

Direct evidence of a biologically active coastal silicate pump: Ecological implications

Abstract—Ecological shifts from diatoms to other phytoplankton species have been related to decreasing Si:N and Si:P nutrient ratios. The Bay of Brest is such a perturbed ecosystem where Si has become limiting but where diatoms continue to dominate the phytoplankton throughout the productive period. Several hypotheses have been invoked to account for this dilemma. The most recent combines suspension feeder activity and Si recycling. Suspension feeder activity, stimulated by the proliferation of the invasive species *Crepidula fornicata*, would be the driving force of a biologically active silicate pump which would (1) retain Si within the Bay during spring and (2) provide the Si necessary for diatoms during summer. During the year 2000, this hypothesis was successfully tested. Direct evidence of silicic acid limitation has been provided, and during summer, benthic fluxes measured at a site with a high density of *C. fornicata* are one order of magnitude higher than those measured at the site with no *C. fornicata*. Seasonal budgets of Si inputs and diatom demand demonstrated that diatom production during summer depends strongly on Si recycling at the sediment–water interface. Thus, if *C. fornicata* decreases benthic biodiversity and perturbs the development of the native Great Scallop (*Pecten maximus*), it also helps the Bay cope with elevated N inputs. The proposed removal of *C. fornicata* might be economically desirable from a fisheries economic viewpoint, but it clearly would be associated, in the present context of excessive N inputs, to a potential risk of harmful algal blooms during summer.

Si and coastal food webs—Evidence is growing that the nutrient silicic acid (DSi) is playing a major role in the functioning of coastal ecosystems in many regions of the world (Conley et al. 1993). The reason is linked to the importance of diatoms in marine food webs (Cushing 1989) and to anthropogenic influences on watersheds and rivers. When DSi is missing, diatoms are replaced by other phytoplankton groups, such as dinoflagellates, that do not have any requirement for this nutrient (Officer and Ryther 1980). A wide variety of coastal ecosystems has been documented where increasing frequency and magnitude of harmful algal blooms have been associated with decreasing Si:N and Si:P ratios, with important consequences for pelagic and benthic food webs (Smayda 1990). Decreasing Si:P and Si:N ratios first find their origin in eutrophication. Urbanization, agricultural, and industrial activities have led to large increases in the delivery of N and P along the land–ocean continuum. On a global basis, the fluxes of these elements to the oceans have increased by a factor of two; at the same time, in rivers unaffected by human activities, DSi fluxes have remained constant because the major source of DSi to rivers comes from the weathering of natural silicate rock (Meybeck 1998). The second source of decreasing Si:N and Si:P ratios is river manipulation, especially the building of dams (Humborg et al. 2000). In the reservoirs behind the dams, growth and sedimentation of diatoms remove biogenic silica (BSiO₂)

from the water column, leading to decreased DSi concentrations (Conley et al. 1993). Whatever the type of perturbation, decreasing Si:N and Si:P ratios in rivers imply potential DSi limitation for diatoms (Dortch and Whittedge 1992), which becomes true limitation when DSi concentrations decrease below the half-saturation constants (K_m values) in the receiving coastal water bodies (e.g., Nelson and Dortch 1996).

The Bay of Brest example—The Bay of Brest is an ecosystem where Si:N ratios in riverine inputs have decreased by a factor of three in the past 30 yr, mostly because of excessive N inputs from agricultural practices (Le Pape et al. 1996). Indirect evidence of DSi limitation has been provided from the declines in diatom populations in concert with DSi concentrations of $<1 \mu\text{M}$ by early spring (Ragueneau et al. 1994). DSi limitation has then been directly demonstrated from kinetic uptake experiments using the ³²Si radioactive isotope (Del Amo 1996; see also Fig. 2). Despite DSi limitation during spring, diatoms typically continue to dominate the phytoplankton during the entire productive period (Del Amo et al. 1997a). Several factors have been hypothesized to account for this (apparent lack of) response of the Bay to excessive N inputs. They include the export out of the Bay of most of this N during winter (Le Pape et al. 1996); the well-mixed nature of the water column, which does not favor the development of flagellates (Ragueneau et al. 1996); and the intensity of Si recycling both in the water column and at the sediment–water interface (Ragueneau et al. 1994; Del Amo et al. 1997b).

