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Influence of Dissolved Silicate on Vertical Flux of Particulate Biogenic Matter

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The influence of dissolved silicate (DSi) addition on primary production, phytoplankton development and subsequent vertical export of particulate matter was studied in enclosures. Blooms of different phytoplankton communities were initiated in the upper part of 10 m deep enclosures supplied with nitrate and phosphate (NP) and nitrate, phosphate and silicate (NPS). Primary production was 31% higher in the NPS enclosure as compared to the NP enclosure over the experimental period of 27 days. Increased phytoplankton growth was mainly caused by mass development of diatoms in the NPS enclosure. Enhanced growth was accompanied by an increased vertical flux of organic matter (86, 15.9 and 16.9% in terms of chlorophyll, particulate nitrogen and particulate carbon, respectively) and was dominated by diatoms. The present study indicates that for each gram of DSi added, vertical flux was enhanced by 3.6 g C, implying that the ratio of DSi added/carbon exported was close to the Redfield ratio. Thus DSi presence appears to decrease the nutrient turn-over time in the euphotic zone by increasing vertical export. This may improve water quality of the surface layer of eutrophicated environments, but can lead to oxygen depletion of bottom waters. © 1997 Elsevier Science Ltd

The sedimentation of phytoplankton at the end of the spring bloom, is a well-known, recurrent phenomena in most temperate coastal ecosystems (e.g. Wassmann, 1991a). However, the relative contribution of total phytoplankton biomass and taxa to the vertical export of organic matter from the euphotic zone may differ between areas (Smetacek, 1984; Olesen and Lundsgaard, 1995). Often, diatoms dominate among the sedimented phytoplankton cells during periods of new production and in coastal or upwelling areas (Smetacek, 1985; Dugdale *et al.*, 1995). These diatoms sink frequently not as single cells and chains, but as large, rapidly sinking aggregates (Alldredge and Gotschalk, 1989; Kiørboe *et al.*, 1994).

Smetacek (1985) hypothesized that the cause of diatom aggregate formation was a deterioration of living conditions such as nutrient limitation. The aggregation of even simple diatom blooms is, however, complicated as aggregation seems neither linked to nutrient depletion nor to the physiological state of cells in a tank experiment simulating a diatom bloom (Alldredge *et al.*, 1995). Results from a large number of enclosure experiments indicate that the quantitative and qualitative development of a phytoplankton community can be manipulated by the composition of nutrients (e.g. Egge, 1993; Egge and Heimdal, 1994), for example silicate (Egge and Aksnes, 1992). While a diatom bloom will usually come to an end after several weeks, continued DSi addition may give rise to diatom-dominated blooms for longer periods, up to 50 days (Doering, 1989; Egge, 1993). Diatoms are less likely to dominate at DSi concentrations < 2 μM. They aggregate, sink and leave the euphotic zone before phosphate and nitrate become depleted. During sinking and in the upper part of the aphotic zone they take up DSi continuously (Rey and Skjoldal, 1986) and often form resting spores (e.g. Pitcher, 1986). The remaining nutrients in the euphotic zone are then used by non-DSi demanding phytoplankton species, such as flagellates, *Phaeocystis* sp., dinoflagellates and coccolithophorids.

Eutrophication in coastal waters such as the North Sea, the Skagerrak-Kattegat area and some Norwegian fiords is characterized by substantial additions of P and N while the supply of DSi is more or less constant or subjected to natural run-off patterns (Bennekom and Salomons, 1981; Skjoldal, 1993). There is also a tendency for DSi supply to the sea to decrease over time in many eutrophied rivers (Turner and Rabbalais, 1994). This is explained by increased growth of freshwater diatoms in the river due to increased N and P concentration and subsequent sedimentation of diatoms beyond dams. Scenarios where the relative concentration of DSi is decreased favours the growth of non-DSi dependent forms such as flagellates. The resulting change in phytoplankton species composition results in increased residence times of the phytoplankton-derived organic matter in the upper layers because

aggregate formation and the relative contribution of rapidly sedimenting diatom blooms decreases. DSi obviously plays an important role for eutrophication as emphasized by Officer and Ryther (1980) and Conley *et al.* (1993).

How does DSi availability influence the vertical export of phytoplankton-derived carbon? While the total annual export of carbon to the aphotic zone can be relatively well predicted from annual primary production rates in coastal areas of the North Atlantic (Wassmann, 1990), the relation between daily carbon export and primary production rates is not well understood. Generally, diatoms have a greater growth potential compared to other phytoplankton groups (Furnas, 1990). In order to realize this high growth potential, however, DSi is required. The common sequence of dissolved silicate-diatoms-aggregation suggests that vertical flux will increase with increased silicate availability (Fig. 1). When N and P is sufficient, but DSi availability is low, vertical flux is assumed to be lower and based on phytoplankton forms which do not demand silicate, such as flagellates. With increasing DSi addition vertical carbon export is assumed to increase. Under conditions of very high DSi availability, diatoms will be limited by other growth factors and the vertical export will thus reach a maximum (Fig. 1).

Many *in situ* observations of aggregate formation and the sinking of phytoplankton cells exist, but experimental evidence from mesocosms (Keller and Riebesell, 1989; Alldredge and Jackson, 1995) and the sea have been carried out lately (Riebesell, 1991a,b; Kiørboe *et al.*, 1994). Experience from the laboratory (e.g. Kiørboe and Hansen, 1993) is not easily applied *in situ*. To improve the understanding of how DSi influences the vertical export of biogenic matter we designed an experimental mesocosm facility where environmental conditions are closer to those found *in situ*. The mesocosms had a mixed upper layer and a stagnant lower layer. Nitrate and phosphate was added to one enclosure, while nitrate, phosphate and silicate was added to a second one. The goal of the investigation was to investigate *1.* the effectiveness of the mesocosm design for experimental studies of nutrient addition and vertical flux, *2.* how vertical flux of biogenic matter would change due to addition of silicate, and *3.* what were the relationship between carbon exported and silicate added.

