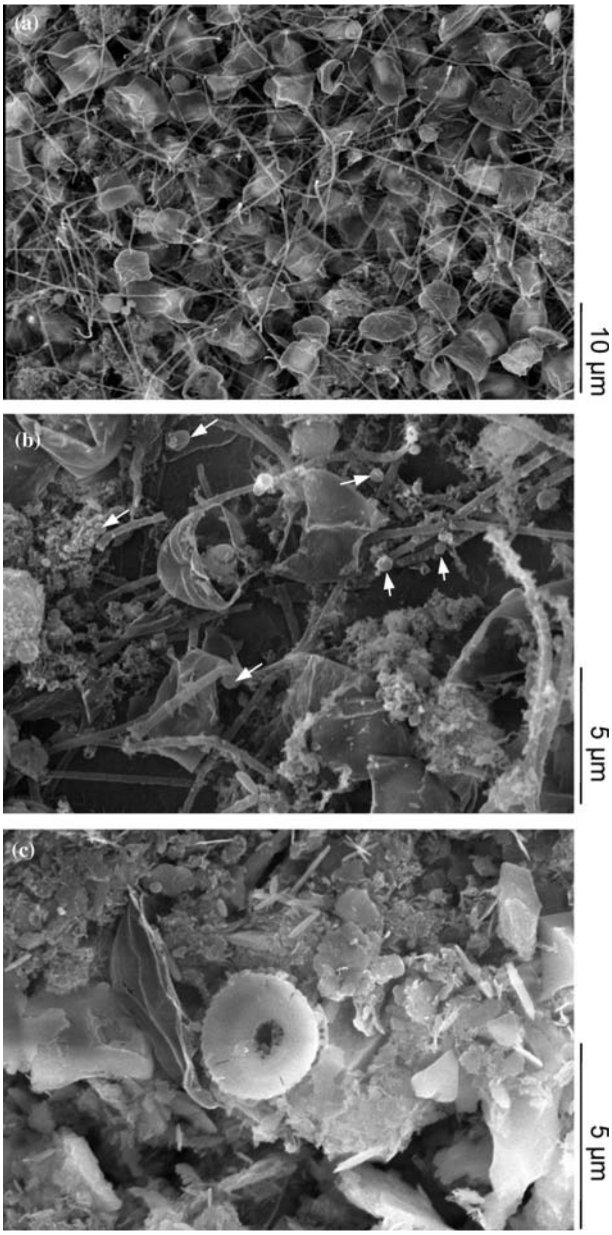

Figure 3. SEM images of diatoms during their transit through the gut of *C. fornicata*. (a) *Chaetoceros calcitrans*, before being consumed; (b) *C. calcitrans* in the gut of *C. fornicata*; (c) *C. calcitrans* in feces of *C. fornicata*.

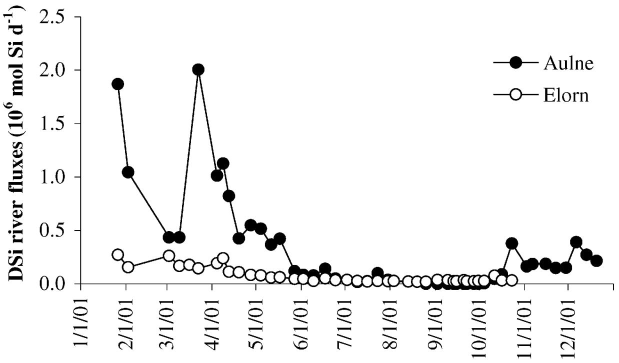

Figure 4. Aulne (black circles) and Elorn (open circles) DSi fluxes measured during the year 2001. Data from the ECOFLUX network (Pohrel et al. 2001).

to note that the spring daily BSi production measured in 2001 is in reasonable agreement with the value of Ragueneau et al. (1994), who estimated indirectly the silica production at 6.2 mmol Si m^{-2} d^{-1} during spring 1992. During the productive period of 2001, the mean Si:C ratio during production was 0.08, in close agreement with the biomass ratio (0.07), measured during phytoplankton blooms of spring 1992 and 1993 by Ragueneau et al. (1994) and Del Amo et al. (1997b), respectively.