Although Si recycling has recently been shown to accelerate under high bacterial activity (Bidle and Azam 1999), it remains slower than the recycling of N and P, which are biologically mediated (Officer and Ryther 1980). In the open ocean, this differential recycling rate is at the basis of the so-called silicate pump (Dugdale et al. 1995), which removes DSi from surface waters for a long time period. In coastal waters, especially in the semienclosed Bay of Brest, the effects of the silicate pump can be reversed because of the tight temporal and spatial coupling between sediment and surface waters. Following the first diatom blooms and the sedimentation of diatom cells, Si can be retained within the Bay at the sediment–water interface instead of being exported to the adjacent coastal ocean. It then becomes directly available for regenerated diatom production because of the shallow depths of the well-mixed waters (Del Amo et al. 1997b).

Synthesizing 20 yr of studies of the Bay of Brest ecosystem, both from a pelagic and benthic point of view, Chauvaud et al. (2000) suggested that the functioning of this coastal silicate pump is under the control of benthic suspension feeders, which dominate the benthic megafauna in the Bay of Brest (Thouzeau et al. 2000). Introduced in 1950, the gastropod *Crepidula fornicata* is now the main benthic sus-

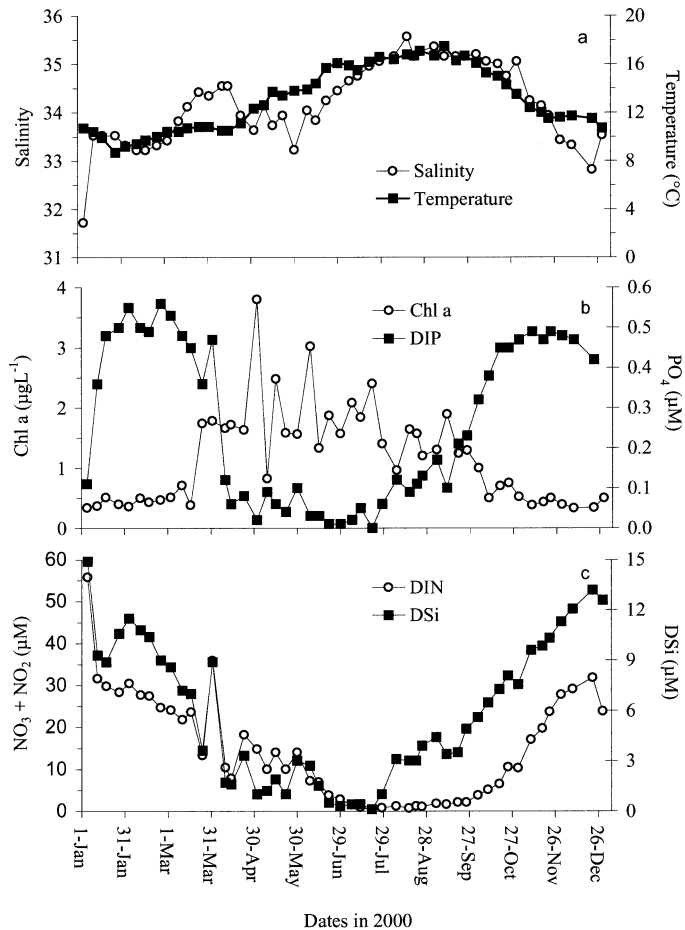


Fig. 1. Physical, chemical and biological parameters measured at the SOMLIT site in the Bay of Brest during the year 2000. (a) Temperature and salinity. (b) Phosphate and Chl *a*. (c) Silicic acid and nitrate.

pension feeder in the Bay (Chauvaud 1998). Chauvaud et al. (2000) have suggested that increased activity of suspension feeders during early spring (filtration and subsequent production of enormous quantities of biodeposits) could lead to an increase in the temporary retention of BSiO_2 in the sediments of the Bay, thereby limiting the export of Si out of the Bay. Subsequent BSiO_2 dissolution during late spring and summer, enhanced by increasing temperature and bacterial activity, would provide the necessary DSi required by diatoms to maintain their dominance throughout the productive period. It is essential to note that the enormous amount of biodeposits produced by *C. fornicata* has no equivalent in the ecosystem.

