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Recruitment of coastal planktonic diatoms from benthic versus pelagic cells: Variations in bloom development and species composition

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Abstract

Although phytoplankton blooms are major events in aquatic systems, the importance of benthic resting stages in seeding planktonic blooms is still unclear. Using microcosms, we tested the influence of benthic versus planktonic inocula on the development and taxonomic composition of diatom communities in a temperate fjord. Experiments in early spring 2002, fall 2002, and late spring 2003 showed that the type and quantity of inoculum influenced bloom development and composition. Species composition was vastly different when seeded by cells from the benthos. Species such as *Detonula confervacea* and *Thalassiosira minima* showed strong dependence on benthic propagules. Populations of *Chaetoceros debilis* and *Thalassiosira nordenskioeldii* were initiated by both benthic and planktonic cells, and benthic seeding was most successful when experiments were preceded by a planktonic bloom. *Skeletonema costatum* was abundant in all treatments but showed variations in size, depending on the type of inoculum. Species that do not have a resting stage, such as *Pseudo-nitzschia* spp., were present only in plankton-treated microcosms. Seasonal factors were especially important in determining the successful growth of newly seeded populations. Our results indicate that benthic resting stages provide an important source for some species. Because the introduction of benthic resting stages to surface waters can greatly influence species composition of the plankton, it is important that studies of plankton blooms include life-history stages from both the sediments and the water column.

Diatom blooms make large contributions to the total phytoplanktonic biomass in coastal regions and are often the major fuel source for grazers in the spring. Sometimes, however, these blooms can be hazardous to marine biota and human health through mechanical injury, excretion of oils and mucilage, and, in some cases, production of toxic compounds (Fryxell and Villac 1999). Despite the importance of diatom blooms, it is still not always clear how these blooms are initiated. Advanced technologies, such as computerized sensors and satellite images, have allowed aquatic scientists to study algal blooms at regional and global scales, and this has led to many advancements in algal bloom research. Although important, these technologies do not consider the detailed life histories that may also be critical determinants of bloom formation (Marcus and Boero 1998). Accurate prediction of algal blooms will depend on a thorough understanding of algal life histories as well as a knowledge of the environmental factors that control the processes of algal growth and loss.

Increasing numbers of aquatic scientists are acknowledging an integral role of benthic life stages in the function and structuring of pelagic systems (Raffaelli et al. 2003). The potential importance of benthic resting stages in diatom ecology has long been recognized in both fresh and marine systems. When environmental conditions become poor for vegetative growth, many diatoms form resting stages. These resting stages sink to the sediments, which afford refuge from adverse conditions in the water column. Laboratory incubations suggest that survival times of at least 2 yr are common in many coastal species, with upper limits of 9 yr (e.g., Lewis et al. 1999) for resting spores. In natural sediments, however, resting stages can remain viable for years to decades (Stockner and Lund 1970; McQuoid et al. 2002). Diatom resting stages require light for germination (Hollibaugh et al. 1981); this is usually accomplished by resuspension into surface waters, where these propagules can germinate and resume vegetative growth (McQuoid and Hobson 1996). Although vertical mixing may introduce resting stages into the plankton, growth and bloom development by newly germinated cells depend on environmental conditions (e.g., critical depth, temperature and day length, nutrient availability) present in the water column. Vegetative growth in the plankton is often restricted to a short period, but benthic survival of resting stages during unfavorable periods ensures that a species will continue in an area (Itakura et al. 1997).

Planktonic blooms can be seeded by pelagic or benthic cells. Actively growing cells may be transported into the surface waters of an area, immediately resulting in a large population (e.g., Godhe et al. 2002). Offshore, frontal zones may also harbor vegetative cells as potential propagules (Smayda 2002). A few vegetative cells may even survive nutrient and grazing stress in an area, and these "fugitive cells" (Kilham and Kilham 1980) can grow and accumulate once favorable conditions return (Backhaus et al. 1999,

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2003). Alternatively, planktonic blooms can be initiated by the germination and growth of benthic resting stages. A single species may use all of these strategies, and so determining the method of inoculation can be difficult.

The influence of resting stages on diatom community dynamics has been examined in lakes (Lund 1971; Schelske et al. 1995). In these studies, regular resuspension of benthic resting stages, especially those of *Aulacoseira* spp., led to changes in the dominant species of the planktonic vegetative population. A similar process may also be operating in some coastal areas. In northern fjords, there are few planktonic cells left in the surface waters after the typically long, dark winters, and benthic resting stages are the most likely supply of cells for the spring diatom bloom (Eilertsen et al. 1995). Resting stages are also an important inoculation source for bloom formation in upwelling areas, because the propagules are brought to the surface with nutrient-rich deep water (Pitcher et al. 1993). In most temperate areas, however, it has been difficult to determine if spores actually seed diatom blooms, because fugitive vegetative cells may always be present in low numbers (Garrison 1981). Although the role of resting stages in coastal diatom populations has been studied for many years, it is still unclear to what extent benthic resting stages contribute to the onset and development of planktonic blooms.

The goal of this study was to compare the development and species composition of temperate diatom blooms seeded with different life stages. Studies were carried out in Gullmar Fjord, Sweden, which is known to have a diverse bank of diatom propagules in the sediments (McQuoid 2002). Microcosms were inoculated with varying combinations of benthic or planktonic propagules, and the development of the community was followed. Microcosm results were compared with the progression of the natural phytoplankton community in Gullmar Fjord. We found that the type of inoculation greatly influenced bloom development and species dominance.

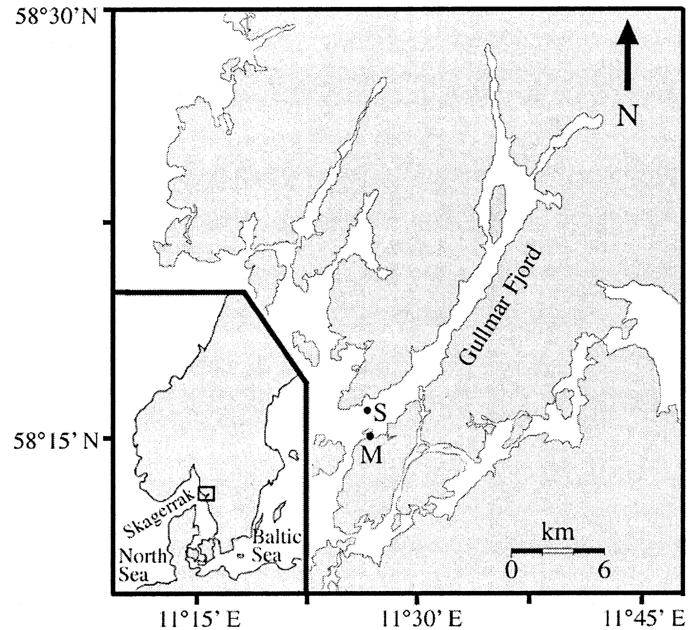

Fig. 1. Location of sampling and experimental sites in Gullmar Fjord, Sweden. Cores were collected at Sta. S. Microcosms were incubated at Sta. M. Planktonic data were collected at both stations.

