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Role of nutrient supply and loss in controlling protist species dominance and microbial food-webs during spring blooms

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ABSTRACT: The species composition of spring blooms varies over open marine regions, displaying both spatial and inter-annual differences. We used semi-continuous cultures to promote species-specific blooms and investigate associated microbial food-web dynamics and inorganic nutrient utilization. Beginning with high-nutrient, low-biomass water from 13 m depth, we compared the changes that took place over 9 d in 2 treatments: (1) NEW, a 'new-nutrient' treatment that simulated horizontal or vertical advection; every 2 d, both particles and dissolved organic matter were removed and ca. 25% of the volume of the container was replaced with nutrient-rich seawater from 200 m depth. (2) REC, a recycling treatment simulating grazing and sinking losses without nutrient replacement, i.e. conditions mimicking sharply stratified water columns; in this treatment the same volume of water was removed, but was then returned to the container following filtration through a 2.0 µm filter. In the NEW treatment, diatoms consumed the added nutrients and dominated the production and biomass of the protist community. Total protist community production in the REC treatment was significantly lower than in the NEW treatment, with either a late or no diatom bloom and prymnesiophytes such as *Phaeocystis* spp. attaining higher proportional biomass. Total production rates for heterotrophic protists, bacteria and viruses did not differ significantly between treatments. Nutrient consumption by the ensuing communities differed between the 2 treatments, with a significantly greater proportion of total inorganic nutrients consumed in the NEW than in the REC treatment. The results demonstrate that the character of nutrient supply and loss influences protist community structure and subsequent bulk nutrient utilization.

KEY WORDS: Nutrient supply · Protist species · Spring-bloom initiation · Succession · Phytoplankton · Marine · Arctic

INTRODUCTION

High nutrient loading and favorable light lead to phytoplankton blooms under both upwelling and stratified conditions. However, predicting the dominant species or species-groups within such blooms has proved difficult. Differences in spatial and inter-annual species composition has been attributed to a broad range of variables, including initial seeding conditions, irradiance, mixing regime, macrozooplankton grazing and nutrient ratios (Wasmund et al. 1998, Cebrian & Valiela 1999). The species composition, timing and duration of blooms is a key determinant of the ratio of annual photosynthetic to heterotrophic biomass production, and therefore has important implications for carbon and nutrient cycling in the ocean (Azam 1998, Buesseler 1998, Arrigo et al. 2000, Anderson & Ducklow 2001).

Persistent long-lived phytoplankton blooms typically occur where nutrients are constantly re-supplied, such

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as in regions of upwelling and lateral advection. The phytoplankton in such environments are exposed to new nutrient inputs, but also experience community losses by advective dilution. To maintain biomass, the community must grow on a scale that exceeds the dilution rate (Dutkiewicz et al. 2001, Lovejoy et al. 2002c). In contrast, classic spring blooms are more short-lived phenomena that begin with water-column stratification and high initial nutrient concentrations. A successional pattern often follows, beginning with diatoms, until silica becomes limiting, and then followed by nanoflagellates that continue to draw down nutrients such as nitrogen (Dale et al. 1999). However, there are exceptions to this classic pattern; in high latitude regions, either diatoms or non-coccolithophorid Prymnesiophytes, such as *Phaeocystis* spp. and *Chrysochromulina* spp., often dominate spring and summer blooms (Barnard et al. 1984, Arrigo et al. 1999). Early work in the Balsfjord, Norway, suggested that the spring bloom commenced with *Phaeocystis* spp., followed by the centric diatoms *Chaetoceros* spp. (Lutter et al. 1989). Other reports for the Barents Sea indicate that pennate diatoms dominate the retreating ice edge, whereas *Phaeocystis* spp., along with a mixture of centric diatoms including *Chaetoceros* spp. and *Thalassiosira* spp., are associated with a later inflow of Atlantic Ocean water (Andreassen & Wassmann 1998). While Barents Sea blooms are often a mixture of *Chaetoceros* and *Phaeocystis* species, in the relatively enclosed Ross Sea polynya, Antarctica, distinct areas are dominated exclusively by either *Phaeocystis* spp. or diatoms (Arrigo et al. 1998). Within the Antarctic Polar Front, the phytoplankton growing within a meander of a frontal jet were a mixture of *Phaeocystis* spp. and *Chaetoceros* spp. (Barth et al. 2001, Brown & Landry 2001), indicating that conditions within this meander were favorable to both taxa. Subtle differences in water-column physical structure may influence species distribution; for example, Mengelt et al. (2001) noted that, irrespective of mixed-layer depth, diatoms generally dominate south of the Polar Front, whereas small prymnesiophytes dominate north of the front.

Correlative studies of the above types have provided valuable insight into the conditions associated with the occurrence of different protist groups. However, such studies cannot provide mechanistic explanations for species success, since they are unable to separate the effects of irradiance, turbulence, and vertical or lateral advection. Successional species sequences must also be separated from sequential species changes; i.e. changes resulting from different water masses moving into a region (Braarud 1935, Barth et al. 2001). Experimental microcosms comprise a tool for isolating a community from such external 'seeding' and facilitate investigations of specific factors that influence successional species progression. The North Water (NOW) polynya (a polar sea of open water surrounded by ice; ca. 80 000 km^2) is a particularly biologically rich region in the Arctic, and is an important region in the life cycles of numerous polar mammal and bird species (Stirling et al. 1981, Deming et al. 2002). The biological importance of this area is due to the unusually prolonged phytoplankton blooms in this region compared to other polar marine sites. In a parallel study, we found that advective nutrient input was an important mechanism for maintaining a diatom-dominated bloom in nutrient-depleted waters (Lovejoy et al. 2002c). In that study, water from the southwestern part of the NOW with high chlorophyll *a* (chl *a*) levels and depleted inorganic nutrients was used to test the effect of advective versus recycled nutrients on species succession. The present study was conducted using water with low chl *a* levels and high inorganic nutrients from the northern part of the polynya, which is typical of Arctic open waters prior to a bloom (Lovejoy et al. 2002b). The goal of the present study was to investigate factors that influence species outcome and timing of an initial spring bloom under conditions incorporating realistic loss terms. This is an important problem, since there has been little success worldwide in predicting species-specific blooms (Hallegraeff et al. 1995). We used an experimental approach to examine the effect of advective dilution versus nutrient recycling on the timing of bloom initiation and species outcome in nutrient-rich high-latitude waters. Microcosms (small-scale incubation containers) were used to compare conditions in which nutrients are replenished (simulated advective conditions) to conditions of nutrient drawdown (simulated stratified conditions, with nutrient recycling). The study was undertaken to examine the effects of a previously under-investigated factor (advective vs recycled nutrient inputs) in determining the dominant species at the onset of a bloom, the dynamics of the phytoplankton and protozoan communities, and the associated variations in bacterial and viral production. While particulate material was removed under the drawdown conditions, both particulate and dissolved material were removed under the advective nutrient replenishment conditions, the hypothesis being that nutrient additions result in a stable diatom community and no new nutrient additions result in a short diatom bloom followed by a flagellate-dominated community. An additional objective was to examine population dynamics of associated microbial food-web components, including bacteria and viruses, that affect ecosystem efficiency (the flow of energy and carbon) under the different loss and nutrient regimes (Anderson & Ducklow 2001).