Testing the working hypothesis—During the year 2000, the hypothesis of a biologically active silicate pump was tested. Figure 1 shows the physical, chemical, and biomass parameters recorded weekly at the monitoring SOMLIT station located near the Bay entrance. These parameters characterize the productive season, which begins in the Bay in late March with the increase in chlorophyll *a* (Chl *a*), corresponding to the decrease in nutrient concentrations. A succession of phytoplankton blooms occur throughout the

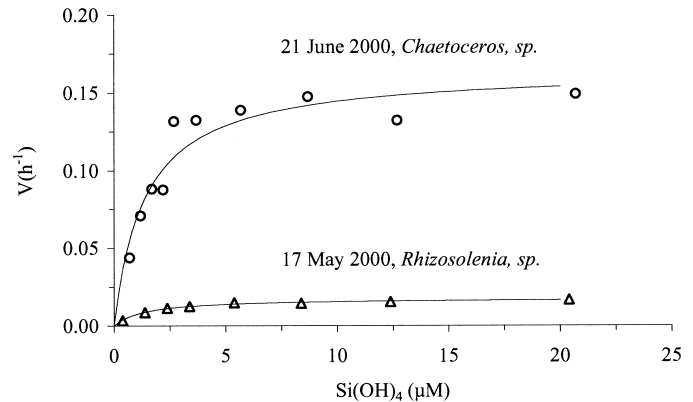


Fig. 2. Two kinetic experiments performed on 17 May 2000, when the diatom *Rhizosolenia* was dominant, and on 21 June 2000, when the diatom *Chaetoceros* was dominant. Experiments have been performed using the ^{32}Si radioactive isotope (Tréguer et al. 1991). A 3-liter water sample was distributed into eight 250-ml polycarbonate incubation bottles. These bottles were enriched with silicic acid up to $20 \mu\text{M}$, spiked with ^{32}Si , and incubated for 24 h at light saturation. Following liquid scintillation counting (Leynaert et al. 1996), the specific uptake rate (V) is plotted against the Si(OH)_4 concentration of the flasks at the beginning of the incubation. These Michaelis–Menten types of curves have been fitted using the nonlinear regression method of Wilkinson (1961), allowing the determination of the maximal uptake velocity (V_{max}) and the half-saturation constant (K_m).

spring and summer. By late July, DSi and DIP start to accumulate again in the water column, followed by DIN 2 months later when the productive period ends. Direct evidence of DSi limitation during spring has been obtained through two kinetic experiments performed when the diatoms *Rhizosolenia* sp. and *Chaetoceros* sp. dominated the phytoplankton population (Fig. 2). Having similar K_m values close to $1.3 \mu\text{M}$, these diatoms were both limited to only 20% of their maximal uptake velocity by late spring/early summer. Note that *Chaetoceros* sp. exhibited a V_{max}/K_m ratio 10 times higher than that of *Rhizosolenia* sp., suggesting a higher affinity and, thus, a greater ability to take up DSi at low concentrations. Thus, diatoms were clearly limited by ambient DSi concentrations and were dependent on Si recycling during early summer. By late summer, DSi accumulated again in the water column (Fig. 1), suggesting that DSi inputs exceeded the diatom demand by that time.