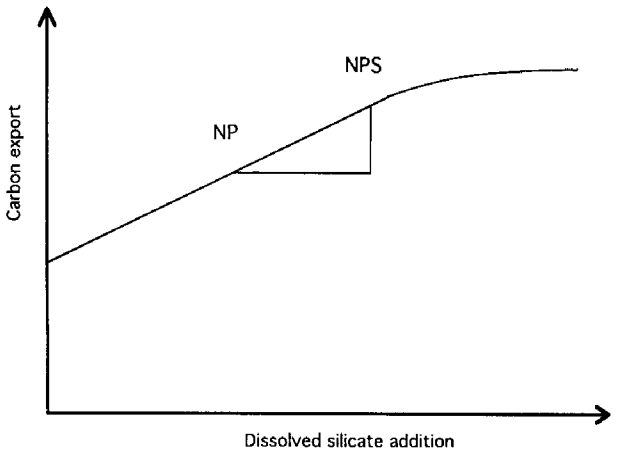

Fig. 1 Theoretical relationship between silicate availability and vertical carbon flux. The relationship is based on the assumption that dissolved N and P is available in non-limiting concentrations while DSi is added in increasing amounts. The vertical export of carbon increases along with the DSi addition until phytoplankton growth becomes limited by other factors for example light. The experiment investigates the increase of vertical carbon export as a derivative along the interval DSi (NP) and DSi (NPS).

Materials and Methods

The mesocosm experiment was carried out between May 13 and June 9, 1994 at the Marine Biological Field Station, close to Bergen, Norway. The enclosures were secured to the southern side of a raft with a floating laboratory (Fig. 2A). The two enclosures presented here were a part of a larger experiment that included 6 enclosures. Each enclosure had a diameter of 2 m, a depth of 10 m, and a volume of 27 m^3 (Fig. 2B). The enclosures were made of polyethylene with 90% light transmission (PAR), and were open to the atmosphere. They were filled by water from 40 m depth. Non-poisoned, gimballed sediment traps with replicate cylinders (heights 450 mm, diameter 74 mm) were placed in the centre of the enclosure at 9 m depth (Fig. 2B).

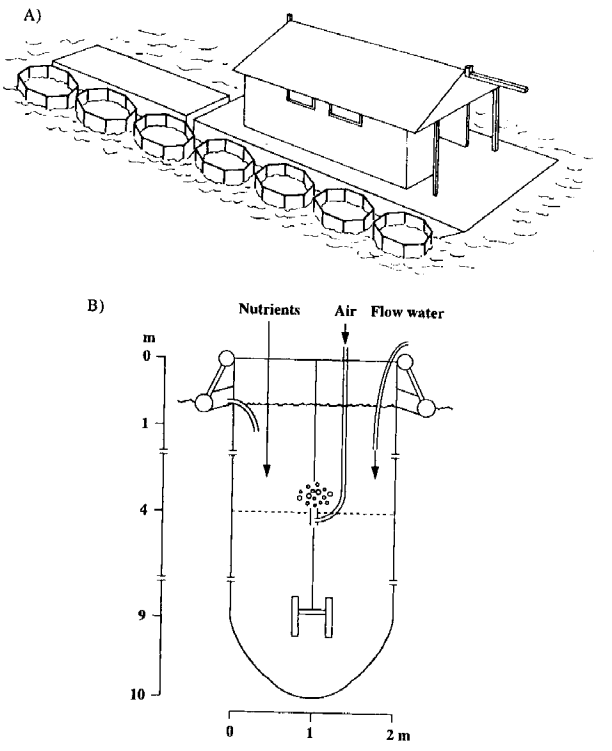

Fig. 2 The floating research laboratory (A) and the enclosures and their construction (B).

In order to generate stratification inside the enclosures, seawater with lower salinity was supplied on top of more dense water. This top layer was renewed continuously. Water was pumped from 1 m depth outside the enclosures, into a tank on the raft, and then into the enclosures. The volume of the renewing water corresponded to 10% of the volume in the upper 4 m of the enclosures per day. The upper 4 m of the enclosures were kept homogeneous using an air lift, while there was no stirring in the lower part of the enclosures (Fig. 2B). Excess water left the enclosures through a small hole in the enclosure wall just below the seawater surface.

The initial water in the two enclosures contained some nutrients (nitrate, phosphate, silicate at 8.0, 0.7, 3.9 μM, respectively), but additional nutrients were supplied to the upper 4 m of both enclosures. One enclosure was supplied with nitrate and phosphate (NP), while the other was supplied with nitrate, phosphate and silicate (NPS). Both enclosures were initially supplied with nitrate and phosphate corresponding to 5 μM and 0.4 μM, respectively. In addition silicate corresponding to 3 μM was supplied to the NPS enclosure. These initial nutrients were supplied on May 14. As 10% of the volume (upper 4 m) was renewed daily from May 16, additional nutrients were supplied to correspond for the loss. 20% of the initial supply of nutrients was supplied every second day to the enclosures at 12.00 h. Due to bright sunlight and favourable growth conditions for phytoplankton additional nutrients corresponding to the initial supply were also added on May 20.

Surface irradiance was measured continuously in close proximity to the enclosures and stored as average values every 10 min in a Li-Cor, Li-1000 data logger. Irradiance attenuation in the enclosures was measured with a 4 π collector (Biospherical Instruments Inc.). Other samples were taken and measurements carried out every second day at 09.00 h. Salinity (PSU) and temperature (°C) were measured daily with a salinotherm (Salinity Temperature Bridge Type M.C.5).

Water samples were collected at 2, 6 and 8 m depth every second day. Analysis of nitrate, phosphate and silicate was conducted on freshly collected samples using a Skalar auto analyser. Samples for suspended particulate chlorophyll *a* (Chl *a*), phaeopigments (Phaeo), carbon (PC) and nitrogen (PN) were filtered onto pre-combusted glass fibre filters (Whatman GF/F) and immediately frozen. The sediment traps were also retrieved every second day. The content of each cylinder along with its 1.7 l of seawater was collected and thoroughly mixed before subsampling. Duplicate subsamples were taken from each cylinder for the determination of Chl *a*, Phaeo, PC and PN. Swimmers were, as far as possible, carefully removed with forceps to prevent zooplankton contamination. PC and PN were analysed a Leeman Lab 440 and Carlo Erba elemental analyser (Wassmann, 1991b). Chl *a* and Phaeo were analysed according to Holm-Hansen *et al.* (1965) using a Turner Design fluorometer.

Primary production was measured using the ^{14}C method according to Steeman-Nielsen (1952) and Gargas (1975). The samples were incubated *in situ* at 2, 6 and 8 m depth between 10.00 and 14.00 h in the centre of the enclosures and after the incubation immediately filtered onto Sartorius filters (0.45 μm). The filters were frozen and subsequently counted in a Pacard Tri-carb, 1900 CA Liquid Scintillation Analyser.

Identification and counting of phytoplankton and faecal pellets (from sediment traps only) was carried out on water column and sediment traps samples preserved with buffered formaldehyde (final concentration 0.4%) using the sedimentation method of Utermöhl (1931). Phytoplankton was individually identified to species if possible, otherwise they were identified to genus.