Materials and methods

Microcosms—Three microcosm experiments were conducted in Gullmar Fjord (58°15.6′N, 11°25.9′E). The experiments ran from 28 February to 20 March and 16 September to 1 October 2002 and from 12 to 26 May 2003. For each experiment, three sediment cores were collected with a box corer in Gullmar Fjord at a water depth of 63 m (Sta. S) (Fig. 1). Cores were immediately sampled on ship. After careful drainage of the overlying water, the top 5 mm of sediment was subsampled into plastic cups. At the same station, phytoplankton at the sea surface were sampled from several net tows (20-μm mesh size) and pooled into three 500-ml bottles. Both sediment and phytoplankton concentrates were analyzed for chlorophyll *a* (Chl *a*) content as described below and then stored in darkness at 5°C overnight.

For each experiment, twelve 20-liter Nalgene bottles were filled with twice-filtered seawater (a 0.3-μm Millipore filtering system) from a 35-m depth in Gullmar Fjord. This water was nutrient rich with a salinity of 32. Three bottles served as controls. The remaining bottles were inoculated with the plankton concentrate (from the three pooled plankton tows), the collected sediment (from each of the three sediment cores), or both, with three replicates of each treatment as described below.

Microcosms were inoculated and set out on 1 March and 17 September 2002 and on 13 May 2003. The bottles were secured between two lines strung across the inner area of a curved floating dock (Sta. M) (Fig. 1) at Kristineberg Marine Research Station on Gullmar Fjord. Each bottle was encased in a rope sling. Two cross lines were woven through opposite sides of the sling and fastened to the lines attached to the dock. The bottles were positioned randomly across the lines with respect to treatment and floated on their sides. Each microcosm had two polypropylene bulkhead fittings in the lid to which polyvinyl chloride (PVC) tubing (6-mm ID) was attached. On the inside of the microcosm, PVC tubing was attached to the inner bulkhead fittings for sample extraction and air intake. The sampling tube was weighted with a short piece of glass rod, and the air intake tube was attached to a small foam float. On the outside of the lid, each bulkhead fitting had a 1.5-m tube secured by a hose clamp. Near the free end of each 1.5-m tube was a polypropylene pinch clamp that was opened during sampling. When not in use, the tubes were clamped closed and secured to the side of the rope sling with Velcro straps.

Microcosms were sampled from a rowboat every 2–3 d until Chl *a* values showed stationary phase or a decline of the population. Bottles were shaken to mix the contents prior to sampling. During sampling, 350 ml was pumped from the sample hose using a hand-operated pump. Samples were transported to the laboratory in a dark box and immediately processed.

Inocula—The ''plankton'' inoculum was designed to give a prebloom concentration of actively growing vegetative cells. Microscopic examination of the net tows could not quantitatively determine the metabolic activity of the collected cells, but they appeared to be healthy vegetative cells. No resting stages were noted in the plankton inocula. Monitoring data from 1986 to the present show that prebloom Chl *a* values in Gullmar Fjord range from <0.1 to >1.0 μg L^{-1}, with a mode of 0.7 μg L^{-1}(unpubl. data). In the two experiments in 2002, the plankton inoculum gave initial chlorophyll concentrations of 1 μg L^{-1} in the treatment bottles—a moderately high prebloom Chl *a* value. In 2003, the plankton inoculum gave initial chlorophyll concentrations of 0.1 μg L^{-1} in the treatment bottles—a low prebloom Chl *a* value.

The ''sediment'' inoculum was designed to simulate the resuspension of 5 mm of sediment and its even distribution through an average water-column depth (~30 m). In all three experiments, 3 ml of surface sediment slurry was added to the treatment bottles. Microscopic examinations showed that the sediment inocula contained resting spores of *Thalassiosira* spp., *Chaetoceros* spp., and *Detonula confervacea* in addition to *Paralia sulcata* and a variety of pennate diatoms. Many *Skeletonema costatum* cells with condensed protoplasts also were observed, and these were likely physiologically resting cells. Because sediment was collected from 63 m, any recently settled cells would have been in darkness for a least 1 week, a condition that would reduce the number of viable vegetative cells to a greater extent than resting stages (Hargraves and French 1983). On the basis of our observations and previous germination studies of sediments in Gullmar Fjord (McQuoid 2002), we believe that the sediment inocula contained many viable benthic resting stages.

The species composition of the sediments was also examined during a laboratory incubation. For each experiment, 1 g of wet sediment was mixed into 50 ml of f/2 medium (Guillard and Ryther 1962) and incubated in a growth chamber at 7°C with 100 μmol m^{-2} s^{-1} irradiance on a 12 : 12 h light : dark cycle. Cultures were scanned after 10 and 16 d, and the species that were present were recorded.

Chl a*, nutrients, and cell counts*—One hundred milliliters of each sample was filtered onto GF/F filters for Chl *a* extraction in 10 ml of 95% ethanol. Filters were extracted overnight in a dark, rotating box and measured with a Turner Designs fluorometer. Calculations were based on equations from Parsons et al. (1984). On the third sampling in September, one Chl *a* sample from a bottle treated with plankton plus sediment was contaminated. Thus, there are only two replicates for that treatment on 23 September. On five sampling dates in each experiment, 5 ml was filtered through a pore size of 0.45 μm and frozen (−80°C) for nutrient analysis. Nitrate, phosphate, and silicate were measured by standard colorimetric methods with an autoanalyzer (TRAACS, Braun-Lubbe). The remaining sample volume (~200 ml) was preserved with Lugol's solution for microscopic analysis with an inverted light microscope at ×200–400 magnification. Early in each experiment, at least half of the chamber was examined. After cells in the microcosms began exponential growth, >350 cells were counted from each sample.

Environmental data—Day length was recorded during all experiments. In March 2002 and May 2003, temperature was continuously measured in Gullmar Fjord by sensors at 1 m below the sea surface. Because of technical problems with the monitoring system in autumn 2002, values of noon surface temperature were collected by a conductivity temperature depth recorder on 16, 17, 23, and 25 September and 1 October. From these data, temperatures were estimated for 20, 27, and 30 September by interpolation.

Phytoplankton in Gullmar Fjord—The natural phytoplankton community in Gullmar Fjord was also monitored throughout the study period. Surface Chl *a* and phytoplankton were collected several times per week near the dock where the microcosms were incubated (Sta. M) (Fig. 1). In addition, Chl *a* values for 2002 and 2003 were obtained from the Swedish Meteorological and Hydrological Institute's biweekly monitoring program at a nearby monitoring station (Sta. S) (Fig. 1).

Calculations and statistics—Bloom development was assessed by calculating the number of days between inoculation and midexponential growth. This was calculated for each replicate by fitting a line through the exponential portion of the growth curve and determining the nearest whole day that corresponded to the midpoint of exponential growth. Bloom development time was calculated on the basis of both Chl *a* and cell abundance curves.

Dimensions of the dominant species were measured, and biovolumes were calculated using formulas for the geometric shapes most closely approximating the species (Sun and Liu 2003). Ten cells of each species from different chains were measured for each treatment. Because *S. costatum* appeared to vary among treatments during the September experiment, we measured 30 cells from different chains in each experiment and treatment, and we compared the biovolume using a single-factor analysis of variance.