Only few measurements have been performed during fall and winter 2001, with a mean value of 1 mmol Si m^{-2} d^{-1}. Integrating this mean (and conservative, in the absence of major phytoplankton bloom) value over the 182 days of the winter/fall period provides an estimate of the BSi production during that period: 0.18 mol Si m^{-2}. Thus, the annual Si production at station R3 was 0.91 mol Si m^{-2} yr^{-1} during 2001, 80% taking place during the productive period. This ^{32}Si-based estimate is in reasonable agreement with the ^{30}Si-based estimate of 1.2 mol Si m^{-2} yr^{-1}, obtained at station SOMLIT by Beucher et al. (2004).

BSi net sedimentation

BSi net sedimentation has been estimated from C net sedimentation and the use of an appropriate Si:C ratio. From monthly measurements of sediment traps deployed during 1991, the C net sedimentation rate was estimated at 7.8 mol C m^{-2} yr^{-1} with a 57% coefficient of variation (Jean 1994). Using an inverse modeling approach of a mass balance benthic food web, C net sedimentation was estimated at 9.4 mol C m^{-2} yr^{-1}, which is in the range of the first estimate using sediment traps (Jean 1994). This last value was adopted in the present study. Because most of the sedimentation flux is due to the filtration activity of benthic suspension feeders and because these organisms feed directly on phytoplankton, BSi net sedimentation can be estimated simply by multiplying the C net sedimentation flux by an appropriate Si:C ratio of the food. Note that the number used for this mol:mol ratio (0.08, see section on biodeposition) is smaller than the value of 0.13 found by Brzezinski (1985), because diatoms are not the only component of the suspension feeders diet, and because the diatoms are limited by DSi availability during spring (Ragueneau et al. 2002a), which typically leads to less silicified frustules (Rousseau et al. 2002). The annual BSi net sedimentation estimated this way is 0.75 mol Si m^{-2} yr^{-1}.

BSi biodeposition

The BSi biodeposition has been estimated using the C biodeposition estimates from Chauvaud et al. (2000) and an appropriate Si:C ratio in biodeposits. C biodeposition has been estimated at 3.5 mol C m^{-2} yr^{-1} (Chauvaud et al. 2000). The Si:C ratio in biodeposits has been estimated using the results from the experiment illustrated in Figure 3. The Si:C ratio measured in the diatom *C. calcitrans* was 0.05. The Si:C ratio measured in the faeces of *C. fornicata* was 0.12. Thus, the Si:C ratio has increased by a factor 2.5 during the transit through the gut of the suspension feeder. Applying the increase of 2.5 to a food with a Si:C of 0.08 yields a Si:C ratio of 0.2 in biodeposits. Multiplying this ratio by the C biodeposition yields a BSi biodeposition of 0.70 mol Si m^{-2} yr^{-1}. This estimate is only slightly lower than that of Si net sedimentation. This agreement was expected, as benthic suspension feeders have no-known requirement for the nutrient DSi, so that all BSi ingested should be accounted for in biodeposits; this consistency simply provides good confidence in these independent estimates.

Benthic fluxes

DSi benthic fluxes measured at the two sites S1 and S2 (Figure 1), exhibiting contrasted densities of the suspension feeder *C. fornicata*, displayed a similar seasonal pattern (Figure 5): maxima were found in June/July at the two sites. Maxima were 5.47 mmol Si m^{-2} d^{-1} at site S1 and only 2.20 mmol Si m^{-2} d^{-1} at site S2, i.e. close to the same values determined at the same sites in 2000 (Ragueneau et al. 2002a). Fluxes were 2–4 times higher at site S1 compared to site S2, during spring and early summer. The difference increased up to 1–2 orders of magnitude during late summer and early fall, as in 2000. Note that in 2000, the maximum of DSi fluxes at site S1 was encountered later in the season, in September.