To study the possible effects of benthic suspension feeders on DSi recycling at the sediment–water interface, benthic fluxes were measured seasonally at two contrasting sites, displaying respectively low (~ 30 individuals m^{-2}) and high ($\sim 1,700$ individuals m^{-2}) concentrations of *C. fornicata*. Sediment cores were retrieved manually at 20-m depths with the use of scuba equipment; three replicates were taken at each site. Following a time 0 sampling (i.e., performed immediately after collection, on deck), 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, Fig. 1). 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 h following the core collection. Homogenization of the overlying

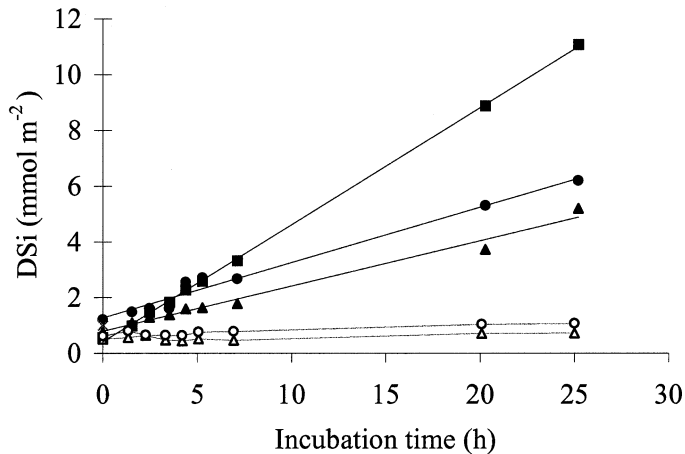


Fig. 3. Sediment core incubation experiments conducted during late summer in the Bay of Brest. Sediment cores were collected at Rozegat by scuba at two sites located within 300 m but exhibiting contrasting densities of the suspension feeder *C. fornicata*. Filled symbols, Rozegat site with high densities of *C. fornicata* (1,243 individuals m^{-2} , Thouzeau et al. 2000). Open symbols, Rozegat site without any *C. fornicata*. Note the difference by a factor of 20 between the mean flux measured at the site with *C. fornicata* (triplicate: mean, $6.3 \text{ mmol Si m}^{-2} \text{ d}^{-1}$) and the mean flux measured at the site without *C. fornicata* (duplicate: mean, $0.3 \text{ mmol Si m}^{-2} \text{ d}^{-1}$).

water was ensured by pumping water, with a peristaltic pump, 2–3 cm above the sediment–water interface and re-distributing it near the water surface. The flow rate was adjusted so that one water volume was renewed every hour. The slopes of the DSi increase measured in the cores during their incubation show a 20-fold difference during late summer depending on whether *C. fornicata* was abundant or rare (Fig. 3). The corresponding DSi fluxes are typical of those encountered in coastal environments (Yamada and D’Elia 1984 and references therein; Friedrich et al. 2002). Mean values at these two contrasting sites were measured every 2 months throughout the productive period (Fig. 4). Two important observations can be made. First, whatever the season considered, fluxes are always higher at the site with *C. fornicata* compared to the site without *C. fornicata*. Reaching only a factor of two by late spring, the difference between the fluxes measured at the two sites becomes more than one order of magnitude by midsummer and fall. Second, maximum DSi fluxes were measured in late spring at the site without *C. fornicata* and in late summer at the site with *C. fornicata*. Thus, both the amplitude of the DSi benthic flux in the presence of *C. fornicata* and the delay in the timing of the maximum of these fluxes provide strong evidence that the BSiO_2 produced during spring is indeed being retained by the activity of the suspension feeders and then gradually released to the overlying waters following dissolution. Owing to the well-mixed nature of the water column in this macrotidal ecosystem, DSi is then immediately available for diatoms production (Ragueneau et al. 1996).