Comparisons of bloom development among treatments were made with a single-factor analysis of variance. Season was not included as a factor in the analysis of variance, since incubations were made only once at the different times of year, and thus, there is no replication for season. Significance was defined as $P < 0.05$. All data were tested for heterogeneous variances with the Cochran's C-test, and no transformation was necessary. The Student-Newman-Keuls (SNK) test was used to determine significant comparisons between pairs of treatments.

Ordination was used to trace community changes in the various treatments over time and to examine the relationships between species composition and environmental factors. Canonical correspondence analysis (CCA; CANOCO version 4.5) (ter Braak and Smilauer 2002) was selected as the unimodal response model, since the gradient was more than two standard deviations. The CCA included five environmental variables (Table 1) and 30 diatom taxa having >2% relative abundance. The inoculation type for each microcosm can be represented by nominal variables, but these are not recognized by CANOCO. Therefore, inoculation type was included as two dummy variables, ''plankton'' and ''sediment,'' which were coded by 0 for no addition or by

Table 1. Means and ranges of environmental variables used in canonical correspondence analysis. Temperature was measured at a 1-m depth in Gullmar Fjord. Nutrients were measured from the microcosms.

	Mar 2002		Sep 2002		May 2003	
	Mean	Range	Mean	Range	Mean	Range
Temperature (°C)	5.2	3.8–6.3	15.6	14.0–17.2	12.6	10.0–12.5
Day length (h)	11.2	10.3–12.1	11.9	11.3–12.5	17.0	16.3–17.3
Nitrate (μmol L^{-1})	5.5	0.4–9.9	1.6	0.2–6.6	1.9	0.2–8.5
Phosphate (μmol L^{-1})	0.4	0.0–0.7	0.2	0.0–0.6	0.1	0.0–0.5
Silicate (μmol L^{-1})	7.4	0.0–14.0	5.1	0.1–12.0	1.4	0.0–9.2

1 for addition. Species abundances and environmental data were log (x + 1) transformed before analysis. None of the data were weighted. CCA was run constrained to each environmental variable in turn to determine the amount of variation that can be accounted for by that variable (axis 1 score). Sampling dates in which all environmental data were available (135) were treated as active cases; the remaining sample dates (63) were treated as passive cases. Significance of the CCA axes was tested using a Monte Carlo analysis with 199 permutations. Results of the CCA were postprocessed to calculate centroids of the sample scores from replicate treatments.

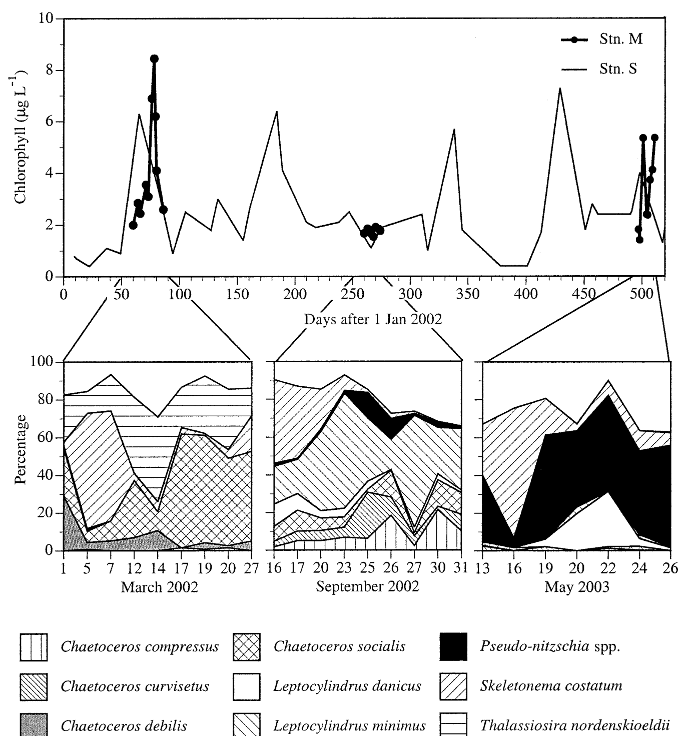

Fig. 2. Chl *a* concentrations and relative diatom species composition in surface waters of Gullmar Fjord, Sweden. Chl *a* measurements were collected at Sta. M and S. Species data were collected at Sta. M during March and September 2002 and May 2003. Note that the first experiment was run during the early spring bloom, the second experiment during a nonbloom period, and the third following the early spring bloom.

Results

Phytoplankton in Gullmar Fjord—During the study period, Chl *a* peaked in spring, summer, and winter 2002 and spring 2003. The March experiment was during the early spring bloom, the September experiment was during a period of low Chl *a* values, and the May experiment was during a late spring peak (Fig. 2). In all three experiments, the phytoplankton were dominated by diatoms. In March 2002, the major diatoms were *Chaetoceros debilis, Chaetoceros socialis, S. costatum,* and *Thalassiosira nordenskioeldii.* In September 2002, dominant taxa were *Chaetoceros compressus, Chaetoceros curvisetus, C. socialis, Leptocylindrus danicus, Leptocylindrus minimus, Pseudo-nitzschia* spp., and *S. costatum.* In May 2003, the phytoplankton was dominated by *L. danicus, Pseudo-nitzschia* spp., and *S. costatum.*

Environmental conditions—Environmental conditions varied with season and throughout the experiments (Table 1). In March 2002, sea surface temperature in the fjord was low, and days were moderately long. The September 2002 experiment had higher temperatures but only slightly longer days. In May 2003, sea surface temperatures were moderate, but days were long. Nitrate, phosphate, and silicate in the microcosms were highest in March. In all experiments, nutrients in the microcosms were highest at the start and near depletion at the end.

Chl a *and cells in microcosms*—Growth in the microcosms was monitored by Chl *a* concentrations, cell abundances, and biovolume (Fig. 3). Replication was good, and with a few exceptions, the coefficient of variation was $<35\%$. Growth was generally slower in March than in September or May. Also, in 2002, treatments with sediment only grew slower than plankton treatments, whereas no difference in growth could be seen among the treatments in May 2003, which had a smaller plankton inoculum. Peak Chl *a* values in March (20–25 μg L^{-1}) were more than double those in September (6–10 μg L^{-1}), and May 2003 Chl *a* values were moderate (13–17 μg L^{-1}) (Fig. 3A–C). Maximum cell concentrations were highest in May 2003 (32–60 million cells L^{-1}) and lowest in March 2002 (2–4 million cells L^{-1}) (Fig. 3D–F). Since cellular Chl *a* content can vary with light conditions and cell physiology and cell concentration is somewhat dependent on cell size (i.e., small cells reach higher concentrations than larger cells), we also calculated the