Integrating these fluxes over the 6-month productive period yields DSi benthic fluxes of 0.086 and 0.313 mol Si m^{-2} for sites S2 and S1, respectively. To derive a similar estimate during winter when sampling was not as intensive, a mean value between those measured in November and March (0.14 and 0.97 mmol Si m^{-2} d^{-1} for sites S2 and S1, respectively) has been used and integrated over the corresponding 6-month period. This integration yields values of 0.009 and 0.101 mmol Si m^{-2} for S2 and S1, respectively. Thus, the annual DSi benthic flux was 0.51 mol Si m^{-2}, 81% of which coming from sites with high densities of *C. fornicata*, and 78% being delivered during the

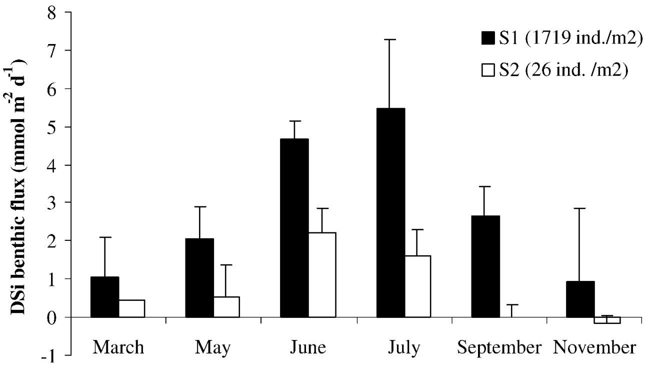

Figure 5. Synthesis of DSi benthic fluxes measured at the two contrasting sites during the productive period of 2001 in the Bay of Brest. Black bars: site S1 (1719 ± 241 ind. m^{-2}); white bars: site S2 (26 ± 5 ind. m^{-2}). These fluxes represent the mean values of the fluxes measured in triplicates. Note that the September value for the site without *C. fornicata* is 0.01 mmol Si m^{-2} d^{-1}, not visible on this graph.

productive period. Note the opposite situation with river fluxes, which bring most DSi during the winter/fall period when diatoms are not very active.

BSi accumulation

A first estimate of annual BSi accumulation in the Bay of Brest can be obtained by substracting the DSi benthic flux from the BSi biodeposition flux. This yields an annual BSi accumulation of 0.19 mol Si m^{-2} yr^{-1}. Note that a remarkably consistent estimate can be obtained by combining the C annual accumulation (0.32 mol C m^{-2} yr^{-1}, Jean 1994) and a Si:C ratio typical of the sediments of continental margins (0.6 on a molar basis, DeMaster 2002). These two estimates suggest that some 23% of DSi river fluxes eventually accumulate in the sediments on an annual basis.

Seasonal and annual budgets of Si fluxes in the Bay of Brest

An annual budget of Si fluxes is shown in Figure 6a. It shows in particular that (i) biodeposition represents some 84% of the river input, (ii) annual preservation of BSi in biodeposits is very good, amounting at 27%, and (iii) retention of Si, i.e. how much of river DSi inputs eventually gets buried in the sediments of the Bay, is close to 23%. This overview of the annual Si cycle will be further discussed, however, it hides two important problems. First, it suggests that river inputs could nearly sustain diatom production, which is not the case during the productive period, as demonstrated by Ragueneau et al. (2002a). Second, it does not provide any explanation to the following discrepancy: net sedimentation represents some 82% of the annual BSi production, whereas Beucher et al. (2004) recently suggested that half of the biogenic silica produced in the Bay redissolves rapidly in the water column.