MATERIALS AND METHODS

Collection and preparation. The NOW (76 to 79° N, centered on ca. 75° W, ca. 80 000 km^2), was intensely sampled between April and July 1998 as part of the International North Water Polynya Project. The NOW occurs annually after an ice bridge forms across Smith Sound (Lewis et al. 1996, Melling et al. 2001). Water from under the arctic ice cap, with high nutrient concentrations but negligible phytoplankton biomass, flows into the NOW (Bâcle et al. 2002). We used this high-nutrient and low-chlorophyll water collected from a station (78° 20.28′ N, 74° 40.68′ W) just south of the ice bridge, to investigate whether the advective supply of new nutrients may be important in determining initial bloom species. The semi-continuous seawater culture experiment was similar to that described in (Lovejoy et al. 2002c). In brief, water for the experiment was collected using a CTD Rosette system and 10 l Niskin-type bottles at 13 and 200 m on board the Canadian icebreaker CCGS 'Pierre Radisson' on 7 June 1998. The 13 m water was randomly dispensed into autoclaved 2.5 l Nalgene polycarbonate bottles after rinsing 3 times with sample water. Initial samples (t_i) for nutrients, chl *a*, protist species identification and enumeration, bacteria and viral concentrations were taken from the same cast. Additional water collected at the same time from 13 and 200 m was filtered though 0.2 µm Nuclepore filters and stored in the dark at 0°C. The polycarbonate bottles used as microcosms were fitted with septum lids and put into bags made of 2 layers of neutral-density shade cloth, which simulated 36% surface irradiance (24 h d^{-1} at these latitudes in June). The microcosms were then placed in an on-deck incubator, where the temperature was maintained between –1 and +1°C by a constant flow of surface seawater. Normal ship movement ensured constant motion, and the round containers moved freely within the incubator. All subsequent manipulations were done using sterile techniques at <4°C. Microcosms were subsampled after gently inverting the containers 5 to 6 times. The loss rates imposed were similar to those in the natural environment (Hargrave et al. 2002).

The experimental microcosms were sampled after 3 d ($t_{i+3} = t_s$), and then every 2 d as follows: 100 ml was removed using a syringe through the septum lid. This subsample was used to determine concentrations of nutrients, protists, bacteria, and virus-sized particles (VSP). An additional 500 ml was then removed and filtered through a 2 µm Nuclepore polycarbonate membrane filter using an autoclaved Nalgene filter-holder and receiver. This filter was frozen at –20°C until chl *a* analysis on shore. In the recycling treatment (REC), the 500 ml of filtrate was returned to the microcosm. The remaining volume, which had been removed (100 ml) was replaced using water from 13 m that had been previously 0.2 µm-filtered; this volume, along with its nutrients, was incorporated into all subsequent calculations (see following subsection). For the NEW treatment (new nutrients, sensu Dugdale & Goering 1967) the entire 600 ml of water that had been removed was replaced with 0.2 µm-filtered 200 m water.

At the end of the experiment, additional water was filtered through a Whatman GF/F filter to determine final total chl *a*. This value was compared to the chl *a* retained on the final 2 µm filter, giving an estimate of the contribution of picophytoplankton (in this case 0.7 to 2 µm) to total chl *a*. Throughout this paper, t_i refers to the day when the initial sample was taken and water was placed in the bottles, t_s refers to 3 d later, when experimental manipulations began and water was either replaced (NEW) or filtered and returned to the bottles (REC), t_{s+2}, t_{s+4} and t_{s+6} refer to subsamples and manipulations 2, 4 and 6 d after t_s, respectively. t_{s+6} was the final day of the experiment.

Calculations. The net increase or decrease in the concentrations (C) of the measured state variables in the NEW treatments was calculated for each 2 d interval during the experiment. Beyond t_s, the net change was corrected for the removal and replacement of the culture with new media. For the first 3 d:

$$\Delta C_{0,3} = C_3 - C_0 \quad (1)$$

and for subsequent intervals:

$$\Delta C_{s,s+2} = C_{s+2} - (1 - \rho_1)C_s + \rho_1 C_{new} \quad (2)$$

where C_{new} is the concentration in the replacement medium and ρ_1 is the 2 d dilution factor (0.6/2.5 = 0.24). The net changes were then summed over the full 6 d period of the experiment to give a total cumulative production or loss.

The same calculations were made for the REC treatments using Eq. (1) for the first interval (t_i to t_s), and the following equation for the subsequent 2 d intervals:

$$\Delta C_{s,s+2} = C_{s+2} - (1 - \rho_1)C_s + \rho_2 C_a + \rho_3 C_b \quad (3)$$

where ρ_2 = 0.1/2.5, with concentration of C_a (the initial concentration in the 13 m water), and ρ_3 is the dilution factor for the filtered returned water (0.5/2.5), with concentration of C_b, in this case subscripts a and b are arbitrary designations used to track iterations. For nutrients, VSP and bacteria, which passed through the 2.0 µm filter, $C_b = C_s$; for all the other components removed by filtration, $C_b = 0$. The 2 d increments or decrements were then summed to give total cumulative production or loss as for the NEW treatments. Nutrient concentrations in the 200 m water added to the NEW treatment were 20.40, 13.05, and 1.16 µmol l^{-1} for Si, nitrate+ and soluble reactive phosphorus

(SRP) respectively. Initial ammonium concentrations were <0.1 µmol l^{-1} for both 13 and 200 m. Given the divergence between duplicates (A and B for each treatment) for some variables, data are presented for all 4 containers.