Integration of nutrients, suspended biomass and primary production were made on the assumption that the measurements at 2 m are representative for the mixed upper 4 m. The measurements at 6 and 8 m depth are assumed to be representative for the 4–7 m and 7–9 m depth intervals, respectively. Budget estimates of nutrient consumption during the entire experimental period ($S_{consumed}$) were obtained according to the following expression:

$$S_{consumed} = S_{start} - S_{end} + S_{add} + S_{in} - S_{out} \qquad (1)$$

where S_{start} is the amount of nutrient (silicate, nitrate or inorganic orthophosphate) in the enclosure on May 14 (start of the experiment), S_{end} is the amount on June 7 (end of the experiment), S_{add} is the amount added to the enclosures, S_{in} is the amount supplied with the intake water, and S_{out} is the amount leaving the enclosure through the outlet. The S_{out}-estimates are based on daily measurements of the nutrient concentration measured in the mixed layer of the enclosure and the flow rate (1 m^3 d^{-1}). Correspondingly, S_{in} was based on flow rate and nutrient concentrations of the intake water.

Results

Hydrography and nutrients

The salinity in the enclosures was approximately 33 PSU at the start of the experiment and the water in the enclosures was homogeneous with respect to salinity (Fig. 3). The renewal of surface water gave rise to increasing stabilization and the salinity decreased slowly to 30.7 in the upper mixed layer. Salinity remained more or less constant at 6 and 8 m depth. Haline stratification was established after May 16, while the temperature remained vertically homogeneous (data not shown). The temperature variations in the enclosures were small at any depth during the experiment. The salinity and temperature differences between the NP and NPS enclosures were negligible. Maximum temperature

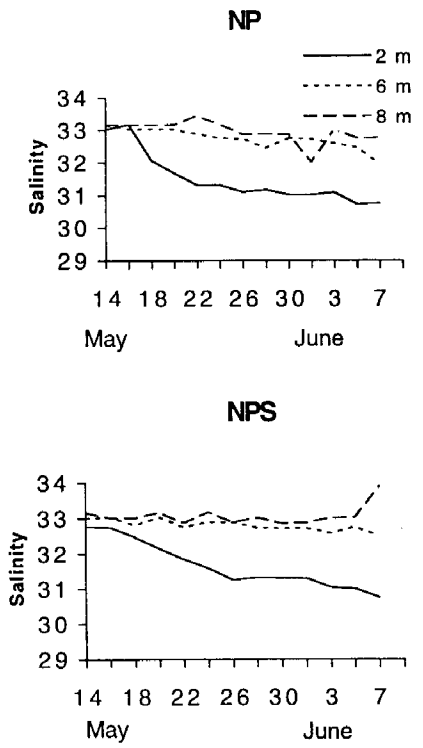

Fig. 3 Salinity at 2, 6 and 8 m depth in the NP and NPS enclosures during the experiment. The salinity at 2 m depth in the sea outside the enclosures varied between 28.93 to 32.67 during the experiment.

(11.3°C) was observed at the end of the fair weather period (May 24), while a minimum (7.3°C) was measured at 8 m at the start of the experiment.

The initial concentrations of nitrate, phosphate and silicate were relatively high (6–8 μM, 0.5–0.7 μM and 3–3.8 μM, respectively), with no significant differences between the NP and NPS enclosures (Fig. 4). All nutrients at 2 m had declined to low levels by May 22 in both treatments, with nitrate concentrations below 0.1 μM. On May 28 the nutrient concentrations below the mixed layer had also decreased to low levels. Silicate concentrations remained < 2 μM and phosphate concentrations < 0.25 μM in both enclosures throughout the experiment. Nitrate concentrations remained < 0.1 μM, except for a temporarily increase in both enclosures on May 30.

Irradiance and primary production

From the onset of the experiment, May 14, and until May 29 the weather conditions were characterized by high and stable irradiance (Fig. 5). The average irradiance during this period was 38.3 mol m^{-2} d^{-1}. In the second half of the experiment, from May 30 to June 9, average irradiance decreased to 16.2 mol m^{-2} d^{-1}.

There was some similarity in primary production rates and time variation was encountered at the three depths in the NP and NPS enclosures (Fig. 6). The bloom started on May 18 and reached its maximum on May 22 in the turbulent layer in both NP and NPS with primary production rates of 54 and 65 mg C m^{-3} h^{-1}, respectively. Primary production fell to low or moderate levels after May 24. At 6 and 8 m depth the variation in primary production was low in both enclosures, never exceeding 11 mg C m^{-3} h^{-1}. Integrated primary production during the entire experiment was 31% higher in the NPS compared to the NP enclosure.

While carbon fixation was far higher in the NPS enclosure, the consumption of N and P did not indicate major differences between the NP and NPS treatments (Table 1). The consumption of DSi was of course much higher in the NPS enclosure. This gave rise to large differences in the C-fixation/DSi-consumption, C-fixation/N-consumption and C-fixation/P-consumption ratios between the NP and NPS treatments (−37%, +60% and +39%, respectively; Table 1).

Suspended biomass and phytoplankton composition

The development of the suspended Chl *a* concentration in the NP and NPS enclosures is shown in Fig. 7 (upper panel). Phytoplankton biomass started to accumulate at all depths mainly on May 18 and decreased to low concentrations at all depths between June 3–5. The maximum Chl *a* concentrations in the NPS enclosure (ranging between 7–15 mg m^{-3}) were 1.4 to 2.1 higher at all depths compared to those of the NP enclosure (ranging between 7–9 mg m^{-3}). The suspended Chl *a* concentrations in the NP enclosure were relatively variable and distinct maxima were not encountered. In the NPS enclosure, however, distinct maxima were encountered at June 1, May 24 and May 24–26 at 2, 6 and 8 m depth, respectively.

The development of the suspended concentration of PC in the NP and NPS enclosures is shown in Fig. 8, upper panel. The variation of suspended PC in the NP enclosure was smaller compared to the NPS enclosure where the concentration were particularly high, but

TABLE 1

Sedimentation, carbon fixation and nutrient consumption during the experimental period (27 days). Nutrient consumption were estimated according to Eq. (1).