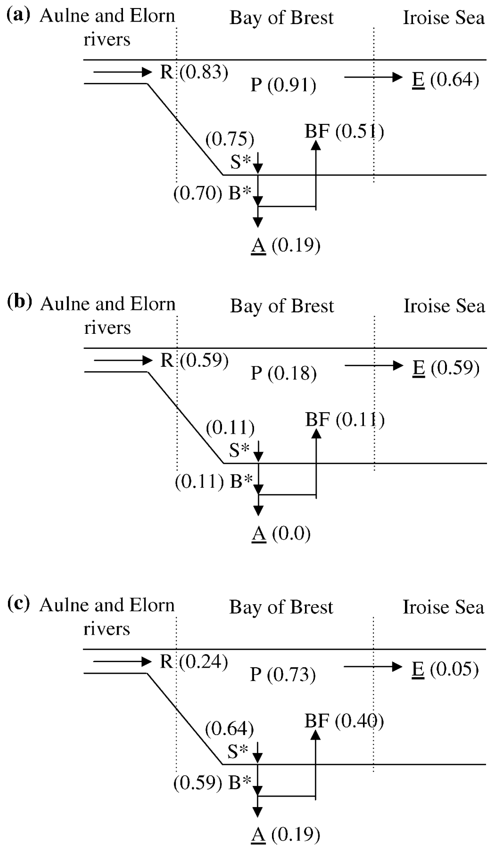

Figure 6. The annual budget of Si fluxes in the Bay of Brest ecosystem (a) and two sub-budgets: a fall/winter budget (b), corresponding to the 182 days between October and March, and a spring/summer budget (c), corresponding to the 183 days between April and September. All fluxes given in parentheses are in mol Si m^{-2} integrated over these 182/183 days. R, River fluxes; P, production; D, dissolution in the water column; S, net sedimentation; B, biodeposition; BF, benthic fluxes; A, accumulation; E, export out of the Bay. Note that numbers underlined correspond to estimates obtained by difference: A (minimum estimate) = B − BF, and E = R − A. See text for calculation details.

To provide a more dynamic view of Si fluxes through the ecosystem, to address the two discrepancies in the budget described above, and to better understand the role of benthic suspension feeders in the ecosystem, two additional budgets have been built. The first budget was for only the fall/winter period, from October to March (Figure 6b). The second budget concerns the productive period, from early April to late September (Figure 6c). The splitting between these two periods of the R, P and BF fluxes, measured directly, has been described earlier, as the integration could be done both annually and for each of these two periods. For the S, B and A fluxes, a small discussion is necessary.

It proved impossible to derive an estimate of the BSi net sedimentation for the winter/fall and productive periods, on the basis of the sediment traps deployed in 1991. Monthly values were reported for C (Jean 1994), with no BSi measurement associated. No rigorous Si:C ratio can be used to estimate monthly BSi sedimentation, as the material was constituted of both autochtone material, and detrital material brought in the Bay by rivers, especially for the winter/fall period, for which we have no constrain at all in terms of Si:C ratio. Therefore, we have used an indirect approach to estimate the BSi net sedimentation during these two periods. Net BSi sedimentation during the 6-month winter/fall period must range between 0.11 mol Si m^{-2}, the value of the benthic flux integrated over this period, and 0.18 mol Si m^{-2}, the BSi production during the corresponding period (Figure 6b). We will assume that BSi net sedimentation was at its minimum possible value during that period, i.e. 0.11 mol Si m^{-2}. Indeed, export out of the Bay is quite efficient during periods of high river flow (Savoye 2001), so that all the biogenic silica produced is not necessarily available for suspension feeders, since river flow was exceptionally high during early 2001 (Figure 4). Using this assumption, the two additional budgets can be built, with spring/summer net sedimentation and biodeposition derived from the difference between the annual and winter/fall fluxes.