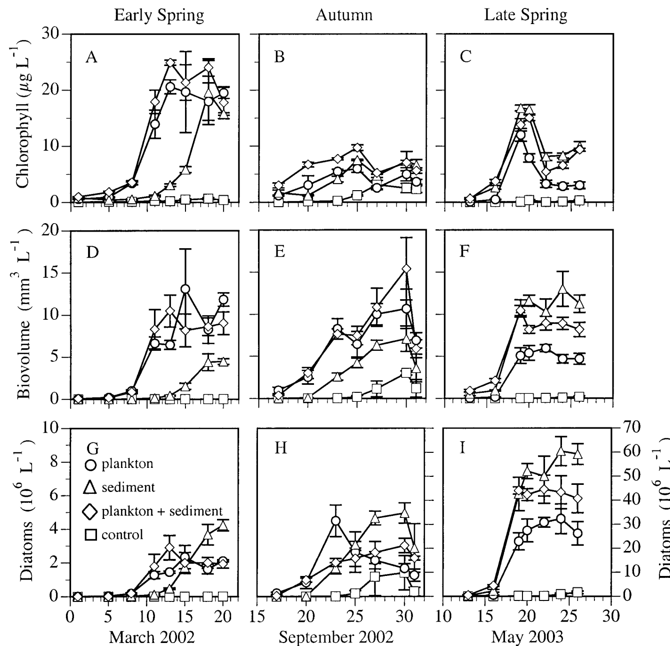

Fig. 3. Growth of diatom populations in the microcosm experiments, March and September 2002 and May 2003. (A–C) Chl *a* concentration. (D–F) Biovolume calculated from microscopic measurements. (G–I) Diatom cell abundance. Symbols are mean ± SE of replicate microcosms ($n = 3$). Plots of diatom abundance have different scales on the y-axes for September and May. Note that in comparing the experiments, Chl *a* and diatom abundances differ, but biovolume estimates are similar.

change in biovolume with time (Fig. 3G–I). Maximum biovolumes were similar for the three experiments.

After 9 d of incubation in the September experiment (on 25 September), some growth of diatoms was detected in control bottles. Contamination could have come from incomplete filtration of experimental water, or cells from the surrounding water could have leaked into the bottles through the pinch clamps. Dominant species in the controls were *L. minimus* and the small form of *S. costatum.* Abundance of these species in treatment bottles may include contamination, especially after 25 September, but we estimate that the contamination is <10%. Calculations of bloom development were based on measurements prior to 25 September; therefore, they should not be affected by the contamination. No contamination was observed in the March 2002 or May 2003 experiments.

Changes in biomass were used to calculate the number of days until growth reached the midexponential phase—our estimate of bloom development. Bloom development time was generally faster in September 2002 and May 2003 (Table 2). For the 2002 experiments analyzed separately, Chl *a* ($P < 0.05$, single-factor ANOVA) and cell concentrations ($P < 0.01$, single-factor ANOVA) both showed significant differences in bloom development time among the three treatments. In addition, treatments where only sediment was added were significantly slower than the plankton treatments ($P < 0.05$, SNK), whereas no difference was found between the treatments with only plankton added and those having plankton plus sediment. In the May 2003 experiment—with

Table 2. Days for populations to reach midexponential growth in microcosms inoculated with plankton, sediment, or plankton plus sediment. Development time was calculated using both Chl *a* and diatom cell concentrations. Mean ± SE (n=3).

Inoculum	Development time (days)	
	By μg of Chl *a* L^{-1}	By cells L^{-1}
March 2002		
Plankton	11.0±0.0	11.0±1.0
Sediment	15.3±0.6	16.0±1.0
Plankton + sediment	10.3±0.6	10.7±0.6
September 2002		
Plankton	5.3±1.1	4.7±0.6
Sediment	7.0±0.0	8.7±0.6
Plankton + sediment	4.7±0.6	6.0±1.0
May 2003		
Plankton	5.3±0.4	5.3±0.4
Sediment	5.0±0.3	4.3±0.2
Plankton + sediment	4.7±0.2	4.3±0.2

the low initial Chl *a* inoculum—there was no statistical difference in development time among treatments on the basis of Chl *a* ($P = 0.63$, single-factor ANOVA) or cell abundance ($P = 0.39$, single-factor ANOVA) estimates.

Species composition in microcosms—Diatom species composition varied among the three experiments and treatments (Figs. 4–6). Microcosms treated only with plankton had communities similar to the diatom population in the fjord; microcosms treated only with sediment had somewhat different communities; and microcosms treated with plankton plus sediment had a mixture of species but looked most similar to the communities in plankton-treated bottles. In March 2002, all treatments contained *C. debilis, C. socialis, S. costatum,* and *T. nordenskioeldii* (Fig. 4). Microcosms treated only with plankton also contained reasonably high amounts of *Chaetoceros diadema,* whereas sediment-treated microcosms were dominated by *D. confervacea* and *Thalassiosira minima.* In September 2002, *C. socialis* and *S. costatum* were found in all treatments (Fig. 5). In this experiment, plankton-treated microcosms were also dominated by *C. compressus, C. curvisetus, L. danicus, L. minimus,* and *Pseudo-nitzschia* spp. In May 2003, *S. costatum* was found in all treatments, whereas plankton-treated microcosms were also dominated by *Pseudo-nitzschia* spp. (Fig. 6). In the sediment treatments of all experiments, *P. sulcata* had a large initial relative abundance but did not continue to reproduce; hence, its contribution to the diatoms was negligible after only a few days. Some resting spores were produced in the microcosms toward the end of each experiment.

Species patterns—Several species showed distinct differences in abundance among treatments. In March 2002, *C. debilis* and *T. nordenskioeldii* had a higher abundance in plankton-treated microcosms, and *D. confervacea, S. costatum,* and *T. minima* reached very high concentrations in microcosms treated only with sediment (Fig. 7). In September 2002, *C. compressus, C. curvisetus, L. danicus,* and *L. min-*

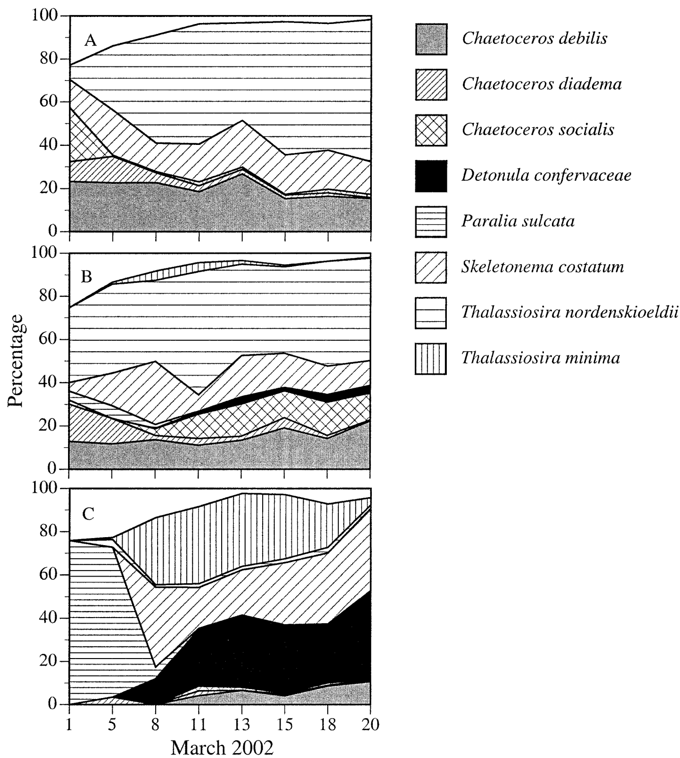

Fig. 4. Relative diatom species composition of microcosms in March 2002. Mean values are shown (n = 3). (A) Plankton treatment. (B) Plankton plus sediment treatment. (C) Sediment treatment.