Phytoplankton and other protists were preserved using a buffered solution of glutaraldehyde and paraformaldehyde, at a final volume of 1 and 0.1%, respectively (Tsuji & Yanagita 1981). Total protist concentrations were estimated using a combination of fluorescence, Nomarski optics and Utermöhl sedimentation (details as in Lovejoy et al. 2002b). Samples were kept in the dark at 2°C until microscopically examined. To ensure that the smallest possible cells were retained, 45 ml of sample was sedimented for several weeks in 50 ml Corning centrifuge tubes. The top 40 ml was then carefully removed using a Pasteur pipette and the final 5 ml placed in a sedimentation chamber and stained with DAPI and Calcofluor for 24 h prior to counting (details in Lovejoy et al. 2002c). The samples were counted at 400 and 1000× magnification, using either Zeiss Axiovert 10 or 100 inverted microscopes. We examined 50 to 200 fields at each magnification, and a total of 400 to 3000 cells were counted for each sample. Phytoplankton and other protists were identified to the lowest taxonomic level possible with light microscopy; taxonomic details and references are given in Lovejoy et al. (2002b). Cells were measured directly using an ocular micrometer and also from images taken with a Dage-MTI CCD-300-RC video; carbon content was estimated from cell volumes (Menden-Deuer & Lessard 2000, Lovejoy et al. 2002c). For ease of comparison with nutrient data, biomass is expressed as molar concentrations of carbon (12.01 g C = 1 mol C) — we do not suggest that biomass is a molar quantity. Broken diatom frustules and protists lacking intact nuclei were rarely seen, indicating that the filtering and experimental manipulations did not damage cells unduly.

Several taxa were grouped, since they could not be routinely separated (see details in Lovejoy et al. 2002b,c). For example, several *Thalassiosira* spp. were grouped together, and this group may also have included chains of *Porosira glacialis* (Grunow) Jørgensen. There were probably several species of small Cymatosiraceae. This family of diatoms is normally lightly silicified and often overlooked in water samples (Hasle et al. 1983). We initially attempted to identify these small cells using scanning electron microscopy, but the fragile cells were crushed during preparation, and other than identifying them as Cymatosiraceae, further taxonomic determination was not possible. *Phaeocystis* spp. have been grouped; *P. pouchettii* (Hariot) Lagerheim is considered to be the most common *Phaeocystis* species in these waters (Tomas 1997). Another prymnesiophyte, *Chrysochromulina* sp., and prasinophytes such as *Pyramimonas* spp. are best identified by scale morphology using transmission electron microscopy, which we did not do.

Chl *a* and nutrients were collected and measured as detailed by Lovejoy et al. (2002c). VSP were collected and enumerated using a modification of the Noble & Fuhrman (1998) technique. We filtered 1 ml of sample, preserved using a mixture of glutaraldehyde and paraformaldehyde (same concentrations as for protists) and stained with both SYBR I and SYBR II green (Molecular Probes) fluorescent DNA and RNA markers, respectively. The slides were stored upright at 2°C for 24 h, then stored frozen until examination (within 2 wk). The VSP were counted at 1000× magnification (details in Lovejoy et al. 2002c). Since virus decay rates are normally shorter than the 2 d interval used herein (Weinbauer & Suttle 1999), the net VSP production was probably systematically underestimated, but it is still useful for comparison purposes.

Samples of bacteria were preserved in 2% final concentration electron microscope grade paraformaldehyde. Not more than 1 wk later, samples were stained with DAPI and filtered onto black 0.2 µm Nuclepore membrane filters (Porter & Feig 1980, Lovejoy et al. 2002c). The slides were frozen and counted within 1 to 4 wk. A total of 400 to 800 cells per slide were counted at 1000× magnification. A factor of 20 fg C per cell was used to convert bacterial numbers to biomass carbon (Fuhrman 1992). For comparison with nutrient data, biomass is expressed in molar concentrations of carbon (12.01 g C = 1 mol C).

RESULTS

Nutrients

Initial nitrate+, SRP and Si concentrations in the 13 m water used in the experiment were high (Table 1). Ammonium concentrations were below the detection limit of <0.1 µmol l^{-1}. At t_s (3 d after collection and before experimental intervention), nitrate+, SRP and Si concentrations had fallen slightly from the initial values (Table 1). During the course of the experiment, cumulative nutrient consumption was greater in the NEW than the REC treatment (Fig. 1). Statistical tests (2-way ANOVA, repeated-measures at t_{s+2}, t_{s+4} and t_{s+6}) indicated significant differences between the NEW and REC treatments for nitrate+ and SRP consumption. Specifically, nitrate+ consumption was significantly greater in the NEW treatment ($p = 0.012$) with no effect of sampling day or significant interactions. For SRP there was a significant treatment effect ($p = 0.007$) and a significant day effect

Table 1. Nutrient and chlorophyll *a* (chl *a*; µg l^{-1}) concentrations. Nitrate+ (nitrate and nitrite), soluble reactive phosphorus (SRP) and Si given as µmol l^{-1}. t_i: initial values at time of collection; t_s: average (SE; n = 4) start values for experiment determined after 3 d pre-incubation; t_{s+2}, t_{s+4}, t_{s+6}: average (SE; n = 2) concentrations at subsequent 2 d intervals. t_{s+6} was final sampling. NEW: 'new-nutrient' treatment; REC: recycling treatment

Day Treatment	Nitrate+	SRP	Si	Chl *a*
t_i	11.08	1.33	25.04	0.32
t_s	9.85 (2.17)	1.16 (0.12)	21.69 (0.89)	0.99 (0.54)
t_{s+2}				
NEW	4.82 (3.01)	0.54 (0.24)	16.19 (4.03)	3.31 (0.75)
REC	9.63 (1.41)	1.11 (0.14)	21.98 (0.51)	1.04 (0.18)
t_{s+4}				
NEW	1.39 (0.21)	0.19 (0.01)	10.27 (4.30)	3.05 (0.25)
REC	7.08 (0.34)	0.86 (0.14)	19.58 (1.01)	1.06 (0.56)
Final, t_{s+6}				
NEW	0.65 (0.17)	0.08 (0.02)	7.06 (3.86)	1.31 (0.09)
REC	2.03 (0.91)	0.54 (0.08)	17.05 (0.42)	3.53 (2.07)

(p = 0.01), with a steady consumption from t_{s+2}, t_{s+4} to t_{s+6}, but no significant interaction. Si consumption was more variable, with no statistically significant difference between treatments (p = 0.154). There was a significant effect of sampling day (p = 0.001) and a significant interaction between treatment (NEW vs REC) and day (p = 0.037). During the experiment, ammonium concentrations were between 0.1 and 0.2 µM, except in the NEW treatment on Day t_{s+4} (4 d after the first intervention), when concentrations were 0.6 to 0.8 µmol l^{-1}.