Figure 6b, c shows that retention of Si in the Bay of Brest exhibits a strong bimodal character. During winter, no Si is being retained in the Bay. On the contrary, during the productive period, the accumulation represents 79% of DSi river inputs. Note that if we assume in the winter/fall scenario that net sedimentation and biodeposition was equal to Si production (assuming no loss of biogenic silica via export out of the Bay and water column dissolution), an accumulation of 0.07 mol Si m^{-2} could be estimated, by substracting BF from B or P. This would represent some 12% of winter/fall DSi river inputs, which would not change the bimodal character of Si retention described above. Thus, during the winter/fall period, the Bay does not act as an efficient filter with respect to Si.

Discussion

Consistency of annual and seasonal Si budgets

Si fluxes through the Bay of Brest ecosystem were quite well constrained during the year 2001, owing to weekly measurements of river fluxes and production of biogenic silica, as well as direct measurements of DSi benthic fluxes every two months, at sites exhibiting contrasting densities of the suspension feeder *C. fornicata*, which dramatically controls the benthic fluxes in this ecosystem (Ragueneau et al. 2002a). Net sedimentation, biodeposition and accumulation were derived indirectly from carbon fluxes and the use of appropriate Si:C ratios. Despite this indirect approach, results appear internally consistent.

As a first example, it was expected that estimates of net sedimentation and biodeposition fluxes would be very close, because benthic suspension feeders do not need any Si. They were indeed very close, thereby providing confidence in these independent estimates. This most probably results from the fact that (i) C fluxes were well constrained, either by observations (Chauvaud et al. 2000) or modeling (Jean 1994), and that (ii) Si:C ratios were also well constrained, owing to direct measurements of this ratio during production, and to the study of its fate upon digestion by gastropods (Figure 3, see below).

Secondly, the two estimates of annual BSi accumulation are remarkably consistent. The annual estimate derived by substracting BF from B equals the one that can be derived using C accumulation (Jean 1994) and a Si:C ratio typical of continental margins, provided by DeMaster (2002). This consistency is quite amazing; it requires further testing, which will be done when the Si:C ratio of continental margin sediments is better constrained, and direct measurements of C and BSi accumulation are performed in the Bay of Brest.

There is one exception however, to the observed balance the Si cycle in the Bay of Brest. On an annual basis, net sedimentation represents some 82% of BSi production, leaving little room for export out of the Bay or dissolution in the water column. Export out of the Bay is important only during periods of high river flow (Savoye 2001), which was not the case during the productive period in 2001, so there is no conflict with this aspect. Concerning dissolution, however, Beucher et al. (2004) have suggested that water column dissolution is a very important phenomenon in the Bay of Brest, supplying 50% of the diatom demand in DSi on an annual basis, and some 30% during the productive period. We believe that by removing the biogenic silica particles from their natural environment during incubation experiments provide estimates of a dissolution flux, which is only potential. It does not account for the fact that the water column is shallow and well-mixed, so that during the incubation time, a particle that was not collected and incubated, has a fairly good chance to be filtered by a suspension feeder, before dissolution can start. In addition, upon bloom termination, diatoms form aggregates that are commonly observed by divers, but cannot be sampled adequately. These aggregates have been shown to affect feeding activity of mollusks, through either gill clogging or oxygen depletion (Lorrain et al. 2000). Dissolution in aggregates is greatly reduced (Moriceau et al. in prep) and such a phenomenon cannot be accounted for during incubation experiments.