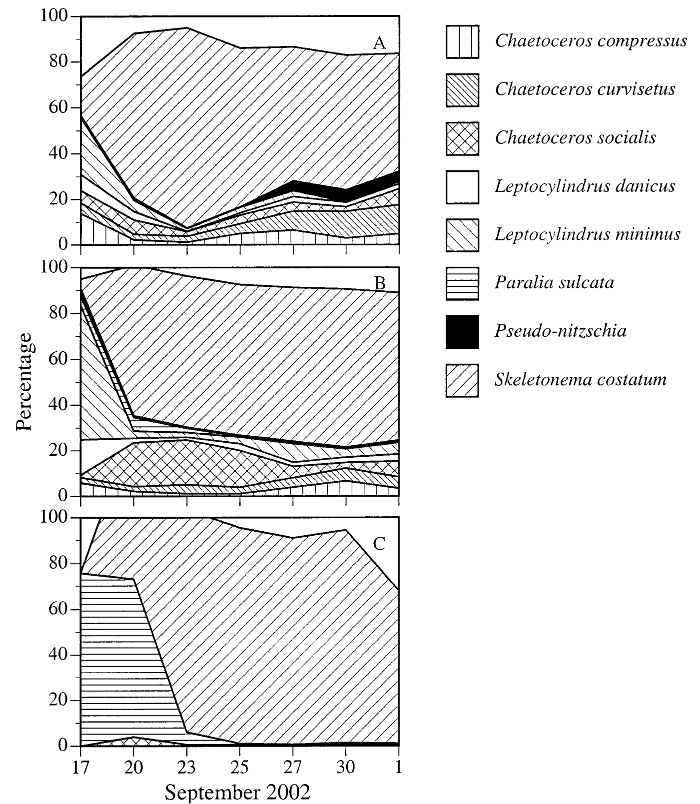

Fig. 5. Relative diatom species composition of microcosms in September 2002. Mean values are shown (n = 3). (A) Plankton treatment. (B) Plankton plus sediment treatment. (C) Sediment treatment.

imus were most abundant in plankton treatments (Fig. 8). In May 2003, *C. curvisetus, T. nordenskioeldii,* and *S. costatum* were most abundant in sediment-treated microcosms, and *L. danicus* and *Pseudo-nitzschia* spp. were present only in plankton-treated bottles (Fig. 9). In both 2002 experiments, *C. socialis* was unusual because it was most abundant in bottles treated with plankton plus sediment (Figs. 7, 8), but this was not repeated in May 2003 (Fig. 9).

S. costatum was abundant in all treatments during the September 2002 experiment (Fig. 8), but the size (biovolume) of *S. costatum* cells was different among treatments ($P <$ 0.005, single-factor ANOVA). Cells of *S. costatum* were significantly larger in samples treated with sediment only than in plankton-treated samples ($P < 0.05$, SNK). Average biovolumes were 65, 100, and 150 μm^3 for plankton, mixed, and sediment treatments, respectively. No size difference was found among treatments in March 2002 ($P = 0.70$, single-factor ANOVA) or May 2003 ($P = 0.39$, single-factor ANOVA) where *S. costatum* biovolumes were 108 and 155 μm^3, respectively.

Laboratory incubations—Species composition of the laboratory incubations primarily matched the species composition from the microcosm experiments, but some additional species were observed. In addition to their presence in the March 2002 culture, *D. confervacea* and *T. minima* were present in the laboratory culture from September 2002, and *D. confervacea* was present in the laboratory culture from May 2003.

CCA—The CCA was significant ($P = 0.002$, Monte Carlo). Axes 1 ($\lambda_1 = 0.24$), 2 ($\lambda_2 = 0.18$), and 3 ($\lambda_1 = 0.09$) explained 27% of the cumulative variance in the species data and up to 90% of the species–environment relation. Contributing to this variance, the ranks of the variables were (1) day length, (2) temperature, (3) phosphate, (4) plankton, (5) nitrate, (6) silicate, and (7) sediment. In our CCA, there was a high correlation among nutrients (Table 3); however, the values of the variance inflation factor (VIF) were low and suggest that each of these environmental parameters contributes new information to the analysis. VIF is related to the multiple correlation among the environmental variables. VIFs for all of our variables were low (<7), showing a low degree of multicolinearity. The species–environment correlations for axes 1 (0.80), 2 (0.90), and 3 (0.83) were high. On the basis of the interset correlations, temperature was most strongly related to axis 1, day length dominated axis 2, and plankton treatment dominated axis 3 (Table 4).

Samples are placed on the CCA biplots on the basis of their species composition and association with the environmental variables (Fig. 10). The length of the environmental arrows and their orientation on the biplot indicate their relative importance to each axis. Environmental arrows represent a gradient; the mean value lies at the origin, and the arrow points in the direction of increase.

The biplot of axes 1 versus 2 shows the distribution of species along the seasonal gradients (Fig. 10A). On the right

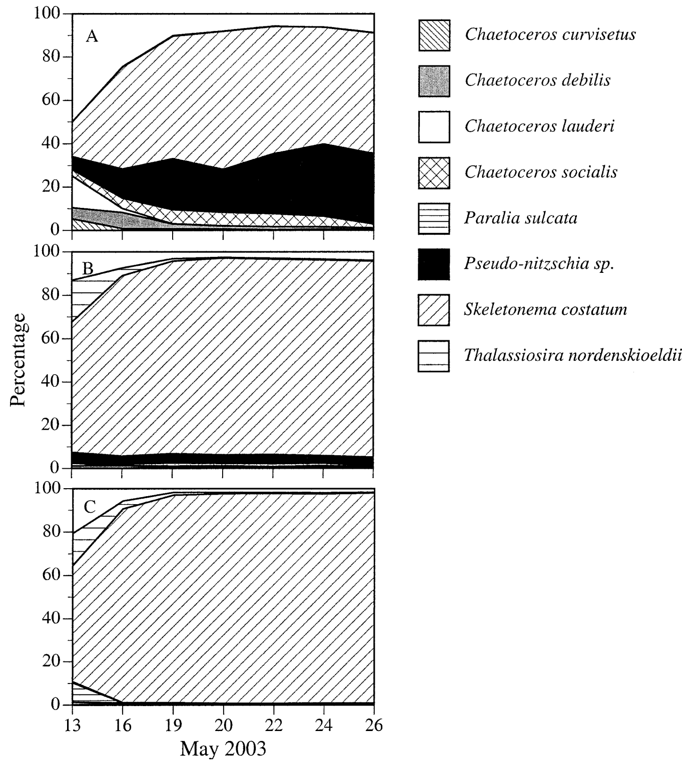

Fig. 6. Relative diatom species composition of microcosms in May 2003. Mean values are shown ($n = 3$). (A) Plankton treatment. (B) Plankton plus sediment treatment. (C) Sediment treatment.

