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Long-term variation of the Bay of Brest ecosystem: benthic-pelagic coupling revisited

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ABSTRACT: Observations over the last 20 yr of the development of pelagic and benthic communities of a western European coastal ecosystem (Bay of Brest) provide complementary hypotheses to the 'silicic acid pump' hypothesis. An increase in nitrogen inputs, independent of silicic acid levels, has lowered the Si:N molar ratios during the last 20 yr in river discharges. Since 1981, maximum concentrations of chlorophyll *a* during the first spring bloom of the annual cycle have decreased, in contrast to the subsequent spring and summer blooms. Concomitantly, extensive spreading of an exotic gastropod *Crepidula fornicata* has modified the trophic structure of benthic communities by increasing suspension-feeder biomass. The following hypotheses on ecosystem functioning are made: (1) the decrease of chlorophyll biomass during the first spring bloom results from silicic acid limitation and increased suspension feeder activity, (2) benthic filtration and biodeposition activities enhance biogenic silica retention at the sediment-water interface, and (3) recycling of trapped biogenic silica maintains diatom populations by providing silicic acid in summer and reduces primary production seasonality. These hypotheses suggest that benthic organisms control the export rate of biogenic silica towards the open-water ocean and thus the specific composition of secondary phytoplankton blooms in the Bay.

KEY WORDS: Coastal ecosystem · Benthic-pelagic coupling · Long-term fluctuations · Silicon cycle

INTRODUCTION

Increasing nutrient inputs into coastal ecosystems are often accompanied by eutrophication phenomena and structural changes within the phytoplankton community (Smayda 1990, Billen et al. 1991, Humborg et al. 1997). In such systems, the increase of anthropogenic nitrogen (N) and phosphorus (P) inputs into rivers, as well as enhanced accumulation of biogenic silica (BSi) in sediments, lowers the Si:N and Si:P ratios in the neighbouring coastal waters, affecting phytoplankton specific composition and allowing for silicic acid (silicate) limitation of primary production in diatom-dominated systems (Meybeck & Helmer 1989, Smayda 1990, Le Pape et al. 1996, Del Amo et al. 1997a,b). It is obvious that the most affected part of the phytoplankton community is the diatoms (Officer & Ryther 1980, Smayda 1990, Conley & Malone 1992). The decrease in their abundance or dominance (van Bennekom et al. 1975, Bodeanu 1990), and more generally the shift from siliceous populations (diatoms) to non-siliceous ones (flagellates; Billen et al. 1991, Fisher et al. 1992) together with the possible emergence of new toxic species (Smayda 1990, Anderson 1995) have been described as a consequence of N and P enrichments.

The Bay of Brest (France) constitutes a coastal macrotidal ecosystem (maximum tidal amplitude: 8 m; tide periodicity: 12 h 15 min; maximum tidal currents: 2.6 m s^{-1}) that receives increasing nutrient inputs of anthropogenic origin (Dauchez et al. 1991, Daniel 1995, Le Pape et al. 1996); it is influenced by both freshwater inputs from rivers and fast mixing exchanges with waters from the Atlantic Ocean (Salomon & Breton 1991). Previous studies have demonstrated the influence exerted by tides on primary production

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dynamics to be the most important (Quéguiner 1982, Ragueneau 1994, Daniel 1995, Le Pape 1996, Ragueneau et al. 1996). In particular, diatom-dominated phytoplankton blooms have been shown to respond to decreasing tidal mixing (Ragueneau et al. 1996). During the last 20 yr, nitrate concentrations in rivers have doubled leading to a long-term decrease in Si:N molar ratios (silicic acid: nitrate + nitrite + ammonium) during summer in coastal seawaters, from 2 in 1975 to 0.33 in 1993 (Le Pape et al. 1996). In the literature, the symptoms of eutrophication cover many aspects of ecosystem functioning including increase in phytoplankton primary production and biomass, oxygen depletion, changes of the phytoplankton community structure with the emergence of harmful or nuisance blooms of microalgae, loss or alteration of macrophyte communities and changes in higher trophic levels (see Smayda 1990, Gray 1992). The Bay of Brest has not undergone any event characterised by high phytoplankton biomass liable to cause oxygen depletion (Le Pape et al. 1996). Numerous studies (Breton 1993, Ragueneau 1994, Ragueneau et al. 1994, Daniel 1995, Del Amo 1996, Le Pape 1996, Le Pape et al. 1996, Del Amo et al. 1997a,b) have demonstrated that the imbalance between silicic acid and N loads is high in the bay waters during spring and summer, but until 1993 only very few transient non-siliceous phytoplankton blooms occurred in the Bay of Brest (see Del Amo et al. 1997b). Resistance to effects of increased nutrient input (both increased primary production and phytoplankton species shifts) has been attributed to several additional factors, such as the relative fast flushing time (Delmas 1981, Delmas & Tréguer 1983), the time-lag between N inputs in winter and primary production in spring and summer (Le Pape et al. 1996, Del Amo et al. 1997a), BSi recycling, both in the water column and at the sediment-water interface (Ragueneau et al. 1994) and strong tidally induced vertical mixing. The latter, which is not favourable to flagellates (Margalef 1978, Ragueneau et al. 1996), would facilitate the replenishment of surface waters in silicic acid recycled at the sediment-water interface during the remaining productive period (see the role of a 'silicic acid pump in coastal waters' in Del Amo et al. 1997a,b).

Deep waters are usually considered as a receiver compartment dependent on, though decoupled from, primary production in the water column. It has been shown that seston deposition follows the seasonality of primary production (Deuser et al. 1981, Billet et al. 1983, Graf 1989). The influence exerted by benthic mineralization on pelagic production has also been demonstrated in coastal systems (Nixon 1981, Pomroy et al. 1983, Hopkinson 1987). However, only a few studies have considered the direct feedback of benthos through energy storage in the organisms or control of phytoplankton populations by benthic filter feeders (Ott & Fedra 1977, Ott 1981, Cloern 1982, Officer et al. 1982, Nichols 1985, Loo & Rosenberg 1989, Herman & Sholten 1990). The present paper considers benthic-pelagic coupling in the Bay of Brest and the way this ecosystem 'withstands' increased nutrient input and the subsequent detrimental effects. In fact, the Bay of Brest sustains benthic communities whose structure is characteristic of eutrophicated ecosystems (Pearson & Rosenberg 1978, Cederwall & Elmgren 1990, Rosenberg et al. 1990). According to the Gray-scale (1992), the shallowest macrobenthic communities show the first symptoms of eutrophication (Grall & Glémarec 1997). The changes in pelagic and benthic compartments during the last 20 yr enable us to reconcile contradictory results about changes in pelagic and benthic communities. The Si:N distrophy has indeed allowed for silicic acid to play a major role in the control of diatom dominance. Here we hypothesize that the silicic pump by which Si is retained within the system and made available to summer diatoms via benthic dissolution and vertical mixing (Del Amo et al. 1997b) is in fact dependent on benthic suspension-feeder activity.