	NP-enclosure	NPS-enclosure	NPS-NP
C-fixation (g C m^{-2})	13.1	19.0	5.9
DSi-consumption (g DSi m^{-2})	0.66	1.51	0.85
N-consumption (g N m^{-2})	1.49	1.35	−0.14
P-consumption (g P m^{-2})	0.23	0.24	0.01
C-fixation/DSi-consumption (a:a)	46.3	29.4	
C-fixation/N-consumption (a:a)	10.3	16.4	
C-fixation/P-consumption (a:a)	85.4	118.8	
C-sedimentation (g C m^{-2})	13.7	16.8	3.1
N-sedimentation (g N m^{-2})	2.0	2.5	0.5
Chl *a* sedimentation (mg Chl *a* m^{-2})	28.7	53.4	24.7
C-sedimentation/N-sedimentation (a:a)	7.99	7.84	
C-sedimentation/Chl *a* sedimentation (w:w)	478	315	

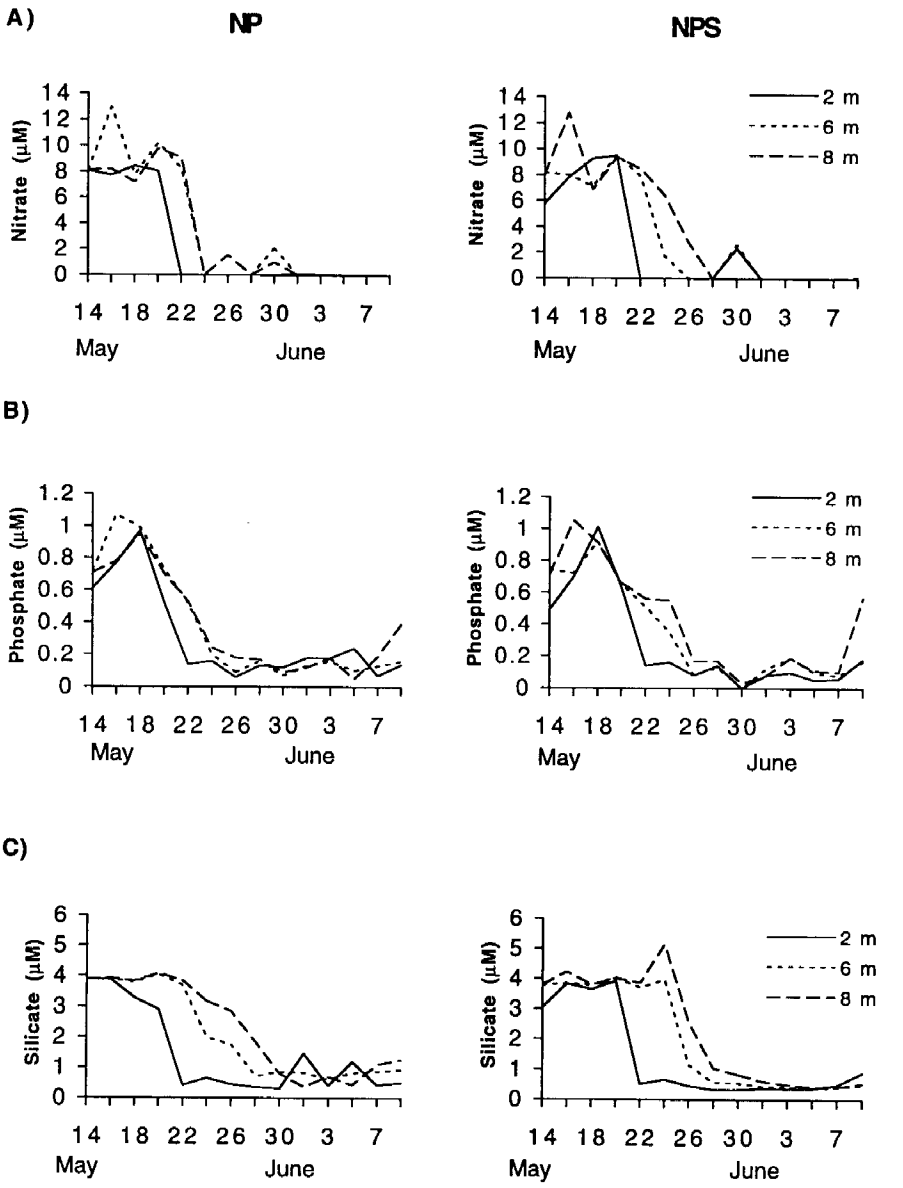

Fig. 4 Nitrate, phosphate and silicate concentrations (µM) at 2, 6 and 8 m depth in the NP and NPS enclosures during the experiment, a, b and c, respectively. The nitrate, phosphate and silicate concentrations at 2 m depth in the sea outside the enclosures varied between below detection limit to 1.5, 0.06 to 0.17 and 0.75 to 1.33 µM, respectively during the experiment.

variable at 2 m depth. PC maximum concentrations were recorded on May 26 and June 1 in the NP and on May 28 while in the NPS enclosure. The maximum concentration in the NPS enclosure were twice as high compared to the NP enclosure.

The phytoplankton cell numbers were low in both enclosures when the experiment started. The phytoplankton community consisted mainly of flagellates between 5 and 10 µm in diameter at both 2 and 8 m depth (Fig. 9). A maximum flagellate concentration of about 3.4×10^6 cells l^{-1} was observed at 2 m depth on May 22. In general, the NP enclosure had higher flagellate concentrations compared to the NPS enclosure. The *Phaeocystis* sp. maximum (colonial stage) was recorded on May 22 with 2.2×10^6 and 2.5×10^6 cells l^{-1} in the NP and NPS enclosures, respectively. In Fig. 9 *Phaeocystis* has been grouped together with flagellates and accounted for 10 to 70% of the flagellate community.

As for flagellates in general, the highest abundance of the coccolithophorid *Emiliania huxleyi* was observed in the NP enclosure. *Emiliania huxleyi* started to increase in numbers in the second half of the experiment and maximum cell numbers, 3.7×10^6 cells l^{-1}, were observed at 2 m depth on June 9 (Fig. 9). An increase was also observed in the NPS enclosure towards the end of the experiment, but the cell numbers were always lower than 1.6×10^6 cells l^{-1}. The abundance of *E. huxleyi* in

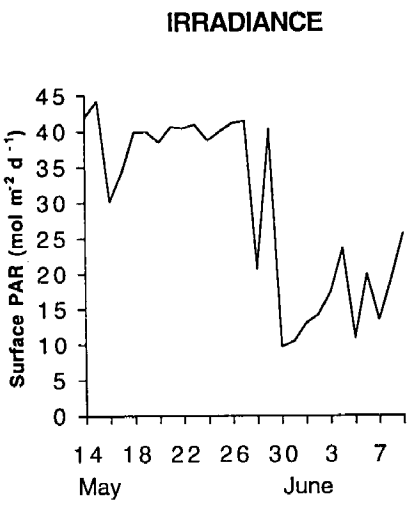

Fig. 5 Surface PAR (mol m^{-2} d^{-1}) during the experiment.

the surrounding seawater also increased during the experiment. The concentration varied between 5.0×10^4 cells l^{-1} to the highest concentration observed, 2.3×10^6 cells l^{-1} on June 3.