A greater proportion of available nutrients were consumed in the NEW than the REC treatment (Fig. 2). On average, >50% of P and nitrate+ was consumed in the NEW treatment in the 2 d following the start of the experiment (t_{s+2}). In contrast, it was only at the end of the REC experiment (t_{s+6}) that >50% of available N had been consumed. For both treatments and all nutrients, overall nutrient consumption was never significantly correlated with ambient nutrient concentration (Pearson's correlation, n = 16, p > 0.05 for all tests).

By the final day of the experiment, an average of 96% of initial plus added nitrate+ in the NEW treatment had been consumed compared to 85% in the REC treatment; this translated into an average total N utilization of 2.52 µmol l^{-1} d^{-1} in the NEW treatment compared to 1.49 µmol l^{-1} d^{-1} in the REC. Similarly 95.4% of the initial + added SRP had been consumed in the NEW treatment by the end the experiment, but only 60% of that supplied was consumed in the REC. In the NEW treatment, 71% of the Si had been consumed compared to only 33% in the REC.

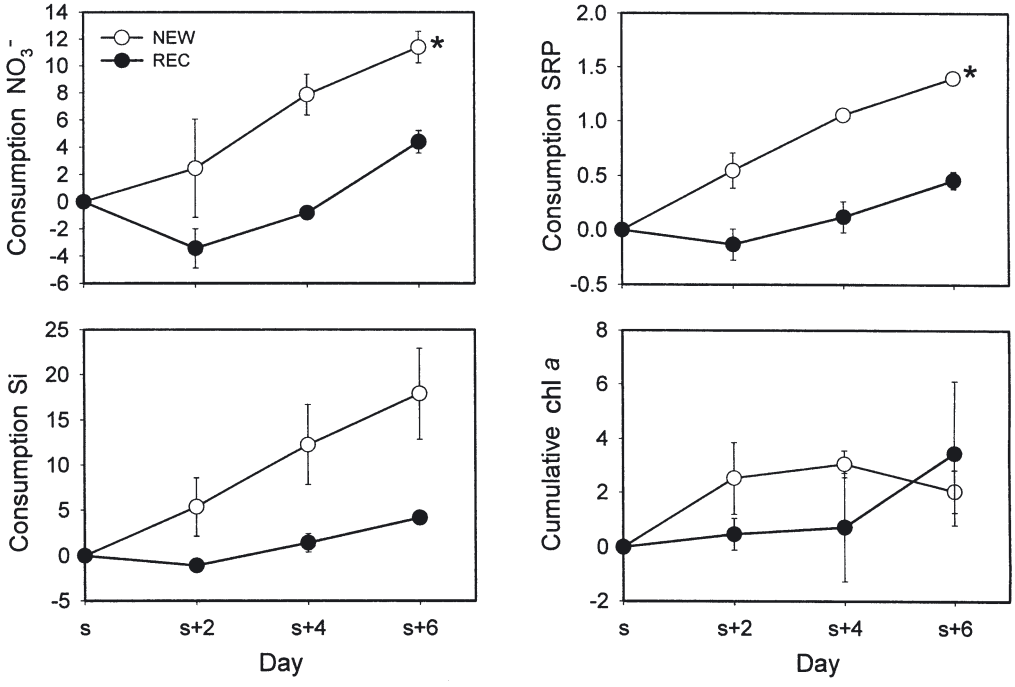

Fig. 1. Average (±SE) net accumulated nutrient consumption (µmol l^{-1}) and chlorophyll *a* (chl *a*) production (µg l^{-1}) from t_s to t_{s+6}. *: Statistically significant differences in final cumulative values. NEW: 'new-nutrient' treatment; REC: recycling treatment; SRP: soluble reactive phosphorus; s: start of experiment; s+2, s+4, s+6: 2, 4 and 6 d from start of experiment, respectively

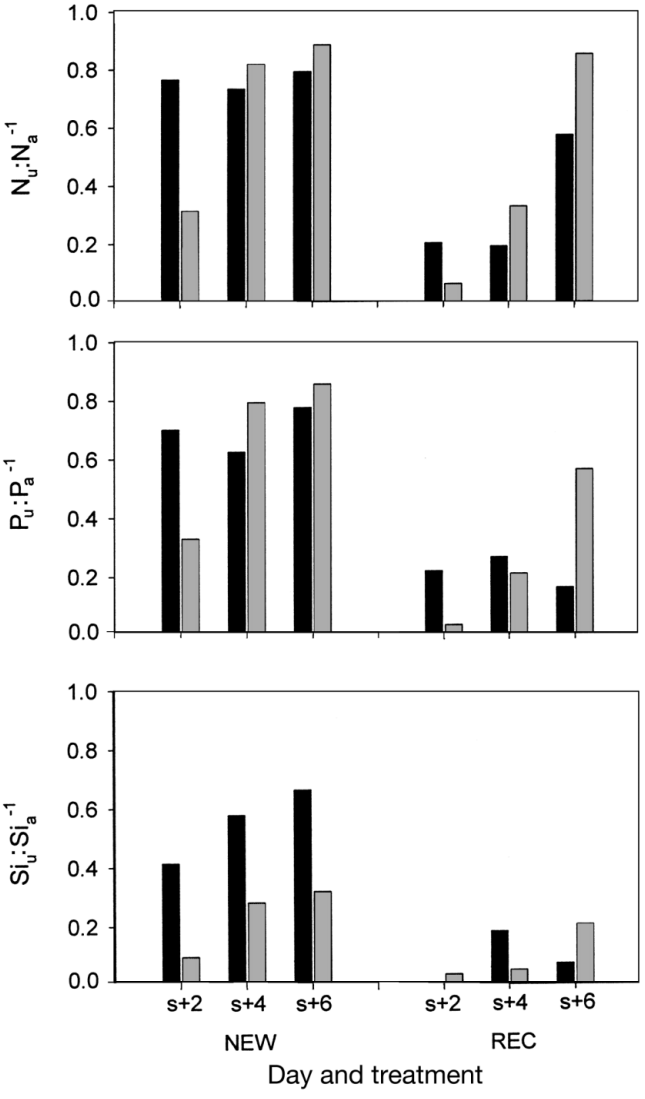

Fig. 2. Net consumption of nutrients (nitrate+, SRP, and Si) as proportion of nutrients available for each period between sub-sampling. Data are for 2 replicate microcosms for each treatment (black bars = A, gray bars = B). Subscripts 'u' and 'a': nutrients consumed and nutrients available, respectively

During the course of the experiment, there was a linear relationship between net nitrate+ and SRP consumption ($r = 0.95$, $p < 0.001$, N:P ratio of 8.8), which was less than the Redfield ratio (16:1). In contrast, there was no overall relationship between nitrate+ and Si consumption. Both nitrate+ and SRP consumption were significantly correlated with total protist production ($r = 0.72$, $p = 0.008$ and $r = 0.84$, $p < 0.001$, respectively).