MATERIAL AND METHODS

Study site. The Bay of Brest is a 180 km^2 semi-enclosed marine ecosystem connected to shelf waters (Iroise Sea) by a narrow (2 km wide) and deep (40 m) strait (Fig. 1). The bay is a shallow basin with 50% of its surface shallower than 5 m (average depth 8 m). There are 5 watersheds responsible for freshwater inputs in the bay, but those from the 2 main rivers, the Aulne (1842 km^2), and the Elorn (402 km^2), comprise 80% of total freshwater inputs. Tidal action induces short-term variability in hydrological parameters and enhances mixing of the water masses (see Quéguiner & Tréguer 1984, Salomon & Breton 1991, Daniel et al. 1995, Chauvaud et al. 1996, 1998). Tidal variation reaches 8 m during spring tides, which represents an oscillating volume of 40% of the high tide volume.

Phytoplankton biomass and communities. The source and nature of the data processed throughout this study are listed in Table 1. Surface-water chlorophyll *a* (chl *a*) and phaeophytin concentrations in 1994, 1995 (Chauvaud et al. 1998) and 1996 (this study) were added to the dataset previously compiled by Le Pape (1996). Bottom-water data, either unpublished or collected from the literature, were also compiled to be added to those determined between 1994 and 1996. The annually integrated chlorophyll biomass was estimated from chl *a* concentrations. Chl *a* and phaeophytin concentrations in 1996 were estimated using a calibrated Turner 111 fluorometer according to

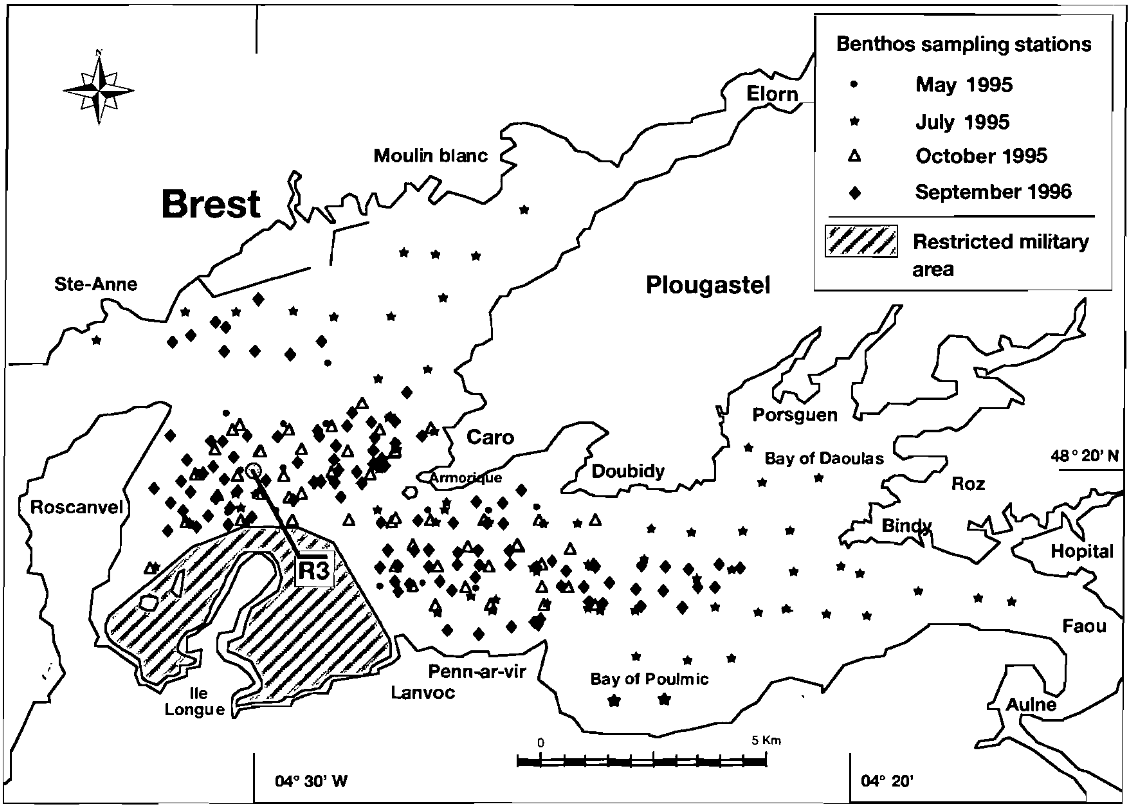

Fig. 1. Study area and location of sampling stations. Water column parameters were measured at Stn R3. Locations of benthos sampling stations were drawn from Chauvaud (1998)

Yentsch & Menzel (1963) and Lorenzen (1967; see also Chauvaud et al. 1998).

Benthic communities. Epibenthic megafauna, including *Crepidula fornicata*, were sampled using a video-monitored sled-dredge AQUAREVE (Thouzeau & Hily 1986, Thouzeau & Lehay 1988, Thouzeau 1989) modified by Thouzeau et al. (1991). AQUAREVE works like an epibenthic sled-dredge sliding on the bottom (tow speed 1 to 1.5 knots) while its knife slices the upper 5 cm of sediments. The working of the dredge is monitored via an underwater video camera mounted on the sled and turned toward the opening of the box. While in operation, instantaneous picture transmission allows the ship to stop the tow before the box overfills and to control dredging efficiency. The distance travelled on the bottom is measured by an odometric wheel providing a precise estimate of the tow length. The collecting box (0.97 m wide × 0.4 m high) is a rectangular steel box drilled with regularly spaced holes of 10 mm in diameter. A box-closing device triggers when the sled leaves the bottom. Samples were collected in May, July and October 1995 and September 1996 (Fig. 1; see Chauvaud, 1998). *C. fornicata* biomass (wet and dry weight) was estimated for each tow, each biosedimentary strata and for the whole Bay (Thouzeau et al. in press).

RESULTS

Main features of the Bay of Brest ecosystem

River flow-rates

Comparing daily flow-rates of the Aulne and Elorn, recorded between 1977 and 1995, has enabled us to select the Aulne flow rate as a climate indicator over a 30 yr period (linear correlation between the 2 sets of data: $r^2 = 0.83$ with $p < 0.01$). A marked seasonal variation of river flow is observed whatever the year considered (Fig. 2). Inter-annual variability is mainly the result of fluctuations in winter rainfall. The geometric moving-average was calculated on 183 Julian days between 1977 and 1995; it did not reveal any characteristic trend in weather conditions during the last 19 yr, except for a major increase in flow-rate between 1992 and 1995.