Validation at the Bay scale—Before budgeting Si fluxes within the Bay of Brest ecosystem, a simple, albeit important, calculation provides strong support that the working

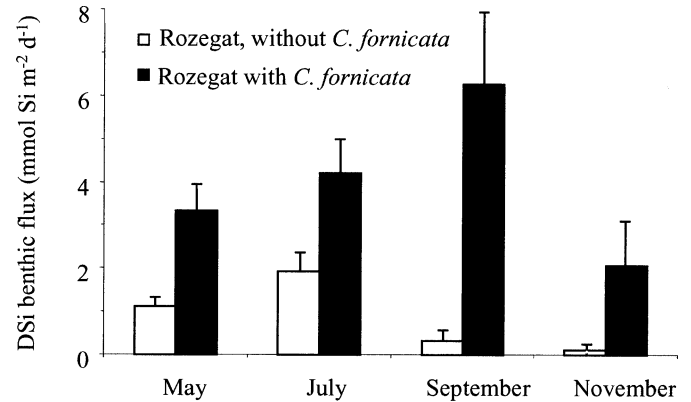


Fig. 4. Synthesis of DSi benthic fluxes measured at the two contrasting sites during the productive period in the Bay of Brest. Black bars, Rozegat site with *C. fornicata*; white bars, Rozegat site without *C. fornicata*. These fluxes represent the mean values of the fluxes measured in triplicate (see Fig. 3); standard deviations are also shown.

hypothesis has significance at the scale of the whole system. Dry organic matter (11,000 tons) is produced by suspension feeders (Chauvaud et al. 2000). By analogy with zooplankton fecal pellets in surface waters (Tande and Slagstad 1985), we can propose the hypothesis that these biodeposits are enriched in biogenic silica because Si is not retained by these organisms for their metabolism. Typically in the open ocean, the Si:C ratio increases by about a factor of five between food and feces, between production and export in surface waters, or between the deposition at the sediment–water interface and the accumulation below the bioturbated layer (Ragueneau et al. 2002). Using this factor and a typical Si:C ratio of 0.04–0.09 for the Bay phytoplankton (Ragueneau et al. 1994; Del Amo 1996) yields a Si:C ratio in the biodeposits close to 0.2–0.5. Thus, the biodeposits can lead to the temporary deposition of $167\text{--}417 \times 10^6 \text{ mol Si}$. Distributed spatially over the 180 km^2 of the Bay and temporally over the whole year, this leads to a potential DSi benthic flux of $2\text{--}6 \text{ mmol Si m}^{-2} \text{ d}^{-1}$. Interestingly enough, this range is of the same magnitude as the fluxes measured using core incubations (Fig. 4).

Preliminary budgets—Having provided direct evidence for (1) DSi limitation and (2) a direct influence of suspension feeders on BSiO_2 retention and DSi availability, one needs to compare the magnitude of the DSi benthic fluxes with both river inputs and the diatom demand (silica production). Nutrient river inputs were measured on a weekly basis by members of the ECOFLUX network in the Aulne and the Elorn rivers, which bring most of the freshwater to the Bay of Brest (Porhel et al. 2001). For comparison purposes, benthic DSi fluxes have been extrapolated to the whole Bay (180 km^2) by applying the fluxes measured at the site with *C. fornicata* to the area of the Bay covered by the gastropod (90 km^2) and the fluxes measured at the site without *C. fornicata* to the area still unaffected (90 km^2) by it. Reasonable estimates of integrated silica production can be obtained on the basis of primary production measurements and the use of appropriate Si:C ratios (Ragueneau et al. 1994). Under