We will provide an interesting comparison to illustrate our purpose. Dissolution rates in the open ocean exhibit a mean value of 10 yr^{-1} (Van Cappellen et al. 2002). With such a high dissolution rate and a sinking rate on the order of 1 m d^{-1}, a particle of biogenic silica has almost no chance to escape the surface mixed layer. However, it is well recognized that diatoms are efficiently exported and Si recycling occurs at deeper depths, compared to the depth of C or N recycling, leading to the so-called silicate pump described by Dugdale et al. (1995). This is because biogenic silica particles are being removed from the surface layers, and exported in the form of aggregates and fecal pellets of large grazers (Ragueneau et al. 2000). Preservation mechanisms, here, are as important as dissolution processes, in controlling the amount of biogenic silica that will be either recycled in the surface layer, or exported. In the Bay of Brest, preservation mechanisms must be very important, because of aggregate formation and because of suspension-feeder filtration/biodeposition activity. Thus, most of BSi dissolution in the relatively shallow Bay of Brest probably occurs at the sediment–water interface, which has been shown to sustaining summer diatom production (Chauvaud et al. 2000; Ragueneau et al. 2002a). This can be seen in a budget such as the one presented Figure 6, but not during an incubation.

Importance of biodeposition in Si retention

Several arguments combined, suggest that biodeposition is playing a major role in the annual retention of Si in the Bay of Brest:

Importance of biodeposition in the Bay of Brest

Biodeposition typically leads to local deposition rates that exceed that of passive sedimentation (Dame 1993; Dobson and Mackie 1998) and create an enrichment of sediments in C and N (Kautsky and Evans 1987; Cranford and Hill 1999). In the Bay of Brest, *C. fornicata* produces annually 850,000 tons of fresh biodeposits (Chauvaud et al. 2000). Sediments have changed from mixed sands to silty sands. Sediment organic matter enrichment due to *C. fornicata* biodeposition has been estimated in the southern basin of the Bay in the year 2001, along a density gradient of *C. fornicata* (Thouzeau et al. in prep). A 300-m long transect, positioned north–south from sites S1 to S2 (Figure 1), perpendicular to main tidal currents, in water depth ranging from 14 to 20 m, has been surveyed seasonally (spring vs. fall sampling) for benthic flux measurements at the sediment–water interface. Sediment organic matter and chlorophyll contents were determined during this survey on core samples collected by Scuba divers. Percent organic matter in sediment was shown to increase from 6.1 to 10.2% of sediment dry weight (+67.2%) for *C. fornicata* density increasing from 26 ± 5 to 1719 ± 241 ind. m^{-2}. The impact of *C. fornicata* grazing on pigment trapping at the sediment–water interface was also quantified in October 2001: the total phaeopigment biomass ranged from 4.9 to 42.3 $\mu g\ g^{-1}$ sediment dry weight between low and high *C. fornicata* density, respectively (8.6-fold increase). These results emphasize the strong impact of biodeposition by *C. fornicata* on sediment enrichment in organic matter. As shown below, the enrichment in BSi is even greater.

Enrichment of biodeposits in Si

Studying Si and C decoupling in the world ocean, Ragueneau et al. (2002b) suggested that grazers must play an important role in this decoupling, be it in surface waters or at the sediment–water interface. Grazers typically have no requirement for the nutrient Si; when they consume diatoms, they retain POM but egest the frustules (Tande and Slagstad 1985). Therefore, the Si:C ratio is expected to increase between the food and the particulate degradation products, i.e. fecal pellets and feces. This has been observed recently by Dagg et al. (2003), who studied the role of copepod fecal pellets in the export of carbon along the AESOPS transect in the Southern Ocean. They showed a strong increase in the Si:C ratio, between the diatoms and the fecal pellets, sometimes reaching one order of magnitude. In fact, with carbon assimilation efficiencies ranging from 50 to 90% (Daly 1997), the Si:C ratio is expected to increase by a factor 2–10 if 100% of the BSi is egested. In surface waters, this process must contribute an important fraction of the factor of 6 increase in Si:C ratio between production and export, observed globally by Ragueneau et al. (2002b).

At the sediment–water interface, from 30 (Sukhotin 1992) to 74% (Deslous-Paoli and Héral 1988) of the C consumed is found in feces and pseudo-feces, with a mean of 46% for 10 different mollusks (Pouvreau 1999). With such a range of C assimilation and still assuming that 100% of the BSi is egested in the feces, the Si:C ratio is expected to increase by a factor ranging from 1.3 to 3.3. It is reasonable to estimate that 100% of the BSi ingested by mollusks is egested in the form of faeces. Indeed, Si is of no food value for mollusks, and the direct measurements of individual mollusk excretion of DSi were below detection limit in the only study where such measurements have been reported (Prins and Small 1994).