Table 1. Bay of Brest. Sources and parameters measured in the water column between 1977 and 1996. N_b = number of bottom measurements, N_s = number of surface measurements. RNO: Réseau National d'Observation (French Ministry of Environment)

Year	Measured parameters				Source
	N_b	Bottom	N_s	Surface	
1977			36	Nutrients Chl *a* Phaeophytin	RNO data
1981	18	Chl *a* Phaeophytin	35	Nutrients Chl *a* Phaeophytin	Quéguiner (1982) RNO data
1982	43	Chl *a* Phaeophytin	49	Nutrients Chl *a* Phaeophytin	Quéguiner (1982) RNO data
1983	18	Chl *a* Phaeophytin	33	Nutrients Chl *a* Phaeophytin	Hafsaoui (1984)
1991	12	Nutrients Chl *a* Phaeophytin	30	Nutrients Chl *a* Phaeophytin	Daniel (1995)
1992	20	Nutrients Chl *a* Phaeophytin	28	Nutrients Chl *a* Phaeophytin	Ragueneau (1994) and Daniel (1995)
1993	27	Nutrients Chl *a* Phaeophytin	27	Nutrients Chl *a* Phaeophytin Phytoplankton Specific composition	Le Pape (1996), Del Amo (1996), and Del Amo et al. (1997a,b)
1994	28	Chl *a* Phaeophytin	28	Chl *a* Phaeophytin	Chauvaud et al. (1996)
1995	32	Chl *a* Phaeophytin	33	Chl *a* Phaeophytin	Chauvaud et al. (1998)
1996	37	Chl *a* Phaeophytin	37	Chl *a* Phaeophytin	This study

Nutrient inputs and phytoplankton biomass

Nutrients. During the last 30 yr, an increase in agricultural production (crop production, fertilizer levels, number of pigs) in the Aulne and Elorn catchments has created large discharges of N compounds to the Bay of Brest (Cann 1995). Tréguer & Quéguiner (1989) have shown a 10-fold increase of N inputs to the bay since the beginning of this century. As most of these nitrogenous compounds are inorganic (98%; Cann 1995), they can be directly used for primary production (Le Pape 1996). Between 1975 and 1991, overall concentrations of nitrite and nitrate at the freshwater/seawater limit increased yearly (Joanny et al. 1993; Fig. 3a). The yearly averaged

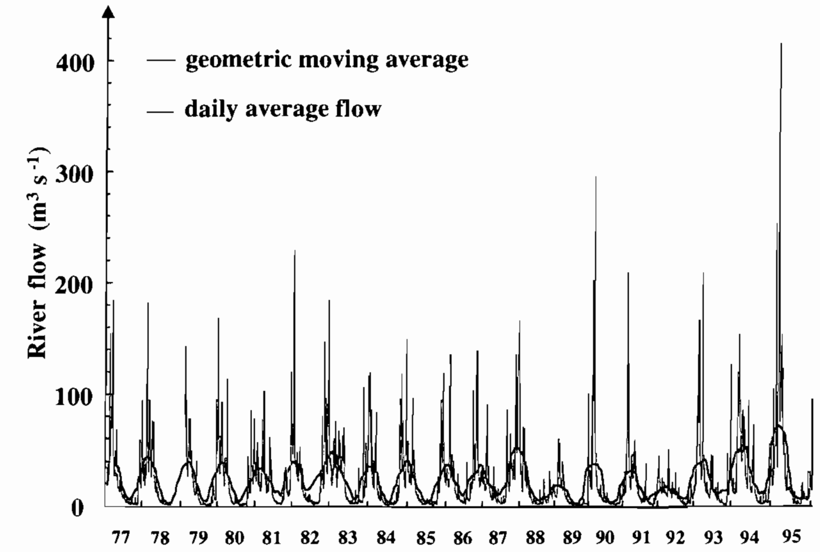

Fig. 2. Average daily flow-rate (m^3 s^{-1}) of the Aulne river between 1977 and 1995 (data provided by the Agence de Bassin Loire-Bretagne) and geometric moving average calculated on 183 Julian days

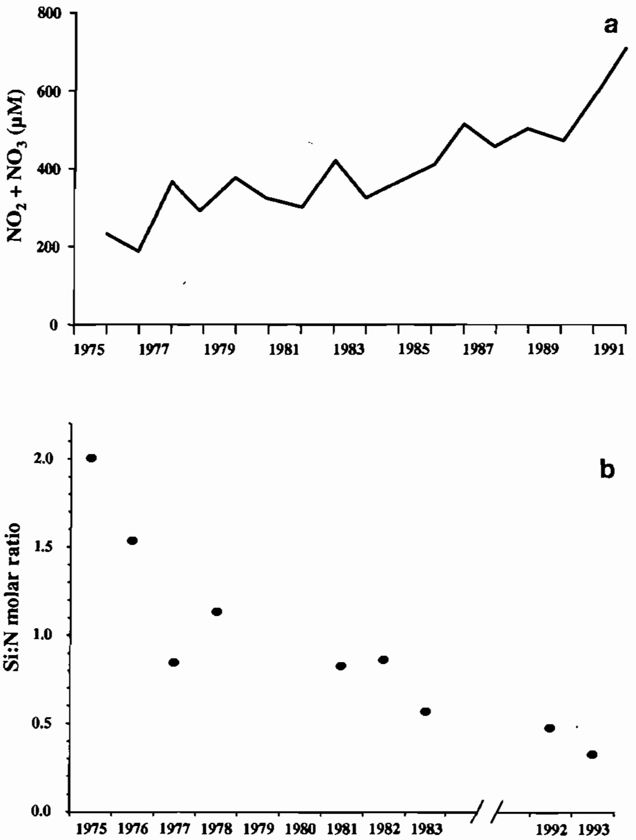

Fig. 3. (a) Nitrate + nitrite concentrations (mean annual concentrations in µM) in the Aulne at the limit between fresh and marine waters (redrawn from Joanny et al. 1993); (b) Si:N molar ratios determined at Stn R3 in surface waters during summer, when nutrients are limiting (redrawn from Le Pape et al. 1996)

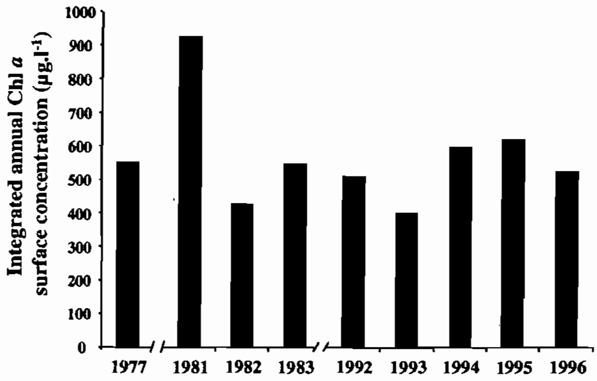

Fig. 4. Integrated chl *a* biomass (µg l^{-1}) in surface waters during the growing season between 15 February and 3 November 1977, 1981–83, and 1992–96

increase of nitrate was about 23 µM in the Aulne and 72 µM in the Elorn during this period (Joanny et al. 1993, Daniel 1995, Del Amo 1996, Le Pape et al. 1996). The annual input of dissolved inorganic nitrogen (DIN) from terrestrial origin in the Bay has been estimated to be 8000 t (Daniel 1995). This increase in N input has lowered Si:N molar ratios during the last 20 yr (Fig. 3b). This ratio was 6 times higher in 1975 than in 1993 (Le Pape 1996, Le Pape et al. 1996).