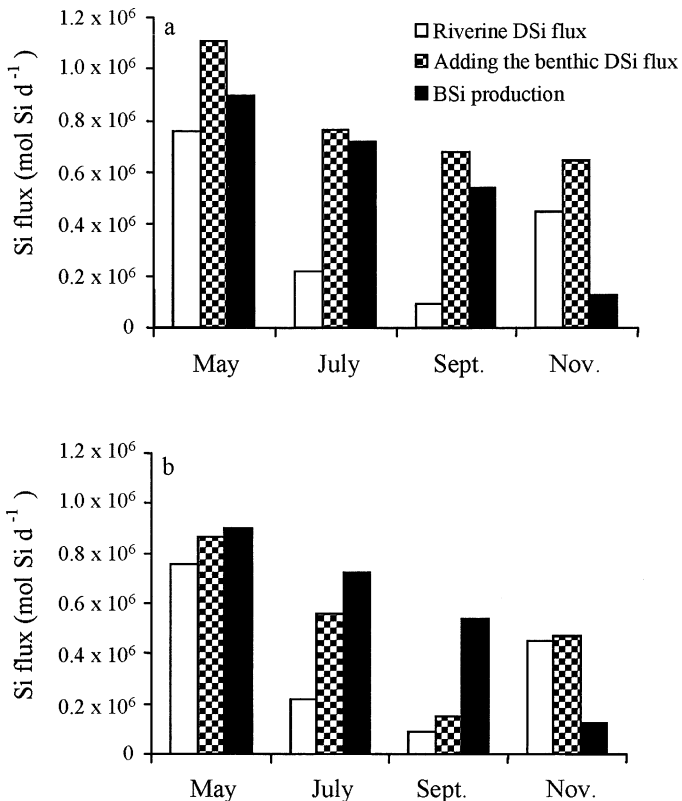


Fig. 5. Seasonal budgets (mol Si d⁻¹) of DSi fluxes in the Bay of Brest. White bars, river fluxes; hatched bars, sum of river and benthic fluxes; black bars, estimates of silica production. See text for explanations on budget calculations. (a) Benthic DSi fluxes have been extrapolated to the whole Bay by applying the fluxes measured at each site (Fig. 4) to half of the Bay (i.e., the present extension of the invasive *C. fornicata*). The grey bars do not represent only the benthic fluxes shown in Fig. 4 and extrapolated to the whole Bay; they represent the sum of the river and benthic DSi inputs, which can be directly compared to the diatom demand (black bars). (b) Same description, only *C. fornicata* has been artificially removed from the system by applying the benthic flux measured at the site without *C. fornicata* (Fig. 4) to the whole Bay and not just to half of it.

nutrient-replete conditions, diatoms grow with a Si:C ratio close to 0.13 (Brzezinski 1985). In the Bay of Brest, this ratio is typically twice as low because of the coupled influence of DSi limitation and the presence of nonsiliceous algae (Ragueneau et al. 1994; Del Amo et al. 1997a). A ratio of 0.06 has therefore been chosen as a reasonable mean for converting C primary production into a BSi production that can then be compared to river and benthic fluxes (Fig. 5).

Four budgets were made for the productive season (Fig. 5a), neglecting DSi inputs from the adjacent ocean because they represent <5% of the diatom demand during the productive period (Ragueneau et al. 1994). These budgets clearly demonstrate the importance of suspension feeder activity on the Si cycle, allowing for DSi to be available for diatom production during late spring and summer. By early spring, river Si inputs can sustain nearly 100% of the diatom demand; diatoms do not depend on recycling at the sediment–water interface, especially if we add the winter stock of DSi that can account for one third of the initial diatom demand (Ra-

gueneau et al. 1994). By late spring, river inputs have decreased by a factor of three and can sustain only 30% of the diatom demand. The rest must be met by recycling at the sediment–water interface. By mid-summer, river inputs are even smaller, and DSi benthic fluxes alone can sustain diatom demand. Because recycling also occurs in the water column, DSi is probably available in excess and starts to accumulate (Fig. 1). Note that in September, DSi inputs exceed the diatom demand by about 140,000 mol Si d⁻¹ (Fig. 5a). The Bay volume is close to 2 × 10⁹ m³ on average, which means that DSi should accumulate at a rate of roughly 0.07 μmol L⁻¹ d⁻¹. From late July onward, DSi increases linearly from 0 to 12 μM in 5 months (Fig. 1). This corresponds to a rate of 0.08 μmol L⁻¹ d⁻¹, which is very consistent with the above budget calculation. During fall, diatom demand decreases sharply, whereas benthic fluxes are still high and river inputs have increased again from rainfall. DSi continues to accumulate in the water column at the mean rate calculated above and will soon reach its winter maximum concentrations.