In the Bay of Brest, *C. fornicata* retains some 63% of the C ingested (Jean 1994; Chauvaud 1998), leaving 37% in feces and pseudo-feces which is low compared to the range given above. Thus, the Si:C ratio is expected to increase by a factor of 2.7 between its value in diatoms and its value in the feces of *C. fornicata*. The results from the experiment illustrated in Figure 3 confirm this increase in the Si:C ratio between food and feces, by a factor measured experimentally at 2.5. Thus, the retention of Si in an ecosystem must increase with increasing biodeposition induced by the proliferation of exotic suspension feeders, because net sedimentation of organic matter is strongly increasing (Thouzeau et al. in prep.) and the biodeposits are enriched in BSi, typically by a factor of 2–3.

Preservation conditions in biodeposits

Most (73%) of the BSi biodeposited gets recycled on an annual basis (Figure 6a). Benthic fluxes reach higher values at the site with high densities of *C. fornicata*, compared to the site where *C. fornicata* is rare or absent (Figure 5), suggesting that this invasive species plays a major role in controlling the intensity of the benthic fluxes. This occurs through the role that *C. fornicata* plays in the coastal silicate pump suggested by Chauvaud et al. (2000) and confirmed experimentally by Ragueneau et al. (2002a). The ecological implications, at seasonal scale, of this retention/recycling process have been explored by Ragueneau et al. (2002a). For our purposes, it is important to observe that although most of the BSi in biodeposits gets recycled and fuels summer diatom production, an important fraction eventually gets buried on an annual basis (Figure 6a). Eighty-four percent of biodeposition occurs during the productive period, and it can be seen that during that period, 32% of BSi in biodeposits get preserved in the sediments.

This preservation efficiency of silica in biodeposits is quite high, approaching preservation efficiencies encountered in the Southern Ocean (Pondaven et al. 2000; Ragueneau et al. 2002b), well-known for being efficient at preserving BSi below the sediment–water interface. Two reasons may explain this good preservation: (i) being embedded *in C. fornicata* mats, a large fraction of the BSi fragments is covered by organic matter (Figure 3), which protects the fragments from dissolution (Lewin 1961; Bidle and Azam 1999); (ii) the sediments of the Bay of Brest are rich in aluminosilicates (Bassoulet 1979), which can provide enough Al to rapidly and strongly decrease the BSi dissolution rates (Van Bennekom et al. 1989; Dixit et al. 2001).

Biodeposition and Si annual retention

Not only does biodeposition lead to the temporary retention of BSi at the sediment–water interface, with important ecological implications at the seasonal scale (Ragueneau et al. 2002a); in addition, it creates the conditions, on an annual basis, for an efficient preservation of the BSi trapped, leading to a retention of Si that represents some 27% of annual BSi biodeposition and 23% of annual DSi river inputs (Figure 6a). This annual retention of Si through the Bay of Brest ecosystem is only slightly higher than the global mean proposed by DeMaster (1981) for estuarine retention, and about two times higher than the most recent estimate (Tréguer et al. 1995). Most importantly, it must be much higher than before *C. fornicata* colonized, perturbating the patterns of pelagic production (Chauvaud et al. 2000) and biogenic sedimentation (Chauvaud 1998; Thouzeau et al. 2003). Indeed, (i) net sedimentation of organic matter has strongly increased with the proliferation (Thouzeau et al. in prep.), (ii) we have shown that the biodeposits are enriched in Si, typically by a factor of 2–3, and (iii) preservation is excellent below *C. fornicata* mats.