side of the plot, the typical spring species lie on the low end of the temperature and day-length gradients. Species dominant in the late spring experiment, such as *Chaetoceros lauderi, Thalassionema nitzschioides,* and *Pseudo-nitzschia* spp., are in the upper left part of the plot where day length is high and temperatures are moderately warm. Species that are adapted to higher temperatures, such as some *Chaetoceros* and *Leptocylindrus* spp., are on the left side of the plot. Species with a wide tolerance range for temperature

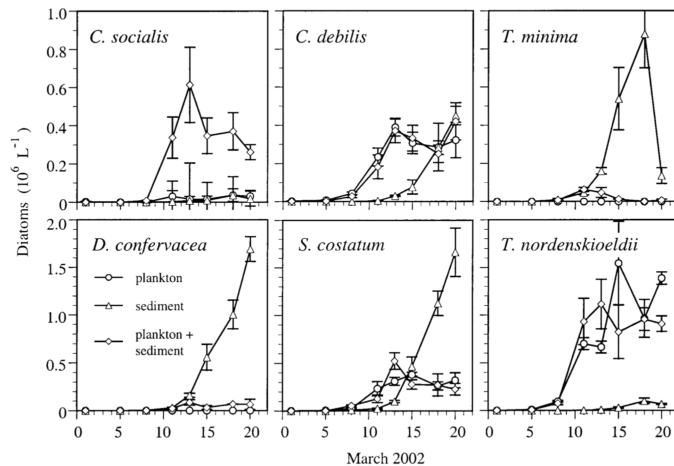

Fig. 7. Patterns of abundance for major diatom species in microcosms, March 2002. Symbols are mean ± SE ($n = 3$). Note that lower panels have 2× the y-axis scale of upper panels.

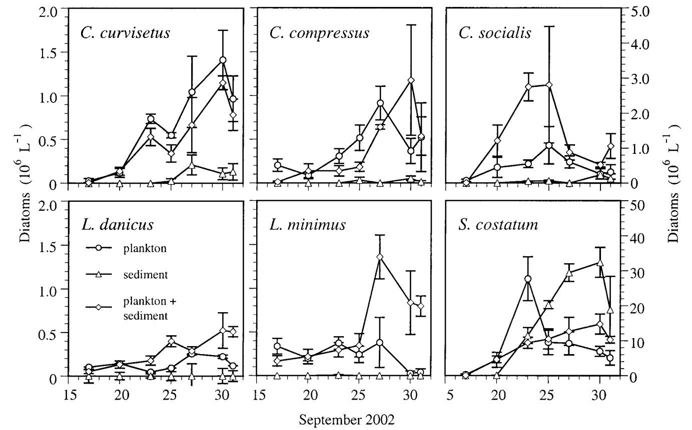

Fig. 8. Patterns of abundance for major diatom species in microcosms, September 2002. Symbols are mean ± SE ($n = 3$). Note that *C. socialis* and *S. costatum* have different scales on the y-axis.

and day length, such as *C. socialis* and *S. costatum,* are plotted near the origin. Nitrate, phosphate, and silicate concentrations were generally higher in March (Fig. 10B); nutrients were also higher in initial samples, becoming depleted in later samples (Fig. 10D). The nominal variables, plankton and sediment, were most important in axis 3, and some spe-

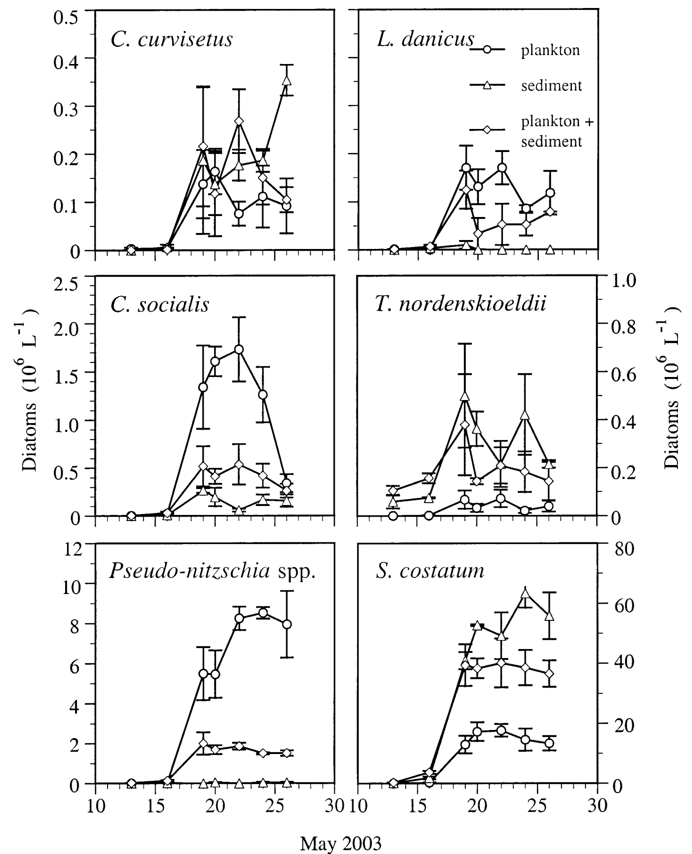

Fig. 9. Patterns of abundance for major diatom species in microcosms, May 2003. Symbols are mean ± SE ($n = 3$). Note that *T. nordenskioeldii* and *S. costatum* have different scales on the y-axis.

Table 3. Correlation among environmental and nominal variables used in canonical correspondence analysis.

	Plankton	Sediment	Temperature	Day length	Nitrate	Phosphate	Silicate
Plankton	1.000						
Sediment	−0.445	1.000					
Temperature	0.066	−0.072	1.000				
Day length	−0.027	0.021	0.447	1.000			
Nitrate	−0.086	−0.043	−0.217	−0.125	1.000		
Phosphate	−0.007	−0.017	−0.251	−0.555	0.767	1.000	
Silicate	−0.033	−0.063	−0.123	−0.532	0.662	0.838	1.000

cies show a strong association with the type of inoculum (Fig. 10C). *C. compressus, C. lauderi, Chaetoceros lorenzianus, Coscinodiscus concinnus, Ditylum brightwellii, Guinardia* spp., *Leptocylindrus* spp., *Proboscia alata, Pseudo-nitzschia* spp., and *T. nitzschioides* were most common in plankton-treated samples. *Asterionellopsis kariana, D. confervacea, Odontella aurita,* and *T. minima* were more abundant in sediment-treated samples.

The plot of centroids for replicate samples shows the seasonal variation and community development in different treatments (Fig. 10B,D). In the biplot of axes 1 versus 2, the different experiments separate on the basis of seasonal factors, such as temperature and day length (Fig. 10B). Development within the microcosms is best shown by the biplot of axes 1 versus 3 (Fig. 10D). Community development generally proceeds from the bottom of the plot to the upper part. One exception is microcosms that were treated only with sediment in September 2002. Compared to other treatments, the plankton-treated microcosms in September showed less change throughout their development. As described above, microcosms treated only with sediment showed exceptionally different communities compared to the plankton-treated samples.