The highest concentration of diatoms was observed in the NPS enclosure. The dominating diatom species was *Skeletonema costatum*, which constituted between 70 and 90% of cell numbers. In the NP enclosure diatom abundance never reached concentrations higher than 0.9×10^6 cells l^{-1}, while the highest diatom concentrations in the NPS enclosure were twice as high, 2.1×10^6 cells l^{-1}.

Dinoflagellates were observed in concentrations less than 1000 cell l^{-1} before May 22. From this date dinoflagellates increased in number reaching maximum concentrations between $5–10\times10^4$ cells l^{-1}. In the sea outside the enclosures low cell numbers were recorded during the entire experiment. In addition to *E. huxleyi* which was mentioned earlier, diatoms, *Phaeocystis* sp. and flagellates were observed in the sea outside the enclosures in concentrations between $0.1–0.6\times10^6$, $02–0.9\times10^6$ and $0.1–1.5\times10^6$ cells l^{-1}. respectively.

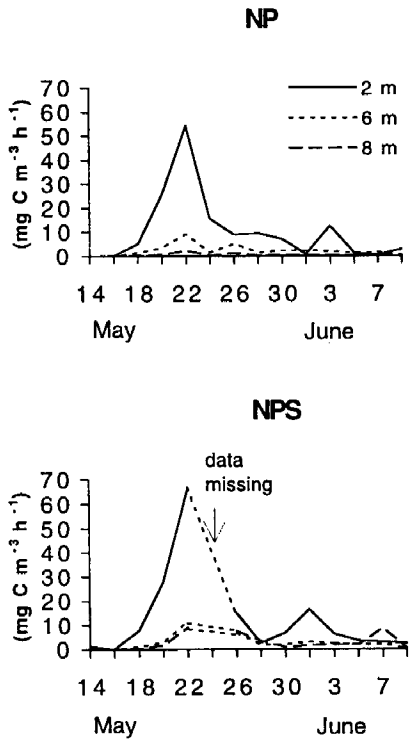

Fig. 6 Primary production (mg C m^{-3} h^{-1}) at 2, 6 and 8 m depth in the NP and NPS enclosures during the experiment. The primary production in the sea outside the enclosures varied between 2–11 mg C m^{-3} h^{-1}, with an average of 6.2 mg C m^{-3} h^{-1} during the experiment.

Sedimentation of organic matter, phytoplankton and faecal pellets

The vertical flux of Chl *a* in the NP and NPS enclosures is shown in Fig. 7 (lower panel). Vertical flux was low in both enclosures until May 20, followed by distinct differences in vertical Chl *a* flux in the two enclosures. Chl *a* sedimentation was obviously more variable in the NPS enclosure, giving rise to a distinct maximum of >20 mg Chl *a* m^{-2} d^{-1} on May 28. The Chl *a* sedimentation in the NP enclosure was always lower than 5 mg Chl *a* m^{-2} d^{-1}. The vertical flux of phaeopigments (data not shown) were of the same magnitude as Chl *a* and were higher than the vertical Chl *a* fluxes in both enclosures after May 30. The integrated Chl *a* sedimentation rate in the NPS enclosure was 46% higher compared to the NP enclosure (Table 1). Both treatments resulted in high PC/Chl *a* ratios, implying that detritus comprised a large part of the vertical export.

The vertical flux of PC in the NP and NPS enclosures was different to those of Chl *a* and are presented in the lower panel of Fig. 8. The sedimentation rates in both enclosures were low until May 22. A broad and distinct maximum in PC sedimentation of more than 2.1 g C m^{-2} d^{-1} was recorded during May 26–28 in the NPS enclosure, followed by reduced fluxes of about 1.2 g C m^{-2} d^{-1} for the rest of the experiment. The variation in the PC sedimentation rate in the NP enclosure was similar to the NPS enclosure, but the maximum was lower (about 2.0 g C m^{-2} d^{-1}) and more narrow. The integrated PC sedimentation rate for the whole experimental period in the NPS enclosure was 18% higher compared to the NP enclosure (Table 1). Both treatments exported organic matter with a PC/PN ratios slightly higher than the Redfield ratio (Table 1).

The vertical loss rates of suspended PC ranged widely between about 4–36 and 5–70% d^{-1} (about 18 and 20% d^{-1}, on average) in the NP and NPS enclosures, respectively. Similar daily, average loss rates were observed for suspended Chl *a* with about 18 and 19% d^{-1}, indicating substantial vertical loss of phytoplankton-derived organic matter during the experiment.

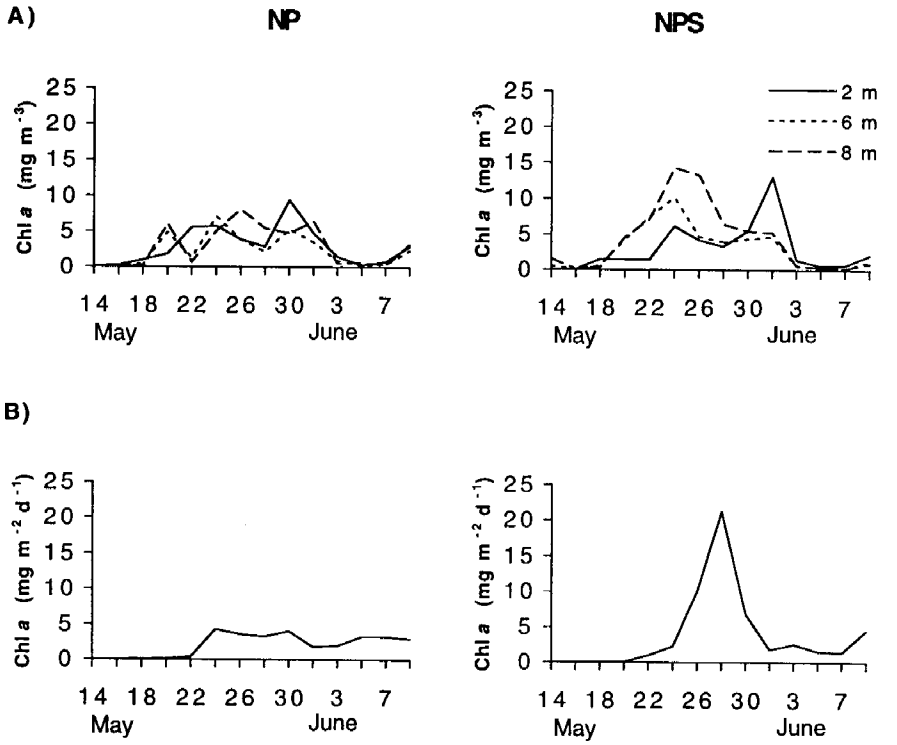

Fig. 7 Suspended chlorophyll a (Chl *a* mg m^{-3}) at 2, 6 and 8 m depth in the NP and NPS enclosures during the experiment (above). The suspended Chl *a* concentrations at 2 m depth in the sea outside the enclosures varied between 1.0 and 4.8 mg m^{-3} during the experiment. Chl *a* sedimentation rate (mg m^{-2} d^{-1}) at 9 m depth in the NP and NPS enclosures during the experiment (below).