Chl a. Though the annually integrated chlorophyll biomass does not exhibit any characteristic long-term trend (Fig. 4), a noticeable reduction in the first spring bloom of the annual cycle can be observed over the years, in contrast to the subsequent secondary blooms (Fig. 5). During the first spring bloom of the year, maximum chl *a* concentrations in surface waters have decreased since 1981. However, near-bottom chlorophyll biomass decreased between 1981 and 1993, but increased in later years. Such trends reduce the seasonality of chlorophyll biomass. A seasonality index, α (Berger & Wefer 1990), was calculated according to the following relationship: $\alpha = (260 - \beta)$, where β is the time (days) required to reach half of the value of the integrated chl *a* biomass in surface waters estimated over 260 d, i.e. the time elapsed between 15 February and 3 November (first and last dates common to all the years investigated). A noticeable decrease of this index was observed over the study period (Fig. 6), thus confirming the time extension of the high biomass period.

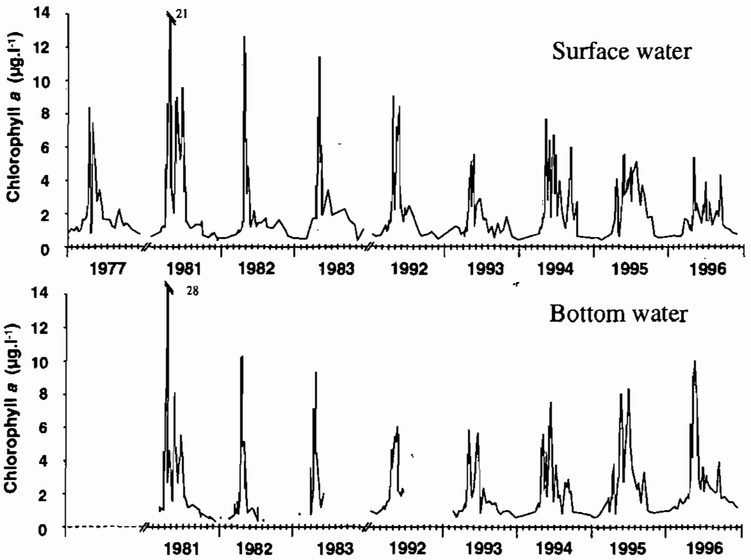

Fig. 5. Surface- and bottom-water chl *a* concentrations (µg l^{-1}) determined at Stn R3 between 1977 and 1996

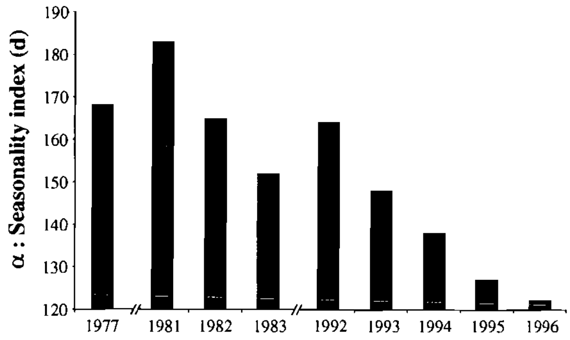

Fig. 6. Seasonality index, α (α = 260 − β), where β is the number of days required to obtain half the integrated biomass assessed over 260 d (from 15 February to 3 November)

Phytoplankton species composition

The specific composition of successive phytoplankton blooms in the Bay of Brest was only weakly influenced by increasing N fertilization (Del Amo 1996, Del Amo et al. 1997b). *Thalassiosira* spp., *Rhizosolenia* spp. and *Chaetoceros* spp. constituting the characteristic succession of diatoms in the Bay of Brest (Quéguiner 1982) have been regularly observed (Ragueneau 1994, Daniel 1995, Del Amo et al. 1997b, Chauvaud et al. 1998). In 1993 and 1995 however, the development of blooms of *Dinophysis* spp., *Gymnodinium* cf. *nagasakiense* or *Phaeocystis pouchetii* was observed (Nézan et al. 1996, Del Amo et al. 1997b). For the first time *G.* cf. *nagasakiense* (a toxic dinoflagellate) dominated the phytoplankton community during the summer of 1995 (Nézan et al. 1996).

Benthic megafauna communities

Many studies on benthic communities have shown the dominance of suspension feeders in the Bay of Brest (Hily 1984, 1989, 1991, Jean 1994, Jean & Thouzeau 1995, Grall & Glémarec 1997, Chauvaud 1998). Since its introduction in 1950, the gastropod *Crepidula fornicata* has been proliferating and is today the main benthic suspension feeder in the Bay (Chauvaud 1998, Thouzeau et al. in press). The area covered by this species expanded from 45 km^2 in 1978 (Coum 1979) to 90 km^2 in 1995 (Fig. 7; Chauvaud 1998). Its biomass was 12 878 t dry weight (DW) in 1995 and varied between 0 and 6900 g DW m^{-2}, depending on sediment type. The faeces and pseudo-faeces produced by *C. fornicata* represented 846 000 t yr^{-1} wet weight (WW) and 11 324 t of dry organic matter. These biodeposits, together with the constant extension of shoals, caused noticeable alterations in the specific composition and structure of benthic megafauna populations. The impact of the extensive spreading of *C. fornicata* onto bottoms like muddy sands and gravels, coralline algae (maerl) and muds previously colonised by specific communities