Biological standing stocks

The concentration of chl *a* at t_i was low (0.32 µg chl *a* l^{-1}) and increased ca. 3-fold over the initial 3 d period (Table 1). At the end of the experiment, chl *a* concentrations were on average slightly higher in the REC than the NEW treatment. This was due to an increase in one of the REC replicates (B) measured on Day t_{s+6}. This meant that there was no significant difference in the average cumulative increase in chl *a* between treatments (Fig. 1). At the end of the experiment, chl *a* concentrations in the <2.0 µm size fraction were <5% of total chl *a*, with no significant differences between treatments. In contrast, there was a significant difference in estimated protist biomass carbon (see next paragraph), resulting in ratios of protist C to chl *a* that were 3 to 4 times higher in the NEW (average 79 µg C $µg^{-1}$ chl *a*) than the REC treatment (average 23 µg C $µg^{-1}$ chl *a*).

Total protist biomass (phytoplankton and heterotrophic protists) was initially low and increased on average 2.5-fold by t_s (Table 2). At t_i, 78% of the protist community biomass C was made up of phototrophs (cells with chl *a*) and 22% heterotrophs. By the end of the experiment, average total protist biomass was greater in the NEW than the REC treatment (Table 2), the result of significantly higher total production in the NEW than the REC treatment (2-way repeated measures analysis of variance, $p = 0.04$). In both treatments, net biomass production from t_s to t_{s+6} was dominated by phototrophs (Fig. 3). However, the patterns of accumulated photosynthetic protist production differed between treatments, with a peak at t_{s+4} in the NEW treatment, but little accumulation in the REC one until the last day, when there was increase in one of the replicate microcosms (REC B). The net accumulated biomass of heterotrophic protists, bacteria and viruses was similar in the 2 treatments (Fig. 3). Initial (t_i) VSP concentrations were ca. 1.4×10^9 l^{-1}, but fell to half after 3 d, when the treatment began, thus raising

Table 2. Concentrations of protists (µmol l^{-1}), bacteria (µmol l^{-1}) and viruses (VSP; µmol l^{-1}). All protists: sum of phototrophic (PhotoP) and heterotrophic (HeteroP) protists. Further details as in legend to Table 1

Day Treatment	All protists	PhotoP	HeteroP	Bacteria	VSP (10^9)
t_i	1.01	0.78	0.22	0.16	1.41
t_s	2.54 (1.49)	2.48 (1.44)	0.06 (0.04)	0.26 (0.05)	0.55 (0.30)
Final t_{s+6}					
NEW	12.8 (0.3)	11.7 (0.1)	0.87 (0.23)	0.85 (0.22)	1.81 (0.89)
REC	7.1 (3.2)	7.0 (3.3)	0.26 (0.05)	1.58 (0.24)	3.48 (0.72)

concentrations again to above the initial values by the end of experiment (Table 2). Initial bacterial concentrations were ca. 0.95×10^8 cells l^{-1}. At t_s, concentrations had increased on average to 1.54×10^8 cells l^{-1} (n = 4, SE = 0.30×10^8). By the end of the experiment, average concentrations had increased to 5.08×10^8 cells l^{-1} (n = 2, SE = 1.37×10^8) in the NEW treatment and 9.52×10^8 cells l^{-1} (n = 2, SE = 1.47×10^8) in the REC. Compared to the initial values, the ratio of VSP to bacteria was lower at t_s (average 3.5) and remained lower throughout the experiment until the final day, when average values were ca. 3.6 for both treatments. Bacterial biomass was always low compared to protist biomass. The estimated bacterial biomass of 0.16 µmol C l^{-1}, calculated using a standard conversion factor of 20 fg C $cell^{-1}$, represents 13.4% of total particulate carbon (protist + bacterial). By the end of the experiment, bacteria made up a slightly greater proportion of the biomass in the REC treatment than in the NEW (Table 2). There was no net production of either large (20 to 200 µm) ciliates and dinoflagellates, or smaller (2 to 20 µm) heterotrophic flagellates in either treatment (data not shown), which meant there were no differences in total heterotrophic protist biomass between treatments at the end of the experiment (pooled data shown in Fig. 3).

Protist species responses

Initially diatoms accounted for ca. 47% of total protist biomass. By the end of the experiment the proportion of diatoms had increased in both treatments with a slightly higher proportion in the NEW (84 to 90%) than the REC (76 to 81%), with 1 or 2 species or species-groups accounting for over 40% of the biomass at the end of the experiment. The remainder of the protist biomass was primarily photosynthetic flagellates, the 2 most abundant species accounting for less than 2.2% in the NEW but up to 16% in the REC treatment (Table 3).

Small, oval, 6 to 8 µm centric diatoms (Cymatosiraceae) were not detected initially at t_i, but had appeared in all microcosms by t_s, before the first manipulation. By Day t_{s+2}, the biomass of this group had continued to increase in the NEW treatment, but had fallen in the REC treatment. In one of the NEW treatments (A), Cymatosiraceae biomass reached maximum levels on t_{s+4} and remained high up to the end of the experiment in that microcosm (Table 3), accounting for 45% of total biomass. In the other NEW container (B), *Navicula granii* (Jørgensen) Gran (a ribbon-forming pennate diatom) was a biomass dominant, achieving maximum biomass at t_{s+4}.