The vertical flux of phytoplankton cells was similar to that of PC and PN, with low rates in both enclosures when the experiment started (lower panel in Fig. 9). Diatoms and 5–10 µm large flagellates (including *Phaeocystis* sp.) dominated the vertical flux. Dinoflagellates and *E. huxleyi* did play a minor role in vertical flux with maximal rates never exceeding 5×10^9 and 0.4×10^9 cells m^{-2} d^{-1}, respectively. Between May 30 and June 3 maximum vertical flux rates of about 1.5×10^{10} and 1.8×10^{10} diatom cells m^{-2} d^{-1} were recorded in the NP and NPS enclosures, respectively. Maximum sedimentation rates of flagellates were similar to that of diatoms in the NP enclosure, but lower in the NPS enclosure (1.0×10^{10} cells m^{-2} d^{-1}). The differences between the suspended and vertical flux phytoplankton group composition clearly indicates *1.* the time lag between a phytoplankton bloom and its subsequent sedimentation, and *2.* that flagellates, although numerically dominant in the upper layers, do not contribute equivalently to the vertical flux.

The dominating diatom species among the sinking cells were *Skeletonema costatum* and *Chaetoceros* sp. Dominating among the flagellates were *Phaeocystis* sp., both single cells as well as whole colonies. The majority of free flagellates in the traps were probably due to collapsed *Phaeocystis* sp. colonies. Only a few diatom resting spores were observed in the traps. The vertical flux rates of faecal pellets were moderate throughout the experiment with maximum rates of 2.6×10^9 and 2.0×10^9 pellets m^{-2} d^{-1} during the phytoplankton flux maximum in the NP and NPS enclosures, respectively. This indicates that meso-zooplankton grazing was moderate throughout the experiment and that faecal pellet flux was probably part of the phytoplankton aggregates giving rise to increased vertical flux along with the phytoplankton cell flux.

Discussion

Experimental set-up

The experimental set-up developed for this study derived from former investigations of manipulation of phytoplankton succession by macro nutrients and phytoplankton species succession (Egge and Aksnes, 1992; Egge, 1993; Egge and Heimdal, 1994; Aksnes *et al.*, 1995). The set-up proved suitable to address the question of how vertical flux of biogenic matter is regulated by macro nutrient availability and composition. Most of the primary production took place in the 4-m deep, mixed surface layer where the nutrients were added. Phytoplankton-derived biomass accumulated there and subsequently also in the stagnant water column below the mixed layer. The assemblage of phytoplankton species during the bloom, the pattern of

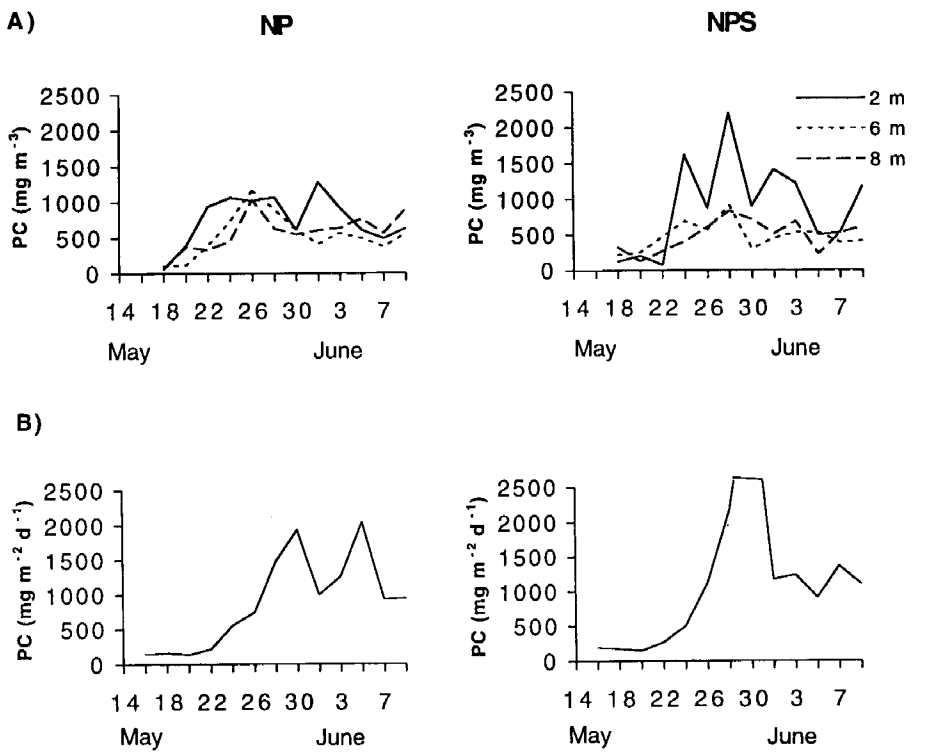

Fig. 8 Suspended particulate carbon (PC) concentration (mg m^{-3}) at 2, 6 and 8 m depth in the NP and NPS enclosures during the experiment (above). The suspended PC concentrations at 2 m depth in the sea outside the enclosures varied between 300 and 1400 mg m^{-3} during the experiment. PC sedimentation rate (mg m^{-2} d^{-1}) at 9 m depth in the NP and NPS enclosures during the experiment (below).

the bloom development and the subsequent vertical export of phytoplankton and phytodetritus were similar to vernal blooms studied during field investigations in relatively shallow Norwegian fjords (e.g. Wassmann, 1991a; Riebesell *et al.*, 1995) and other coastal environments (e.g. Hargrave and Taguchi, 1978; Peinert *et al.*, 1982; Laws *et al.*, 1988; Olesen and Lundsgaard, 1995). While the patterns and daily loss rates of suspended matter through vertical export in the present experiments were similar to *in situ* observations, the absolute rates were up to two times higher than maximum rates recorded in coastal environments. This was probably caused by the fact that *1.* nutrients were supplied into the upper 4 m of the water column without significant dilution, and that *2.* euphotic zones with a nutrient rich, mixed upper and a stagnant layer below as well as constant nutrient supply are rare in nature.