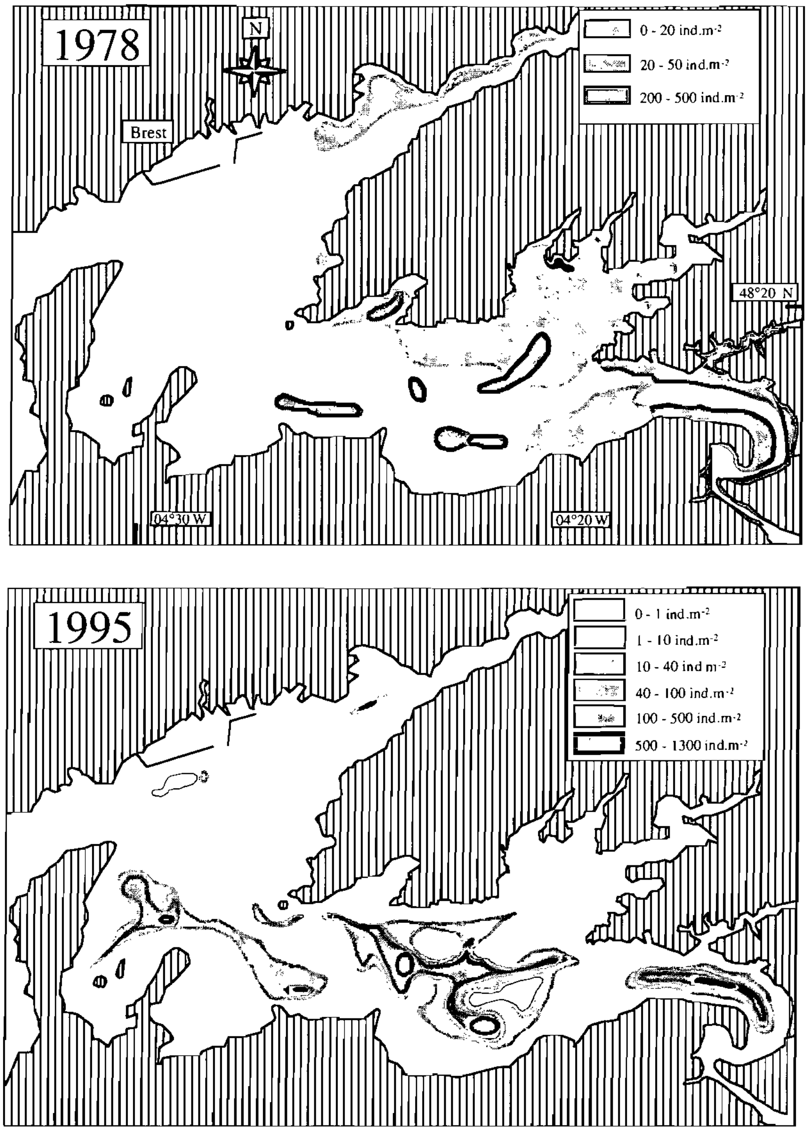

Fig. 7. Distribution (ind. m^{-2}) of *Crepidula fornicata* in the Bay of Brest in 1978 (from Coum 1979) and in 1995 (modified from Chauvaud 1998)

can be quantified. A comparison of the density and biomass of the communities living in these strata with the present *Crepidula*-based community highlights the increase of the suspension-feeder biomass within the latter community (Fig. 8). This biomass increase corresponds to a 101-fold increase for colonised areas consisting of sand dunes and to a 570-fold increase for muds. Even though *C. fornicata* is mainly responsible for these increases, the biomass and density of other associated megafaunal suspension feeders have also increased since 1950, whereas species diversity among this trophic group remains stable at the biosedimentary stratum scale.

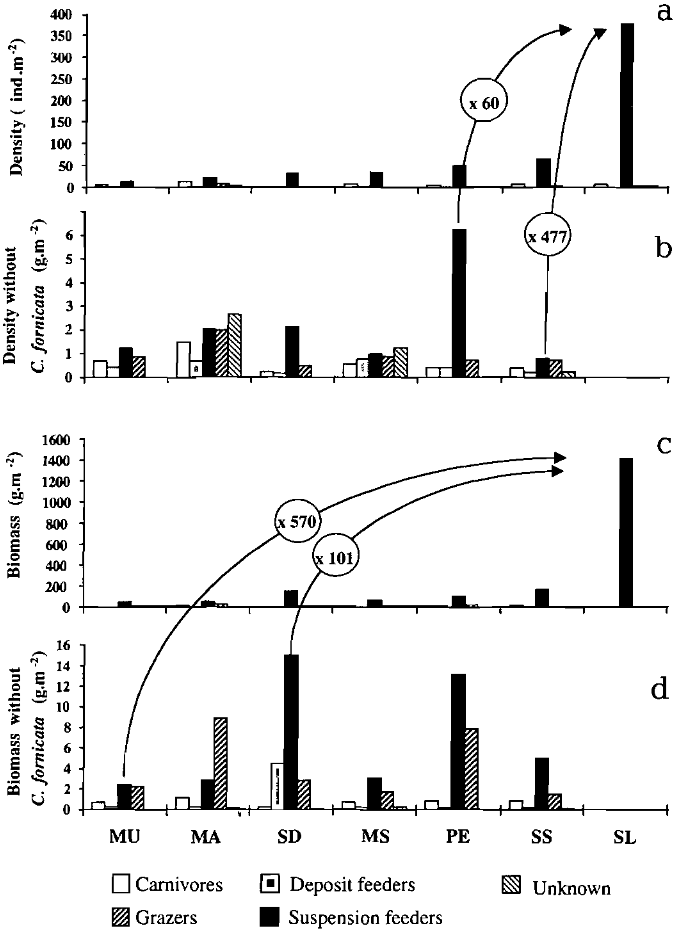

Fig. 8. Density and biomass of benthic megafaunal assemblages in each biosedimentary stratum. (a,c) With *Crepidula fornicata*; (b,d) Without *C. fornicata*. MU: mud; MA: maerl; SD: sand dune; MS: muddy sand and gravel; PE: pebbles; SS: sand shell; SL: slipper limpet

Benthic-pelagic coupling

One of the main features of the long-term chlorophyll biomass fluctuations in the Bay relates to the steady decrease of maximum chlorophyll concentration during the first spring bloom (Fig. 5). Such a trend could have different causes:

(1) Variable sampling scheme. A variable sampling frequency in spring would not enable one to systematically obtain chl *a* concentrations corresponding to the true maximum of the first annual bloom. However, spring has systematically been the most investigated period and sampling frequency cannot be the source of chlorophyll biomass fluctuations that occurred throughout the first bloom. Table 1 shows that the number of samples collected over 1 yr cannot be related to the inter-annual fluctuations of chl *a* maximum.

(2) Unfavourable variations in weather conditions (light and rain). River flow-rate fluctuations (indicator of rainfalls) between 1977 and 1995 do not show any specific trend. The decrease of both the seasonality index (α; Fig. 6) and chlorophyll biomass (Fig. 5) measured during the first annual spring bloom over the 1992 to 1995 period was concomitant with a steady increase in river flow rate (Fig. 2); this result could signify light limitation for primary production due to water-column stratification and increased turbidity.