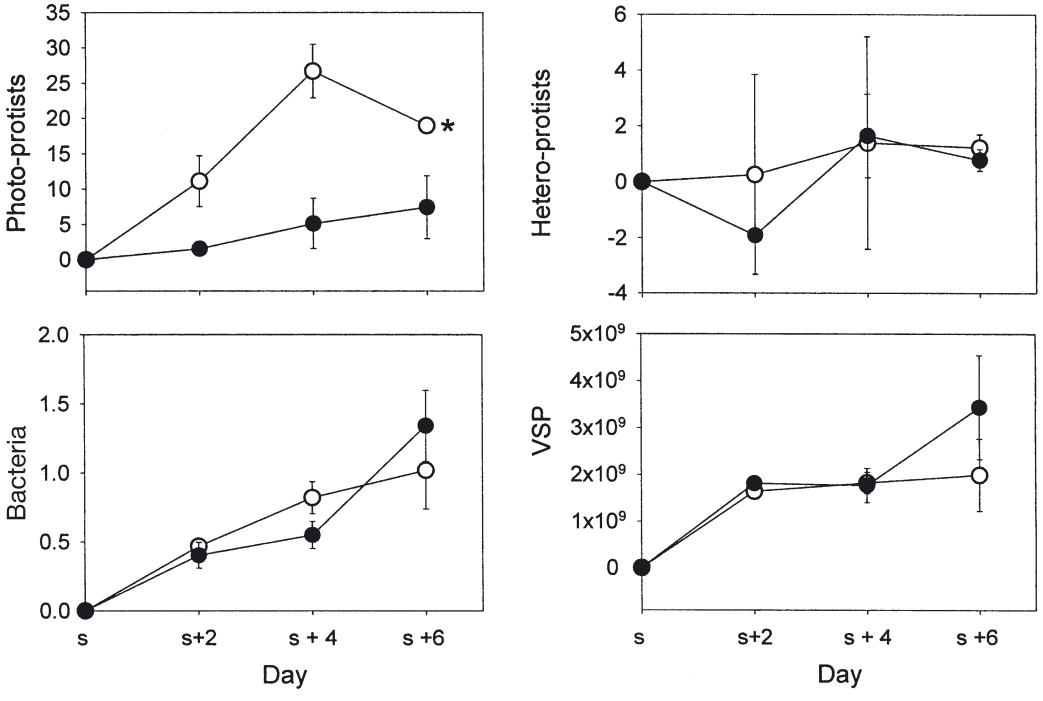

Fig. 3. Net cumulative biological production averages (±SE) for the 2 treatments (µmol C l^{-1}) from t_s (starting from 0 net production) to t_{s+6}. (○) NEW treatment; (●) REC treatment. Phototrophic protists (Photo-protists) comprise all protists containing chlorophyll (including photosynthetic flagellates and dinoflagellates); heterotrophic protists (Hetero-protists) are non-photosynthetic organisms including flagellates, dinoflagellates and ciliates. Cumulative net production of virus-sized particles (VSP) is expressed as virus l^{-1}. *: Statistically significant differences in final cumulative values

Table 3. Biomass (µmol l^{-1}) at each sampling of the 2 most abundant diatom and photosynthetic flagellates (PNAN) taxa (i.e. functional taxonomic units, FTU) that comprised dominants at the end of the experiment. A, B: replicate microcosms. Percentage contribution of each FTU to total biomass on each sampling occasion is given in parentheses. nd: not detected

Taxon	Time interval		
Microcosm	t_{s+2}	t_{s+4}	t_{s+6}
Diatoms			
NEW A			
Cymatosiraceae spp.	5.61 (49.2)	6.15 (19.5)	5.65 (45.2)
Thalassiosira spp.	1.62 (14.2)	3.93 (12.4)	1.97 (15.8)
NEW B			
Thalassiosira spp.	9.51 (37.9)	8.77 (51.0)	4.48 (31.0)
Navicula granii	4.49 (26.1)	6.63 (44.8)	1.31 (10.0)
REC A			
Navicula transitans	0.09 (2.8)	0.18 (2.7)	1.30 (32.8)
Nitzchia fridgida	0.98 (31.9)	0.14 (2.1)	0.44 (11.1)
REC B			
Thalassiosira spp.	1.27 (25.9)	3.51 (35.2)	7.11 (68.5)
Pauliella taeniata	0.32 (6.4)	0.13 (1.3)	0.28 (2.7)
PNAN			
NEW A			
Eutriptiella sp.	nd	nd	0.18 (1.4)
Chrysochromulina spp.	0.03 (0.2)	0.04 (0.1)	0.16 (1.3)
NEW B			
Phaeocystis spp.	0.19 (1.2)	0.29 (1.9)	0.27 (2.1)
Pelagophyte (unidentified)	nd	nd	0.00 (0.04)
REC A			
Phaeocystis spp.	0.05 (1.5)	0.05 (0.7)	0.34 (8.5)
Pyramimonas spp.	nd	0.02 (0.3)	0.10 (2.6)
REC B			
Phaeocystis spp.	0.06 (1.3)	0.97 (9.7)	1.62 (15.6)
Micromonas pusilla	0.03 (0.7)	0.06 (0.6)	0.04 (0.4)

Thalassiosira spp., large chain-forming centric diatoms, were among the final biomass dominants in the 2 NEW and 1 of the REC treatments (Table 3). In the NEW treatment, the maximum biomass of *Thalassiosira* spp. occurred early, as described above for other diatoms, and declined by t_{s+6} (Table 3). In the REC treatment, diatom growth was delayed compared to the NEW treatment. In the REC A microcosm, 2 pennate diatoms, a large single-celled *Navicula* species (*N. transitans* Heimdal) and *Nitzchia fridgida* Grunow, which forms arborescent colonies, were biomass dominants. These 2 species made up over 40% of the t_{s+6} biomass-C; however, the total was <2 µmol l^{-1}, markedly less than final values of the 2 dominant diatoms in the other microcosms (>5 µmol l^{-1}, Table 3). In the REC B microcosm, *Thalassiosira* spp. had increased between t_{s+4} and the final day and *Pauliella taeniata* (Grunow) Round & Basson, another ribbon-forming pennate diatom, had the second highest biomass (Table 3).

Prymnesiophytes were the dominant flagellates in both treatments, with 6 to 10 µm *Chrysochromulina* spp. in the NEW A microcosm, and small colonies and single cells of *Phaeocystis* spp. in the others. In the REC treatment, *Phaeocystis* spp. made up 8.5% of the final biomass in Microcosm A and 15.6% in B. Maximum biomass of *Phaeocystis* was in REC B (>1.6 µmol l^{-1} at t_{s+6}; Table 3).

Ciliates and dinoflagellates were also present, but were not among biomass dominants at t_{s+6}. Maximum dinoflagellate biomass was noted at t_{s+4} in the REC B microcosm for *Protoperidinium bipes* (Paulsen) Balech (2.19 µmol l^{-1}) and *Actiniscus pentasteria* (Ehrenberg) Ehrenberg (1.43 µmol l^{-1}). Both these species are heterotrophic and ingest diatoms and flagellates. While these 2 species accounted for over 50% of the biomass on t_{s+4} in the REC B microcosm, they did not contribute substantially to the biomass on t_{s+6}.

In summary, with the exception of the small Cymatosiraceae, all the eventual dominants at t_{s+6} were present in low numbers in the original water. Net production of the Cymatosiraceae was substantial in the NEW but not the REC treatment. Net production of *Thalassiosira* spp. was high in 3 of the 4 microcosms. Ribbon-forming diatoms were also an important part of phototrophic biomass, contributing 4 to 7 times more production in the NEW than in the REC treatment. Net *Phaeocystis* spp. production comprised a much greater proportion of total production in the REC microcosms, but in absolute terms the production of *Phaeocystis* spp. in the NEW B microcosm was nearly as high as in REC A. The protist communities in the microcosms were taxonomically diverse, with 151 taxa observed in the NEW and 155 in the REC treatment.