The budgets presented demonstrate unambiguously the importance of recycling at the sediment–water interface in sustaining diatom demand throughout the productive period. It has been suggested that *C. fornicata* be removed from the ecosystem because this invasive species has drastically reduced the native *P. maximus* fishery in the Bay of Brest. A theoretical removal of *C. fornicata* was made in 2000 by applying the DSi benthic fluxes measured at the site without slipper limpets (Fig. 4) to the whole Bay of Brest (Fig. 5b). The budget suggests that during summer, DSi inputs from rivers and from the sediment–water interface would not be sufficient to sustain diatom demand. Diatoms would then probably be replaced by other algae not requiring DSi, leading to the potential of harmful algal bloom with severe consequences for pelagic and benthic food webs. The massive bloom of the toxic dinoflagellate *Gymnodinium nagasakiense*, encountered during the summer of 1995 in the Bay of Brest, illustrates this theoretical removal scenario. *C. fornicata* was present but inactive. Indeed, feeding activity has been deeply affected by the mass sedimentation of the diatom bloom that occurred by late spring, through either gill clogging or oxygen depletion (Lorrain et al. 2000; Chauvaud et al. 2001). As a consequence, biodeposits were produced in much lower quantities and Si was exported out of the Bay in the form of BSiO₂, instead of being stored at the sediment–water interface as biodeposits. Less DSi was then available for diatoms during late spring and summer, especially because river inputs were particularly low, and *G. nagasakiense* dominated the phytoplankton throughout the summer (Chauvaud et al. 2000).

Ecological implications—Until quite recently, the Bay of Brest did not experience any sign of “true eutrophication,” and more subtle shifts toward nondiatom species have been sparse. Our results suggest that it is the proliferation of the invasive *C. fornicata* that might well have masked, for years, the potentially negative effects of elevated N and P inputs through its role on the coastal silicate pump mechanism. Truly, *C. fornicata* endangers benthic biodiversity (Chauvaud et al. 2000) and the development of *P. maximus* (Thouzeau et al. 2000). However, the proposed removal of *C. fornicata* can

clearly be associated, in the present context of excessive N inputs, to a potential risk of harmful algal blooms during summer. The 1995 *Gymnodinium* event, explained by a complete stop of the silicate pump mechanism, had dramatic effects on benthic food webs. In particular, it led to a major interruption in the growth of *P. maximus* (Chauvaud et al. 2000; Lorrain et al. 2000) and to differential larval and/or postlarval mortality, depending on the species sensitivity to toxic substances (Chauvaud and Thouzeau pers. comm.). Interestingly, most indigenous species are more sensitive to *Gymnodinium* toxicity than the introduced mollusk (Chauvaud 1998), suggesting that nutrient enrichment would indirectly favor the successful colonization by nonindigenous species.

Both eutrophication (Schelske and Stoermer 1971) and river manipulation (Humborg et al. 2000) have modified Si retention along the aquatic continuum from land to ocean, with important consequences for the receiving coastal waterbodies. Enhanced retention due to increasing activity of suspension feeders, such as was encountered in the Bay of Brest ecosystem, provides a third means of perturbing the Si cycle in the coastal environment. By analogy with the observed enhanced retention in river systems and the consequences for the receiving coastal waters, we believe that studying the possible ecological and biogeochemical effects of enhanced Si retention in embayments onto the adjacent continental shelf warrant further investigations.

The mechanism described herein also affects primary production seasonality, with important feedbacks for benthic food webs. The Bay of Brest is showing a long-term change in the seasonal timing of phytoplankton biomass development (Chauvaud et al. 2000). The spring blooms have become smaller in amplitude, but the summer biomass has become higher. These subtle seasonal-scale changes might lead to positive or negative feedbacks in the benthic system and in other components of coastal ecosystems (Grall and Chauvaud 2002). How these responses might be used as early warning indicators of systemic responses to nutrient enrichment (Cloern 2001) warrant further investigations. Mass populations of invasive mollusks are developing throughout the world as a result of human introduction. Biotic invasions are an important component of human-driven aquatic alteration as major agents of global change (Mack et al. 2000; Grosholz 2002). Changes in primary production seasonality and alteration of the Si cycle provide additional potential impacts from such translocation of species.

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