(3) Changes in the species composition of spring blooms inducing a drastic decrease in phytoplankton production at this time of the year. Del Amo (1996) has reported large inter-annual variations in primary production since the 1980s (280 g C m^{-2} yr^{-1} in 1981; Quéguiner & Tréguer 1984; 255 g C m^{-2} yr^{-1} in 1982; Hafsaoui 1984; 148 g C m^{-2} yr^{-1} in 1993), but there has been no indication of increases in primary production. In addition, species composition of the first blooms was not radically modified between 1981 and 1993 (Del Amo et al. 1997b).

(4) Increased zooplankton grazing. In the Bay of Brest (Quéguiner 1982), like in many temperate coastal

Table 2. Concentrations (µM) of dissolved inorganic nitrogen (DIN; nitrate + nitrite + ammonium), silicic acid and phosphate measured in surface waters at Stn R3 (48° 20′ N, 4° 30′ W), just prior to the first spring bloom

Year	DIN	Phosphate	Silicate
1977	40[a]	0.4	15[a]
1981	19[a]		7[a]
1982	10[a]		5[a]
1991	28.8	0.49	8.75
1992	15.7	0.45	3.59
1993	24.9	0.2	6.29
1994	29.3	0.43	8.69

[a] Estimated from authors' values (see Table 1 for references)

ecosystems (see Båmstedt 1985), the first spring bloom develops when zooplankton biomass is the lowest. Zooplankton grazing is thus negligible at this time of year.

(5) Reduction of nutrient concentrations before the first spring bloom. There is no indication of any long-term trends in nutrient concentrations (Table 2).

(6) Increasing suspension-feeder grazing. Increasing biomass of epibenthic suspension feeders would lead to increasing phytoplankton grazing by the benthos from year to year. It has been shown that when nutrient inputs in a coastal ecosystem increase while the production rate and species composition of phytoplankton populations are stable and suspension feeders biomass is growing, then the decrease of phytoplankton biomass can result from increasing benthic grazing. In particular, flume experiments (Oviatt et al. 1993, Peeters et al. 1993, Smaal et al. 1994) and *in situ* investigations conducted in lakes (Lehman 1980) and in coastal ecosystems (Cloern 1982, 1996, Motoda et al. 1987, Alpine & Cloern 1992) have shown that phytoplankton biomass was controlled by the benthos in nutrient-enriched and shallow systems. Hily (1991) has suggested that, in the Bay of Brest, benthic suspension-feeding activity would be sufficient to explain the paradox observed by Quéguiner (1982) between high phytoplankton production and low chlorophyll biomass in summer. However, benthic grazing can totally control phytoplankton biomass only in the systems where the water residence time is long (several mo), as in the Bay of San Francisco (Cloern 1982, 1996, Officer et al. 1982). A mean residence time of about 25 d in the Bay of Brest (Anonymous 1980) could prevent total control of phytoplankton biomass by the benthos, but benthic grazing might explain the decrease in chlorophyll biomass during the first spring bloom of the annual cycle.

Role of the benthos in the silicic acid pump (hypothesis)

Most recent studies focusing on the role of silicic acid in phytoplankton dynamics in the Bay of Brest have shown (1) Si uptake limited by silicic acid availability in early spring (Del Amo 1996), (2) efficient retention of Si within the sediments of the Bay during spring (Ragueneau et al. 1994) and (3) the important role of vertical mixing in making silicic acid recycled at the sediment-water interface available for diatoms in surface waters, despite a temporal decoupling between physical and biological processes (Ragueneau et al. 1996). Del Amo et al. (1997b) suggested that these processes together may be described as a 'silicic acid pump' that—in such a coastal, shallow and well-mixed ecosystem—would act differently than the scenario described by Dugdale et al. (1995) for stratified oceanic waters. The silicic acid pump mechanism restricts the potentially dramatic Si-limiting period and allows diatom production during summer, contrary to stratified deep-water systems, where silicic acid is depleted from the euphotic zone after spring bloom sedimentation (Del Amo et al. 1997b).

Our results suggest that benthic suspension-feeder activity may control the efficiency of this silicic acid pump in the Bay of Brest. We hypothesize that benthic filtration and biodeposition activities would (1) enhance BSi trapping and retention at the sediment-water interface, (2) help BSi dissolution by biological activity (grazing) and (3) control the export rate of BSi towards the open-water ocean and thus the specific composition of secondary phytoplankton blooms in the Bay.

DISCUSSION

Evidence for benthic grazing with seasonal fluctuations

The feeding activity of benthic suspension feeders is highly influenced by the species composition and the intensity of phytoplankton blooms (Beukema & Cadée 1991). Ingestion rate by suspension feeders is usually positively related to cell concentration in the water, up to a critical value (Winter 1977). Previous studies dealing with the Bay of Brest ecosystem (Le Pape 1996, Chauvaud 1998, Chauvaud et al. 1998) have shown that benthic suspension feeders consume only a part of the chlorophyll biomass. The amount of microalgae consumed can be detected when feeding activity of some species, or the whole trophic group, is stopped. With the exception of either toxic events or phytoplankton biomass in excess, the amount of phytoplankton cells in the water column does not limit *Pecten maximus* growth (Chauvaud et al. 1998). In 1994 and 1995, the spring shell growth of Age 1 *P. maximus* restarted synchronously with the first *Thalassiosira* sp.-*Cerataulina* sp. bloom and coincided with maximum food intake (Chauvaud et al. 1998). Over the remainder of 1994, *P. maximus* growth was not limited by low chl *a* concentrations and no competition for food between this species and other suspension feeders was evident (Chauvaud 1998). However, shell growth decreased during the following spring and summer blooms in 1995 (Fig. 9). Reduction in feeding and growth occurred because of toxicity of *Gymnodinium* blooms during June-September 1995, and gill clogging and termination of feeding (Chauvaud et al. 1998) or hypoxia when major *Rhizosolenia delicatula*-*Chaetoceros sociale* blooms developed. However, not all suspension feeders stopped feeding on these diatom