Discussion

Microcosm bloom development and composition—Our results show that the development and taxonomic composition of a planktonic bloom is influenced by the inoculum type. In our microcosms and in the natural phytoplankton community, we observed Chl *a* values comparable to other Chl *a* measurements for Gullmar Fjord (Belgrano et al. 1999). During the course of our experiments, Chl *a* reached higher values in the microcosms than in the fjord phytoplankton because, in the former, light and nutrients were plentiful, and the communities were not disrupted by physical dispersal or grazers. Nevertheless, the microcosms that were treated with plankton developed a species composition similar to the natural phytoplankton community in the fjord, suggesting that our experiments approximated the natural community. In March 2002, microcosms were inoculated just prior to the spring bloom in the fjord, and they provide a good simulation of early spring bloom development. The May 2003 results represent how resuspension influences the plankton in late spring. Because the May experiment took place several weeks after the major spring bloom, the collected sediments contained benthic cells that were probably younger than those collected in March 2002. Planktonic blooms are also known to occur in the fjord during September and October (Belgrano et al. 1999) but were not detected in our study. Consequently, the community that developed in our microcosms in September 2002 reflects a bloom that might have developed (a potential bloom) in the fjord if conditions there had been more conducive. In September 2002, nutrient concentrations in the fjord were less than one fortieth of the starting concentrations in our microcosms (unpubl. data) and could have limited the growth of the natural population.

Table 4. Interset correlations between the first three species axes and the environmental variables in canonical correspondence analysis.

Variable	Axis 1 ($\lambda_1 = 0.24$)	Axis 2 ($\lambda_2 = 0.18$)	Axis 3 ($\lambda_2 = 0.09$)
Plankton	−0.315	−0.091	−0.697
Sediment	0.202	0.101	0.351
Temperature	−0.684	−0.013	0.099
Day length	−0.366	0.785	0.073
Nitrate	0.449	0.084	−0.386
Phosphate	0.448	−0.333	−0.337
Silicate	0.313	−0.434	−0.239

Previous microcosm experiments have shown that the size of a seed population is important in determining the time required for bloom development (Pitcher et al. 1993). Our results suggest that bloom development also depends on the nature of the inoculum and the relative quantities of different inocula types. In the experiments with a plankton inoculum of 1 μg of Chl *a* L^{-1}, bloom development was faster in treatments inoculated with plankton and slower in microcosms treated only with sediment. Diatoms do not require a dormancy period prior to germination (Hargraves and French 1983). There is some evidence, however, that resting spores may show a 1-d lag period before growth, whereas vegetative cells can grow almost immediately (Hollibaugh et al. 1981; Kuwata and Takahashi 1999), and this may have influenced the timing of bloom development. Although we do not know the exact number of propagules in each inoculum type, there may have been a greater number of actively growing cells in the plankton inoculum. We saw no difference in bloom development among treatments when the plankton inoculum was reduced to 0.1 μg of Chl *a* L^{-1}. Because the plankton used to inoculate the May 2003 experiment should have been just as metabolically active as in the previous experiments, the similar (across treatments) development times can probably be attributed to a lower number of propagules compared to the plankton inocula in 2002.

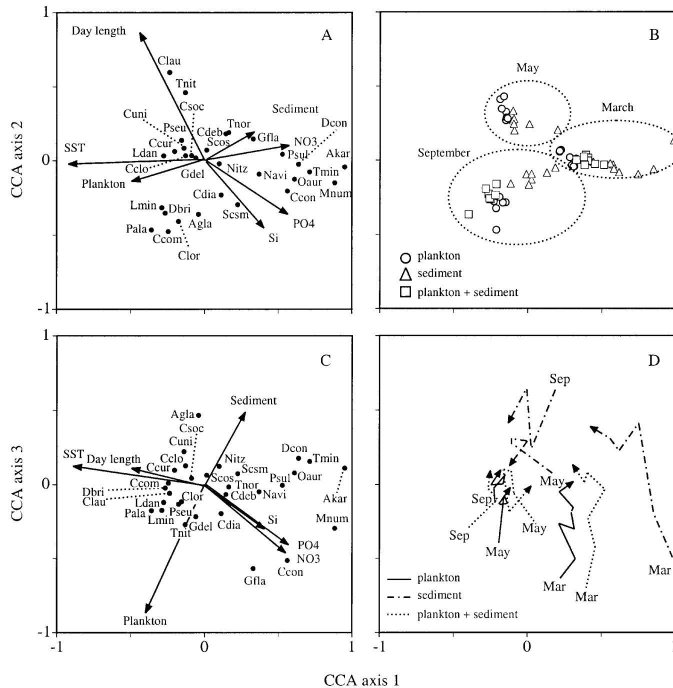

Fig. 10. Canonical correspondence analysis biplots for diatom abundance in microcosms and environmental variables. (A) Species scores and environmental vectors (arrows) on axes 1 and 2. (B) Centroids of replicate samples on axes 1 and 2. (C) Species scores and environmental vectors (arrows) on axes 1 and 3. (D) Centroids of replicate samples on axes 1 and 3. Lines connect sequential samples from an individual treatment, and arrowheads indicate the last sample date. Environmental variables were omitted from (B) and (D) for clarity but would be arranged as in (A) and (C), respectively. Agla, *Asterionellopsis glacialis;* Akar, *Asterionellopsis kariana;* Cclo, *Cylindrotheca closterium;* Ccom, *C. compressus;* Ccon, *C. concinnus;* Ccur, *C. curvisetus;* Cdeb, *C. debilis;* Cdia, *C. diadema;* Clau, *C. lauderi;* Clor, *C. lorenzianus;* Csoc, *C. socialis;* Cuni, *Chaetoceros simplex + Chaetoceros tenuissimus;* Dbri, *D. brightwellii;* Dcon, *D. confervacea;* Gdel, *Guinardia delicatula;* Gfla, *Guinardia flaccida;* Ldan, *L. danicus;* Lmin, *L. minimus;* Mnum, *Melosira nummuloides;* Navi, *Navicula* spp.; Nitz, *Nitzschia* spp.; Oaur, *O. aurita;* Pala, *P. alata;* Pseu, *Pseudo-nitzschia* spp.; Psul, *P. sulcata;* Scos, *S. costatum;* Scsm, small *S. costatum;* SST, sea surface temperature; Tmin, *T. minima;* Tnit, *T. nitzschioides;* Tnor, *T. nordenskioeldii.*

Our results suggest that the effectiveness of seeding by benthic propagules will be greatest when natural phytoplankton biomass is low.

In the microcosm communities, the most significant effect of inoculum type was on species composition. Sediment versus plankton inocula generally resulted in different suites of species. Species richness was highest in microcosms treated with both inocula types because they were a mixture of the two assemblages. Because the natural phytoplankton in the fjord looked primarily like our plankton-treated microcosms, it appears that the sediments we collected in Gullmar Fjord contributed relatively little to the natural phytoplankton populations growing at the time of these experiments.

The CCA traces community development in the microcosms in relation to seasonal as well as experimental conditions. The three experiments clearly separate along the first two axes according to seasonal combinations of temperature and day length. That the samples remain separated by season indicates that the communities produced by the experiments were, in this respect, a realistic simulation. Variations along the third axis reflect primarily the type of inoculum given. Although the type of inoculum may alter plankton species composition, the resulting community will ultimately be influenced by season. In the CCA, several species showed a strong association with a particular inoculum type. This correlation with inocula type may reflect different seeding strategies.