This suggests that this exotic species of suspension feeders, by producing huge amounts of biodeposits, has the potential to substantially alter the retention of Si along the land–ocean continuum. One way of testing this hypothesis would be to collect sediment cores below *C. fornicata* mats, and look for changes in BSi accumulation through time.

Increasing biodeposition throughout the world

Biodeposition has increased throughout the world coastal ocean, as a result of human introduction, both deliberate or accidental, of alien mollusk species (Strayer et al. 1999; Mack et al. 2000; Budd et al. 2001; Perrings et al. 2002). *Dreissena polymorpha*, *Ruditapes philipinarum*, *C. fornicata*, *Potamocorbula* *amurensis* or *Corbicula fluminea* are among the most common invasive aquatic organisms, for which large scale impacts have been reported in the last two decades (Carlton et al. 1990). These invasions will continue, as mollusk aquaculture production is growing rapidly and biological invasions will continue as expanding international commerce increases the translocation of fauna from one geographic realm to another (Carlton and Geller 1993). For instance, the rate of reported invasions (second main group: Mollusk, Figure 7) of coastal marine communities in North America has increased exponentially over the past two centuries. Finally, the main invasive mollusks in freshwater (*Dreissena polymorpha*, *Corbicula fluminea*, *Rangia cuneata*), and in marine/estuarine ecosystems (*Crepidula fornicata*, *Corbula gibba*, *Maoricolpus roseus*, *Mytilus galloprovincialis*, *Musculista senhousia*, *Limnoperna fortune*), all suspension feeders, continue to spread worldwide.

The calculations presented herein suggest that production of biodeposits and preservation of BSi in the biodeposits may well be high enough to sustain an important Si annual accumulation flux in the Bay of Brest ecosystem; important with respect to the other sources and sinks of Si in this ecosystem, and

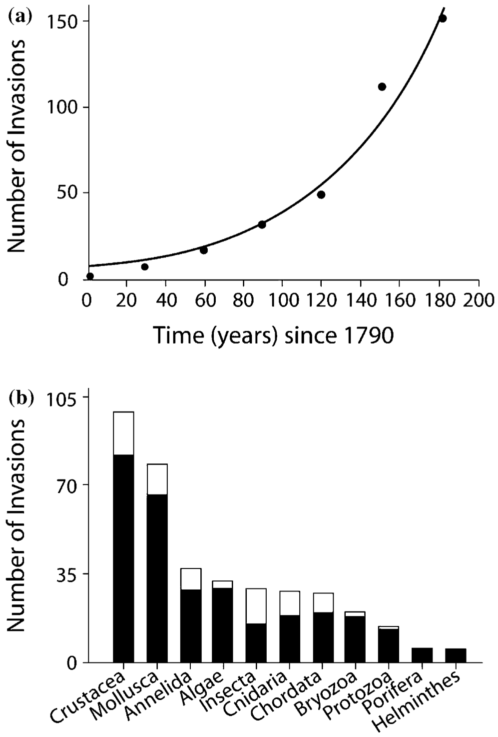

Figure 7. Total number of established non-indigeneous species of invertebrates and algae reported in marine waters of north america shown by: (a) rate of invasion, (b) taxonomic group. Redrawn from Ruiz et al. (2000).

possibly, important with respect to what this flux was before the invasion started. In such ecosystems where suspension feeders continue to spread, Si retention along the land–ocean continuum may increase with time. Interestingly, but to be tested in appropriate places, this mechanism could constitute a third route in the silica depletion mechanism (Van Bennekom and Salomons 1981). This route would not require enhanced diatom production (contrary to eutrophication), but simply enhanced BSi preservation, following increasing biodeposition due to the proliferation of invasive species of benthic suspension feeders. Given the importance of increasing biodeposition throughout the world and the role of DSi in coastal food webs, we believe it is important to look closely at nutrient monitoring stations and search for possible long-term changes in DSi concentration, seaward of areas subject to such proliferation of biodepositing organisms.

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