A quantitative comparison of primary production, nutrient consumption and the export of organic matter in the experimental set-up is not straight forward. The form of the enclosures, the relative movement of the PVC walls, growth on the walls and the position of the sediment traps in the lower end of the enclosures (Fig. 2B) implies focusing of sinking organic matter in the lower centre. As compared to the area of primary production in the upper layer, vertical export is probably overestimated. Consequently, the export of PC and PN was as high or even higher then the total C fixation and N consumption (Table 1).

Differences between the two enclosures

All three biomass measures (Chl *a*, PN, PC) indicated increased sedimentation in the NPS-experiment compared to the NP experiment (Table 1). This increase in sedimentation by adding DSi was 86, 15.9 and 16.9% in terms of Chl *a*, PN and PC, respectively. Diatoms of the genus *Skeletonema costatum* and *Chaetoceros*, sp. dominated the vertical flux and the high Chl *a* value is consistent with the fact that diatoms have a high Chl *a* content (Furnas, 1990). Hence, the idea that increased DSi availability is likely to promote increased diatom dominance, and thereby increased sedimentation, is supported by the present experiment. It should be noted, however, that the NP-experiment was not devoid of diatoms (Fig. 9). Dissolved silicate was initially present and also supplied with the intake water in small quantities during the experiment. Hence, we estimated a DSi consumption of 0.66 g Si m^{-2} in the NP compared to a value of 1.51 g Si m^{-2} in the NPS-experiment (Table 1). It is likely that the sedimentation regimes of the two enclosures would have differed more if the DSi

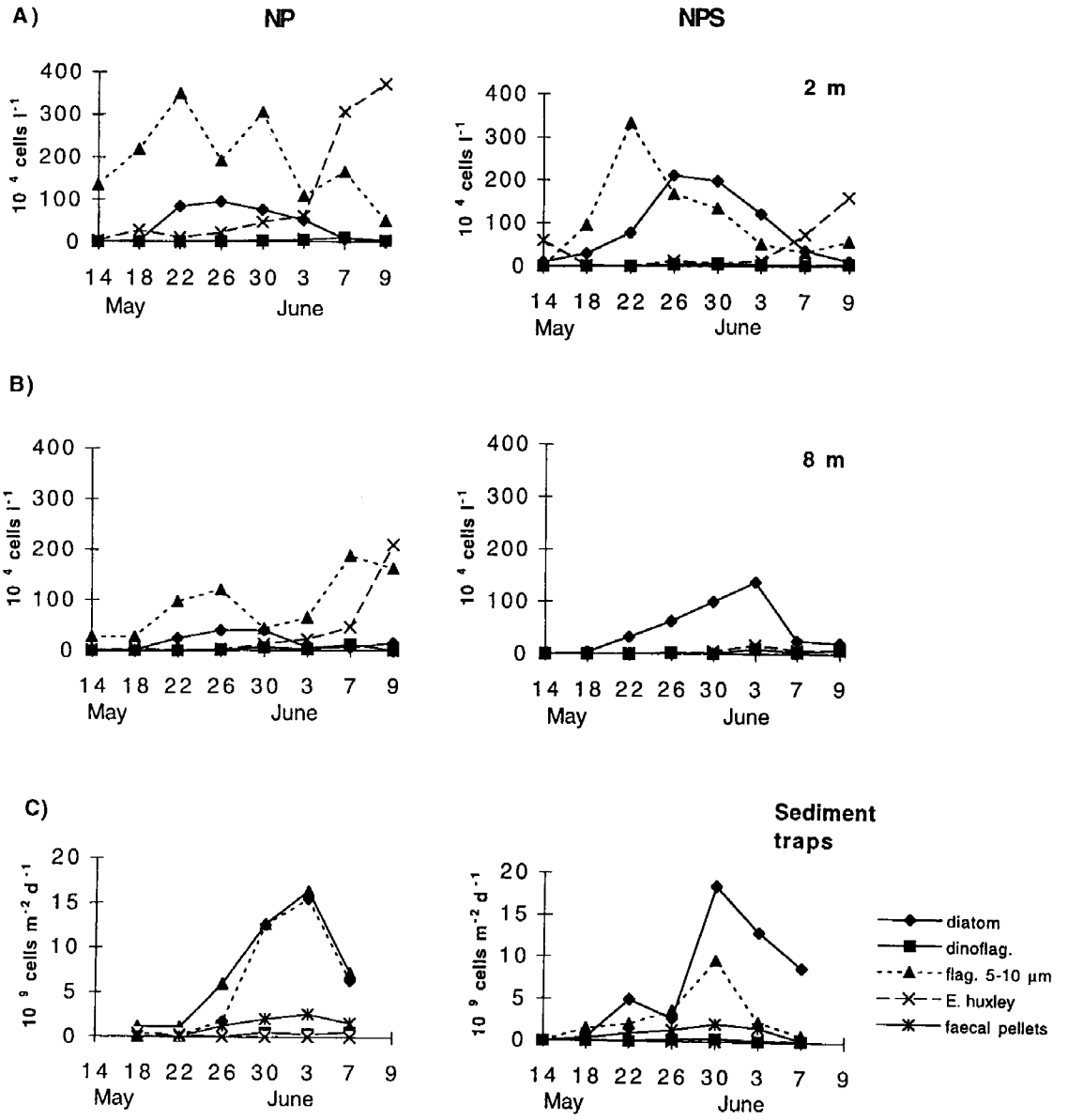

Fig. 9 Suspended concentration of diatoms, dinoflagellates, flagellates and *Emiliania huxleyi* (10^4 cells l^{-1}) at 2 and 8 m depth in the NP and NPS enclosures during the experiment (upper two panels). Sedimentation rate of diatoms, dinoflagellates, flagellates, *Emiliania huxleyi* and faecal pellets (10^9 cells or pellets m^{-2} d^{-1}) at 9 m depth in the NP and NPS enclosures during the experiment (lower panel).