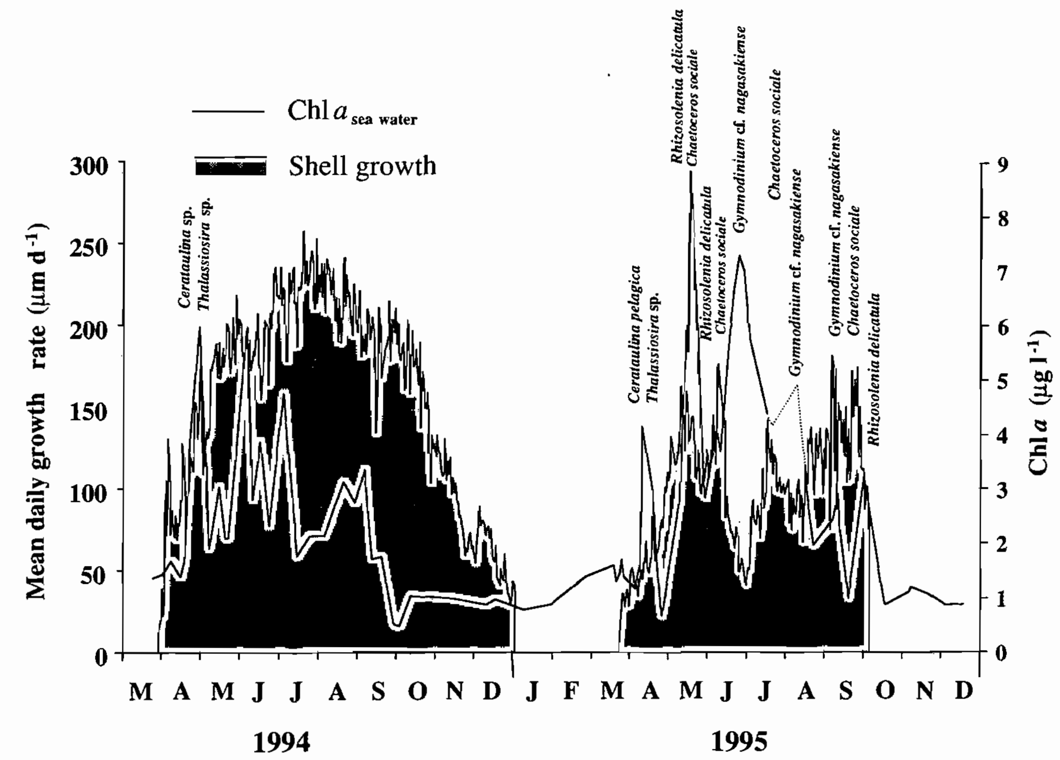

Fig. 9. Chl *a* concentrations (µg l^{-1}) in bottom waters and mean daily growth rates (µm d^{-1}) of Age 1 and Age 2 *Pecten maximus* juveniles (redrawn from Chauvaud et al. 1998). Main phytoplankton species are mentioned according to Nézan et al. (1996)

blooms. The high phaeophytin concentrations recorded in the water column during these events (Fig. 10) may partly result from zooplankton grazing. By contrast, during the *Dinophysis* (1993) and *Gymnodinium* (1995) toxic blooms, the bottom and surface chl *a* concentrations increased while phaeophytin concentrations were lowered (Fig. 10). Such phenomena may indicate that grazing by zooplankton (Poulet et al. 1994, Buskey & Hyatt 1995) and/or benthos (Summerson & Peterson 1990, this study) stopped completely.

Evidence for enhanced BSi retention at the sediment-water interface?

Active pumping and biodeposition by benthic suspension feeders are known to increase the downward particle fluxes near the sediment-water interface. De Vries & Hopstaken (1984) have estimated that, in the Lake of Grevelingen (The Netherlands), biodeposition due to benthic suspension feeders would increase particulate matter fluxes to be 3- to 4-fold greater than those resulting from passive sedimentation. In the Bay of Brest, Barnes et al. (1973) stated that biodeposition by *Crepidula fornicata* and higher architectural complexity within *C. fornicata*

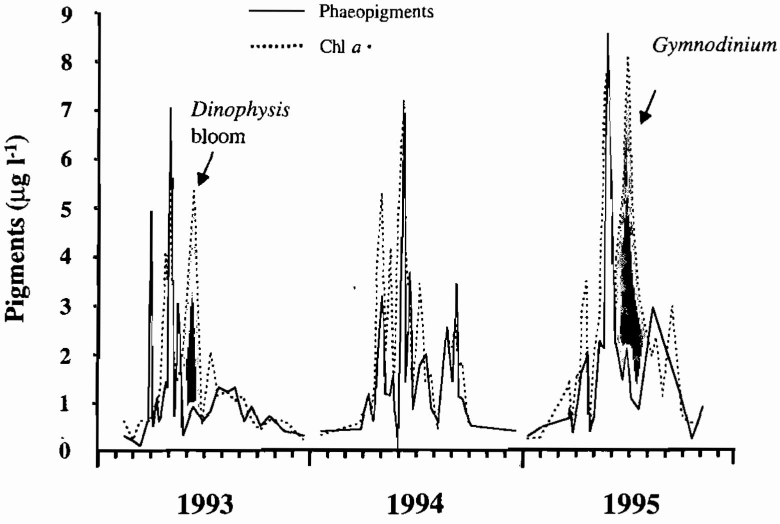

Fig. 10. Phaeophytin and chl *a* concentrations (µg l^{-1}) at Stn R3, 1 m above the bottom. Unusual discrepancies between phaeophytin and chl *a* concentrations (shaded areas) indicate no phytoplankton grazing by zooplankton or benthic suspension feeders

shoals led to siltation of sediment and reduced particle resuspension. *C. fornicata* has been reported to speed up the sedimentation process (Haven & Morales-Alamo 1968, Newell 1979, Hamon & Blanchard 1994), due to active pumping and biodeposit sedimentation rate being faster than that of other suspended matter (Haven & Morales-Alamo 1968, Sornin 1981). Since biodeposits contain ca 22 to 26% organic matter (% DW; Manac'h 1995), biodeposition leads to sediment organic-matter enrichment. In 1995, faeces and pseudo-faeces contained 3.5 ± 1.1 and 4.7 ± 2.4 µg chl *a* g^{-1} respectively (Manac'h 1995), which is higher than the concentrations usually found in upper sediment layers nearby (1 to 2 µg g^{-1}; Riaux 1977, Sagan & Thouzeau 1998). Therefore, *C. fornicata* feeding activities are likely to enhance BSi retention at the sediment-water interface.

Can BSi recycling sustain diatom populations in late spring and summer?

The maintenance of diatom populations in summer implies that the time required for BSi recycling is comparable to the time-scale of phytoplankton succession. The lowest specific rate for BSi dissolution in surface waters has been recorded in Antarctica (3×10^{-4} h^{-1}; Nelson & Gordon 1982, Tréguer et al. 1989, Nelson et al. 1991) corresponding to a BSi residence time of nearly 3 mo. The highest values have been measured in tropical waters (5 to 8×10^{-3} h^{-1}; Nelson & Goering 1977, Brzezinski & Nelson 1989) and correspond to a residence time of ca 5 d. Water temperature in the temperate Bay of Brest usually increases from 10 to 20°C from spring to summer. Disregarding any other factor liable to influence frustule dissolution, the residence time of BSi in the Bay of Brest sediments would be on the order of 1 mo. This pattern is in agreement with the spring Si budget estimated by Ragueneau et al. (1994), and corresponds to the increase of Si recycling from the sediment-water interface with temperature from April to June. Even though BSi reactivity in the sediment may be reduced by many processes involved during early diagenesis (see van Cappellen & Qiu 1997), suspension-feeder activity is most likely to enhance BSi dissolution kinetics by removing the organic matter coating the opal surfaces, just like zooplankton (Miller et al. 1990) and bacteria (Jacobson & Andersen 1986, Bidle & Azam 1999). Thus, the time-scale needed to mineralize BSi seems compatible to sustain diatom secondary blooms. Confirmation of enhanced silicic acid recycling due to benthic grazing can be inferred from a preliminary study conducted during summer 1997: a 2-fold increase of the silicic acid efflux from the sediment-water interface has been measured using a core incubation technique in the southern Basin as *Crepidula fornicata* biomass increases from 300 to 4600 g m^{-2} (WW; unpubl. data).