Seeding strategies in coastal diatoms—Diatoms may employ a variety of seeding strategies for initiation of planktonic growth, and our results suggest that a few species rely strongly on benthic propagules as a seeding mechanism. Some species in our study (e.g., *C. concinnus, Pseudo-nitzschia* spp., *T. nitzschioides*) are not known to form a resting stage and must rely on planktonic propagation. In the microcosms, *D. confervacea* and *T. minima* were present only when sediment was added. Thus, at least during the study period, benthic propagules were very important for planktonic growth of these diatoms. Also, *D. confervacea* and *T. minima* were observed only in the March 2002 microcosms. Results from our laboratory incubations show that these species could germinate from September 2002 and May 2003 sediments when temperature was low. The lack of germination by *D. confervacea* and *T. minima* in the September 2002 and May 2003 microcosms confirms that benthic germination also can be regulated by seasonal factors (Eilertsen et al. 1995; McQuoid and Hobson 1995).

C. debilis and *T. nordenskioeldii* could grow from both our plankton and sediment inocula. In March 2002, these species were more abundant when propagules originated from the plankton. In September 2002, these species were more abundant in sediment-treated microcosms and may have originated from benthic cells that were deposited during the spring bloom. In May 2003, *T. nordenskioeldii* was also most abundant in sediment treatments. Monitoring data from 27 March 2003 show that *T. nordenskioeldii* was very abundant in the plankton of Gullmar Fjord (Edler 2003), and this bloom may have contributed to the benthic cells that we used in our May sediment inoculum. In contrast, *C. debilis* was more abundant in the plankton treatment in May 2003. Because this species was abundant in plankton samples taken on 5 May 2003 (Edler 2003), it may be that the population had not yet deposited cells in the sediments. For *T. nordenskioeldii* and *C. debilis,* the initiation of blooms by benthic cells is most effective when recently preceded by a large planktonic population.

The growth of *S. costatum* from sediment inocula in all three experiments agrees with other work showing that this species has viable propagule banks in Scandinavian coastal sediments (McQuoid 2002; Josefson and Hansen 2003). Similar to *C. debilis* and *T. nordenskioeldii, S. costatum* was able to germinate in all seasons. In March 2002, it contributed 20–30% to the total number of diatoms in all treatments, whereas in September 2002 and May 2003, it made up >60% of the community. Although successful in all cas-

es, the higher dominance of *S. costatum* in September and May probably reflects enhanced vegetative growth in warmer temperatures and longer days (Curl and McLeod 1961; Sakshaug and Andresen 1986).

In September 2002, we found that *S. costatum* cells arising from sediment propagules were 2.3 times larger than cells coming from the plankton inoculum. Repeated vegetative division reduces diatom cell size. Accordingly, if cells from the plankton inoculum had come from a population that had been dividing for many generations, they might have been smaller than younger cells arising from the sediment. *S. costatum* cells in the sediment treatment grew slower than those in the plankton treatment (0.34 vs. 0.87 divisions d^{-1}), but we did not see any significant size reduction of cells in the sediment treatment over time, despite the growth of at least three generations. Another possibility is that benthic *S. costatum* cells had undergone cell enlargement prior to our incubations. Cell enlargement in diatoms is usually associated with sexual reproduction rather than production of dormant stages; however, vegetative cell enlargement is more common in *S. costatum* (Gallagher 1983). Gallagher (1983) observed that clones of *S. costatum* from Narragansett Bay increased in diameter in the period preceding the summer bloom. Similarly, our measurements of *S. costatum* biovolume were largest in May 2003. If cell enlargement had also occurred prior to summer in 2002, the large cells could have been deposited in the sediments that we collected in September. If the deposited *S. costatum* cells remained large in the sediments throughout the summer and the cells remaining in the plankton continued to get smaller, this would explain why the cells in the September sediment treatments were larger than those in the plankton treatments. A third possible explanation for the variation in size between treatments is that the different-sized *S. costatum* are genetically different clones or even different species (Medlin et al. 1991). Earlier work has shown that *S. costatum* resting stages can survive for several decades buried in the sediment of a Swedish fjord (McQuoid et al. 2002)—a much longer time than has been estimated from laboratory studies (Hargraves and French 1983; Lewis et al. 1999). A periodic supply of propagules from long-term storage in the benthos may provide a mechanism to connect cohorts many generations apart (Marcus and Boero 1998). Therefore, possible genetic differences between benthic and planktonic diatom populations could provide valuable information about sources of planktonic blooms.

Material settling after a bloom may contain intact and viable diatom cells (e.g., Riebesell 1991), which may accumulate at the sediment surface (Josefson and Hansen 2003). If a bloom is terminated by physical processes rather than nutrient limitation (Tiselius and Kuylenstierna 1996), the settling material may be dominated by vegetative cells rather than resting spores. Although resting spores generally survive longer than vegetative cells, some vegetative cells have been found to survive several weeks in laboratory incubations (Hargraves and French 1975). Consequently, planktonic populations of some diatoms may be successfully seeded by vegetative cells that are resuspended from sediments.

Resuspension of resting stages for bloom inoculation—The success of a bloom depends on an adequate inoculum of cells and the subsequent growth of the initial population. A few numerical models have included resting-stage density and excystment rates (Eilertsen and Wyatt 2000; Yamamoto and Seike 2003). Model results suggest that resting stages are an important source of bloom inocula, but the overall bloom size also depends on environmental controls of vegetative growth. In accordance with the models, our experiments showed an influence of the inoculum on bloom development, whereas bloom size and overall composition were also related to environmental factors (e.g., temperature, day length, nutrient concentrations).

Benthic propagules are a potential inoculum for any phytoplankton bloom, given that a sufficient number are brought up to the sea surface. Large-scale passive resuspension of individuals from deep water to the sea surface can occur via tidal forcing, other turbulent mixing (e.g., winds, surface waves), upwelling, convection, or human activities such as fishing with bottom trawls and dredging. The importance that seasonal overturn and wind resuspension have for production and development within the phytoplankton community is well recognized in lakes (Schelske et al. 1995). Satellite imagery has documented regular sediment resuspension in the Great Lakes (Eadie et al. 2002). The diatom community within these sediment plumes is significantly different from that in surrounding waters, probably because of benthic seeding. In coastal areas, there is also evidence that vertical mixing by storms and wind can bring benthic stages from the sediments to the sea surface. In the East China Sea, storms resuspend resting stages in early spring, and these cells can grow to bloom proportions in about 1 week (Ishikawa et al. 2001). Phytoplankton in the southern Benguela upwelling region are seeded by inoculations of diatom resting stages through upwelling (Pitcher 1990).

Opportunity is one of the keys to success. Planktonic cells may be metabolically ''primed'' to take quick advantage of favorable growth conditions, but a benthic resting stage offers an extra level of insurance for survival of a species, especially if planktonic cells are too few. Our results show that if benthic propagules are brought to the surface, germination and growth of these cells can lead to large planktonic populations. Furthermore, the species composition of populations seeded from the benthos can be greatly different from those that arise from planktonic cells.

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