DISCUSSION

Species outcomes

Following the initial bloom of small cymatociracians between t_i and t_s, the net production by individual species or species-groups between t_{s+2} and t_{s+6} varied in the microcosms over time and between treatments. These results underline the dynamic nature of protist community structure over short time intervals

(days), even at extreme cold temperatures. Under relatively controlled environmental conditions there were some divergences in species outcomes between duplicates. Certain species made brief appearances for 1 or more sampling intervals and then became minor constituents. Despite this, there were clear differences between treatments in the timing of the onset of high production by phototrophs, in overall production, and in nutrient utilization. In the NEW treatment that simulated advective conditions, diatoms dominated phototrophic biomass within 2 d and consumed 30 to 80% of the available nitrate. *Thalassiosira* spp. co-occurred with other diatoms under these conditions. In contrast, in the REC treatment that simulated a stratified water column, there was either no bloom after 6 d, or *Thalassiosira* spp. co-occurred with the prymnesiophytes *Phaeocystis* spp. In polar waters, *Thalassiosira* spp. commonly co-occurs with other diatoms or *Phaeocystis* spp., and this genus is considered to be extremely opportunistic (Kang & Fryxell 1993). The rapid diatom response in the NEW treatment was typical of a spring bloom (Sieracki et al. 1993), with both N and Si being rapidly consumed (Figs. 1 & 2). This bloom community and high nutrient consumption were maintained over 6 d under the simulated advective regime. In contrast to our initial prediction, there was no initial bloom in the REC treatment, despite the favorable nutrient concentrations.

Ratio of C to chl *a*

The ratios of C to chl *a* varied 3.5-fold between treatments. The ratios were within theoretical limits (Cloern et al. 1995, Geider et al. 1997): at the lower limit in the REC treatment and at the upper limit in the NEW treatment. The taxonomic differences between the communities may be one reason for the large differences in the C:chl ratio. Chloroplasts occupied a relatively small proportion of the cell volume of both the ribbon diatoms and the Cymatosiraceae that dominated the NEW microcosms (ca. 15 to 25%; C. Lovejoy pers. obs.). The higher C to chl *a* ratio of the NEW treatment may also have indicated physiological differences in the 2 communities, as C to chl ratios increase under nutrient stress (Laws & Bannister (1980). At $t_{s+6,}$ the final day, the ratios were lower in the REC treatment (20 to 24; calculated from Tables 1 & 2), which remained nutrient-replete, than in the NEW treatment (67 to 90; calculated from Tables 1 & 2), in which final nutrient concentrations were low, and in which the rapidly growing community had utilized 89 to 90% of available nutrients (Fig. 2).

Bacteria and heterotrophic protists

There were no differences between treatments in net accumulated bacterial or heterotrophic protist biomass. Ciliates and dinoflagellates are important diatom grazers and have been credited with the prevention or delay of nitrate-dependent diatom blooms (Levinsen & Nielsen 2002). Protistan (microzooplankon) grazing has also been associated with the maintenance of high-nutrient, low-chlorophyll regions (Landry et al. 1997). Ciliates and dinoflagellates (20 to 200 µm microzooplankton) are also major flagellate predators. Although no macrozooplankton were present, the experimental design ensured that in both treatments 25% of the larger ciliates and dinoflagellates (flagellate predators) and nanoflagellates (2 to 20 µm bacterial predators) would have been removed every 2 d by filtration. Total heterotrophic protist growth fluctuated over time and among microcosms; however, there was no net biomass gain of either micro- or nano-sized heterotrophs in either treatment on the final day of the experiment, suggesting that the trophic interactions between these 2 groups were similar in both treatments.

Net bacterial growth was positive in both treatments (Fig. 3). We expected that bacterial growth would be greater in the REC treatment, in which there was no cell loss (the <2.0 µm fraction, which included bacterial cells, being returned to the cultures) and higher concentrations of DOM would have been available; however, there was no difference between the 2 treatments. Viral biomass was also returned to the REC treatment along with DOM, but we detected no differences in viral production between treatments (Fig. 3). Recently, pico-eukaryotes have been identified as potentially important bacterial grazers (Guillou et al. 2001). We did not specifically search for <2 to 3 µm heterotrophs, but these small predators have been identified in a variety of marine systems (Moreia & López-García 2002), including recently from the Arctic (C. Lovejoy, C. Pedrós-Alió & R. Massana unpubl. data). Any increase in bacterial production in the REC treatment may well have been offset by a concomitant increase in inter-size-class grazing. Alternatively, the higher overall photosynthetic production in the NEW treatment may have resulted in an increase in bacterial substrate due to DOM release by the photosynthetic community. The average net production by photosynthetic protists by the end of the experiment was 20.7 µmol C l^{-1} in the NEW versus 8.3 µmol C l^{-1} in the REC (Fig. 3) treatments. An average DOM release of 30% would provide an additional 3.6 µmol C l^{-1} available for bacterial growth in the NEW treatment, and at bacterial growth efficiencies of ca. 33%, this would account for 1.2 µmol C l^{-1}, equal to the net bacterial

production over the course of the experiment (Fig. 3). These assumptions are not unreasonable, in that Mei et al. (2002) found similarly high levels of DOC release by NOW phytoplankton in the summer of 1998. These calculations suggest that bacteria in the REC treatment may have been substrate-limited, as were bacteria in the NOW polynya later in the season (Middelboe et al. 2002). In summary, in both treatments there was net bacterial growth but no net heterotrophic protist (2 to 200 µm) growth. Either increased substrate in the NEW, or inter-size class grazing in the REC, or a combination of the two, could account for these results.

Nutrient utilization and biological responses

We found statistically significant differences between treatments, with nutrients taken up at greater rates and more quickly in the advective (NEW) treatment than the recycled (REC) treatment. Since irradiance levels and >2.0 µm loss rates were the same for both treatments, either the nutrient supply rate or the removal of dissolved constituents and <2.0 µm particles, or both, triggered the initial diatom growth in the NEW treatment. Within the dissolved fraction, the concentration of dissolved inorganic C may have varied between treatments. Dissolved CO_2 concentrations are reported to influence phytoplankton assemblages, with diatoms favored under low CO_2 (150 ppm) concentrations and *Phaeocystis* spp. favored under high CO_2 (750 ppm) concentrations (Tortell et al. 2002). However, Tortell & Morel (2002) suggested that in experiments lasting <11 d, community composition is not affected by CO_2 concentrations. In our experiment, there was poorer diatom growth in the REC treatment after only 2 d, so other factors are more likely to have influenced the species differences between our NEW and REC treatments. However, given that we did not measure CO_2, it is not possible to eliminate CO_2 levels as a potential influence on species composition.