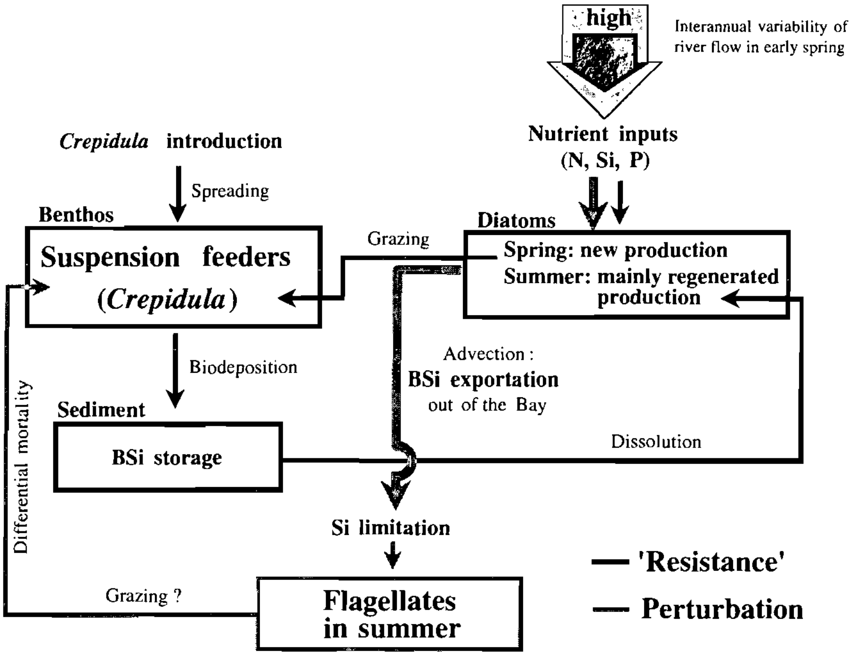

Fig. 11. Synthesis diagram highlighting the role of hydroclimatic conditions and benthic grazing on ecosystem functioning. Interannual variability of fluxes and process intensity is depicted by the variable thickness of arrows

Physical versus biological forcing

From a pelagic point of view, the Bay of Brest seems to be resistant to the potentially negative effects of N enrichment. If several physical, chemical and biological factors can be advanced to explain such a resistance, the distrophy itself is a sign of potential nuisance blooms, as harmful phytoplankton blooms have been observed as a consequence of Si:N distrophy in many coastal areas (reviewed in Smayda 1990). The Bay of Brest would act as a differential filter for nutrients (N exportation vs Si retention) due to its hydrodynamic properties and biological activities. Such characteristics would explain the resistance of the bay to eutrophication of the pelagic system. However, the composition and intensity of secondary blooms would remain under the control of environmental conditions. Two scenarios may occur during the primary production period: (1) low or moderate rainfall (and thus river and nutrient discharges) in early spring would induce diatom-dominated phytoplankton successions in spring and summer similar to those observed in 1993 (e.g. March: *Skeletonema costatum*; April-May: *Thalassiosira* spp.-*Rhizosolenia* spp.; June-September: *Chaetoceros* spp.-dinoflagellates; late September: cryptophyceans; Del Amo et al. 1997b) or in 1981 (Quéguiner 1982). Active filtration by benthic suspension feeders does occur in those cases. (2) Conversely, higher rainfall in early spring would be responsible for high spring phytoplankton biomass inhibiting suspension-feeder food intake either due to excessive food, too many inedible species or hypoxia. In that case, the ecosystem's ability to trap Si would dramatically drop, Si would be exported out of the Bay, thereby allowing dinoflagellates to develop in summer while N concentrations are still sufficient (e.g. in 1995; Fig. 11). It seems therefore evident that changes in the hydroclimatic conditions or in the benthic suspension feeder biomass are likely to influence phytoplankton biomass and species composition.

By contrast, in the absence of toxic blooms a longer primary production period, compared to 20 yr ago, would favour the development of benthic suspension feeders (secondary production) and would explain why zoobenthic communities exhibit increasing biomass in the Bay of Brest. Such increases constitute the first level of disturbance in enriched coastal ecosystems (particulate organic matter enrichment-based disfunction, Type-2 benthic communities; Grall & Glémarec 1997), associated with organic enrichment (Pearson & Rosenberg 1978, Cederwall & Elmgren 1990, Rosenberg et al. 1990). According to Gray (1992), the shallowest macrobenthic communities in the Bay (Daoulas Bay, Caro Cove) show initial symptoms of eutrophication, including a modified species composition (Grall & Glémarec 1997). Thus, the Bay of Brest displays significant disfunctioning at the benthos level.

The variable sensitivity of coastal ecosystems to nutrient enrichment can originate from the qualitative and quantitative variability of benthic systems (Cloern 1996). If benthic suspension feeders partly control phytoplankton biomass, and thus dampen the effects induced by increasing N input, regulation will depend on ecosystem depth, residence time, hydrodynamics and benthic community structure. Due to bottom types, the Bay of Brest benthic fauna is characterised by numerous assemblages with specific trophic structure, diversity and biomass (Hily 1989, Jean 1994, Jean & Hily 1994, Jean & Thouzeau 1995, Chauvaud et al. 1996, Grall et al. 1996, Chauvaud 1998, Thouzeau et al. in press). More than 130 benthic suspension-feeding taxa have been recorded in the Bay of Brest (Grall & Chauvaud unpubl.). Such diversity would allow optimised consumption of pelagic primary producers, whatever the size of phytoplankton cells, and would contribute to the resistance of this ecosystem to eutrophication and toxic events. The proliferation of *Crepidula fornicata*, which is contemporary with increases in N input into the Bay of Brest, may have masked the changes that occurred in the ecosystem's functioning. If the apparent phytoplankton dynamics is the same today as it was 20 yr ago, the system's stability now depends not only on environmental conditions but also on benthic suspension-feeder activity.

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