availability in the two enclosures had been more contrasting. This is indicated in the hypothetical relationship of Fig. 1, which suggests that a DSi load will have a larger effect on vertical flux of organic matter in systems characterized by low DSi availability. Nevertheless, based on our experiments, the effect of DSi on vertical carbon flux can be estimated as the ratio:

$$DC_{sed}/DSi_{consumption} = (C_{sedNPS} - C_{sedNP})/(Si_{consumptionNPS} - Si_{consumptionNP}) \quad (2)$$

This ratio corresponds to the derivative of the relationship suggested in Fig. 1 at some place to the right of the x-axis. Based on the values provided in Table 1 we obtain an estimate $DC_{sed}/DSi_{consumption} = 3.1$ g C $m^{-2}/0.85$ g Si $m^{-2} = 3.6$ g C/g DSi (PC:DSi = 8.4). Thus, it is indicated that for each gram of silicate added the vertical flux is enhanced by 3.6 g C which is close to the Redfield ratio (PC:DSi = 7.1). Having in mind that vertical export of PC is slightly overestimated we conclude that export production under moderate DSi addition is determined by the Redfield ratio. This conclusion is also supported

by Brezinski (1985) who reported a PC:DSi ratio of 7.7 for marine diatoms. The relationship between DSi added and carbon exported (Fig. 1) seems thus to be linear to the left of the NP-NPS position of the present experiment, i.e. vertical export of C is regulated by the Redfield ratio in the lower range of the DSi addition. Correspondingly, for nitrogen we find that for each DSi added the increase in vertical N-flux is 0.6 g N which corresponds to a C/N ratio of 6.14, i.e. close to the Redfield ratio. More experimentation,(however, is needed in order to see to what extent these ratios depend on the actual location on the x-axis in Fig. 1.

Eutrophication and silicate

Marine environments may contribute to increased carbon sequestration from the atmosphere, for example by eutrophication. However, the extent to which human intervention to fertilize the oceans can increase carbon fixation and sequestration remains a matter of speculation (Wassmann and Wong, 1995) as the role of the ocean for increased carbon sequestration seems rather limited compared to the present level and rate of increase of CO_2 in the atmosphere. Altered, relative nutrient concentrations in eutrophicated ecosystems result in changes in species composition, changes in food web dynamics and altered nutrient-recycling processes. This is also true for silicate (Conley *et al.*, 1993). For eutrophication the role of silicate has been much less frequently studied than that of N and P. While additions of N and P generally increases algal biomass, the decreasing, relative contribution of DSi limits an analogous increase in diatom growth. Increased phytoplankton biomass due to eutrophication is, therefore, frequently caused by non-silicate demanding forms such as flagellates, which do not rapidly sediment. Many of the flagellated forms are toxic. Recent analyses of toxic algae blooms in the North Sea and Skagerrak area suggest that the proliferation of these species might have been caused by nutrient addition in general, but also by changes in the relative nutrient availability (Skjoldal, 1993; Aksnes *et al.*, 1995) and lack of silicate in particular. Along with the general increase in suspended biomass caused by eutrophication, the effects of the anthropogenic modification of the silica biogeochemical cycle have far-reaching consequences for temperate marine ecosystems, since DSi availability effects algal species composition and pelagic-benthic coupling (Conley *et al.*, 1993).

The results of the present investigation indicate that moderate DSi addition increased vertical carbon export by about 18% (Table 1) and reduced the residence time of phytoplankton in the upper layers. The decreased residence time of phytoplankton-derived biomass in the euphotic zone is probably caused by aggregate formation during diatoms blooms and the subsequent increase in sinking speed and bulk sedimentation (Smetacek, 1985; Passow *et al.*, 1994). Addition of DSi, favouring diatom growth, could be one strategy to decrease the effect of eutrophication in surface waters. This would remove suspended biomass and essential nutrients from surface layers and increase their supply to the benthos. A thorough investigation of the DSi addition vs vertical carbon export relationship characterized in Fig. 1 could be the instrument to regulate and control this manipulation. How will such management practises effect coastal marine environments?

Traditional reasoning implies that the negative consequences of eutrophication, such as increased suspended biomass, decreased transparency and the development of toxic algae, are minimized by *reduction* in nutrient supply. At present low DSi discharge, as compared to N and P, characterize all eutrophicated environments, giving rise to high suspended biomass, low vertical export and proliferation of potentially toxic algae. However, silicate *addition* to nutrient discharge would result in a more balanced N/P/Si ratio, a more natural phytoplankton community, and hence to increased diatom growth, increased vertical flux and hopefully less potential toxic algae. Silicate addition may be an interesting alternative method to reduce the negative consequences of eutrophication in marine surface waters. Diatoms are often the preferred food of herbivorous zooplankton and therefore increase the potential food resources of commercially important pelagic fish. For example, the worlds largest protein production per unit area, the cultivation of blue mussels in the rias of Gallicia, northern Spain, is mainly based on extensive diatom growth caused by large-scale upwelling during spring and summer (Blanton *et al.*, 1987; Alavarez-Salgado *et al.*, 1993).

Silicate addition will also give rise to increased supply of high quality biogenic matter to the sediment. The increased supply to the benthos might increase benthic growth, but increase also the probability of hypoxic or anoxic conditions in the bottom water. The improvement of the environmental conditions in the euphotic zone caused by the stimulated vertical export of suspended biomass and an increase of potential biomass which can be exploited from the ecosystem, may be neutralized by increased benthic oxygen demand and the deterioration of the oxygen conditions in bottom waters.

Dissolved silicate addition to eutrophied ecosystems is a measure of *1.* to promote water quality, *2.* to reduce the proliferation of toxic algae, and *3.* to improve the feeding grounds of pelagic organisms of interest for extensive aquaculture and fisheries. The hypothetical relationship shown in Fig. 1 could be the instrument regulating the DSi relative to the N and P discharge. However, before such management procedures are applied, the construction of oxygen and carbon budgets for benthos and deep water are necessary. Such studies would determine the capacity of the sediment and deeper waters for increased carbon supply and guide the authorities to reduce the negative impact of hypoxic and anoxic bottom water on the environment.

Conclusion

- The experimental facility developed for this investigation proved useful for experimental studies of variable macro nutrient composition and addition, and of primary production, phytoplankton development and the subsequent export of particulate matter.
- There was an increase in vertical flux of organic matter when silicate was added (86, 15.9 and 16.9% in terms of Chl *a*-, PN and PC, respectively). For each gram of silicate added the vertical flux was enhanced by 3.6 g C, implying that export production under moderate DSi addition is determined by the Redfield ratio.
- More experimentation with variable DSi addition, turbulence and scenarios of zooplankton grazing, must be carried out in the near future in order to describe more thoroughly the functional relationship between silicate addition and vertical export of organic matter.

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