Over the course of the experiment, until t_{s+6}, nutrients were abundant in both the NEW and REC treatments. This was a consequence of the experimental design in the NEW treatment (where deep [200 m] nutrient-rich water was added every 2 d) and the slow consumption of available nutrients in the REC treatment (Figs. 2 & 3). The community difference between treatments implied that factors other than nutrient concentrations affected the timing and intensity of the diatom bloom. Diatoms are the most important photosynthetic protists in polar waters, where nutrients tend to be high and the growing season is short. In particular, ribbon-forming pennate diatoms and centric colonial diatoms, including *Chaetoceros* spp., and *Thalassiosira* spp., are frequently reported as dominants (von Quillfeldt 2000, 2001). *Phaeocystis* spp. are also frequently reported prior to, in conjunction with, or following diatom blooms. The timing and species composition of blooms is frequently related to hydrological events (Pondhaven et al. 1999, Strom et al. 2000, Wassmann et al. 2000), and while dominant species and the conditions during a bloom are often reported, species, nutrient concentrations and the mixing history of waters prior to blooms are rarely known. There is no agreement on what or how physical factors determine the population growth and dominance by diatoms versus prymnesiophytes such as *Phaeocystis* spp. (Wilson et al. 1986, Kang & Fryxell 1993, Schloss & Estrada 1994, Eilertsen et al. 1995, Leventer & Dunbar 1996, Andreason & Wassmann 1998). This question is important, since the relative importance and timing of blooms by these groups is thought be a major factor determining biogenic carbon fixation and sequestration in polar waters (Smith et al. 1991, Arrigo et al. 1999, 2000, DiTuillo et al. 2000).

The dominant loss mechanisms under advective and stratified conditions differ markedly. Both dissolved organic matter and particulate material are lost under advective conditions, while under stratified conditions the primary loss is particulate material due to grazing by protozoan and metazoan zooplankton (Levinsen et al. 1999, 2000) or by sinking out of the euphotic zone as individual cells, cellular aggregates or fecal pellets. This implies that DOM would be retained under stratified conditions, and taxa such as *Phaeocystis* spp. that are able to use DOM (Peperzak et al. 2000) should follow the initial diatom bloom. Other species may be favored in the absence of DOM or constituents of DOM such as dissolved organic nitrogen (DON). For example, nitrate consumption is frequently inhibited in the presence of ammonia and DON (Harrison et al. 1996). Phytoplankton constantly release some DOM (up to 50% of fixed biogenic carbon in the NOW, Mei et al. 2002) and DON is released when phytoplankton are stressed or damaged by grazers (Ward & Bronk 2001). DON could accumulate in the absence of advective processes and suppress nitrate consumption, irrespective of nitrate concentrations. Biochemical constraints of molecular processes may explain this sort of regulation in nitrogen metabolism. The regulatory P_{II} transduction proteins (enzymes that control the activity of other key metabolic enzymes) largely control microbial nitrogen metabolism, and genes encoding for these proteins are regulated by external concentrations of ammonium, nitrate, nitrite and carbon sources (Arcondéguy et al. 2001). In our REC treatments, the accumulation of DON may have inhibited nitrate+ consumption. Further experiments specifically investigating the effect of DON pools on protist food webs are required to test this proposition.

Aside from DOM and the major nutrients, there are several other differences between advective and recycled systems. For example trace-metal composition and chelation state are altered by biological activity, which in turn may have feedbacks to the microbial community (Morel & Price 2003). The trace-metal characteristics in the REC treatment would be expected to be different than in the deep (200 m) water used in the NEW treatment. In addition, metabolites from both protists and bacteria would accumulate under recycled conditions. Metabolites of several groups of bacteria are highly toxic to specific protist groups (Lovejoy et al. 1998, Long et al. 2003), and selective mortality may have been important in determining the species outcome in the REC treatment. Similar selective pressures may occur in non-advective regions such as stratified water columns or gyres.

The NOW polynya is extremely dynamic, and characterized by interleaving and layering of different water masses (Melling et al. 2001, Lovejoy et al. 2002a). Between April and July 1998, ribbon pennate diatoms and *Thalassiosira* spp. were among the major contributors to biomass in the NOW polynya. *Phaeocystis* spp., although frequently seen as single cells, did not reach high concentrations or form colonies except for a few isolated stations where there was little water-mass interleaving (Lovejoy et al. 2002a,b). As with all experiments using small containers, some caution is required to avoid over-interpretation. For example, we did not consider the effects of higher trophic levels on either differential losses or nutrient recycling. Bacteria and protist populations at the end of the experiment were similar to those in the polynya in June, suggesting that container effects were minimal. Our experimental results concur with our field observations that diatoms are favored under advective conditions in the NOW polynya. Our results also imply that in other regions intermittently cut off from advective nutrient supply, prymnesiophytes such as *Phaeocystis* spp. could become common. The late-onset *Phaeocystis* spp. blooms in areas such as Terra Nova Bay in the Ross Polynya, Antarctica (Arrigo et al. 1998), may be an example of these conditions.

Our results indicate that some groups of protists, such as diatoms, are sensitive to advective nutrient supply and losses, and that bulk nutrient concentrations are relatively less important. High production along fronts and eddies, as well as the occurrence of diatom-dominated communities along horizontal surfaces of shear flow (Dekshenieks et al. 2001, Alldredge et al. 2002) suggest that advective processes are crucial in maintaining sustained production by diatoms. These interfaces may contribute substantially more to net oceanographic production than bulk parameters such as chl *a* and nutrient concentrations would suggest. Our results indicate that, in addition, nutrient cycling and consumption may have unique characteristics along these frontal regions. We found a similar response by diatoms to advective conditions in another experiment conducted several weeks later (Lovejoy et al. 2002c), when starting conditions were markedly different. Prior to that later experiment, there had been a persistent diatom bloom in that region of the NOW polynya for over a month, with *in situ* nutrient concentrations close to detection limits; in the experiment, large ciliates and dinoflagellates became dominant in a recycled treatment, whereas the diatom bloom (dominated by *Thalassiosira* and *Chaetoceros* species was maintained in an advective treatment for a further 8 d. The results of the present study extend our previous conclusions. Here we found that the diatom response to advection was not an artifact of depleted nutrients and pulsed supply. More importantly, in the current study, we found a surprising lack of early nutrient utilization under recycled conditions. This was not observed in the subsequent study, as nutrients remained exhausted during the recycling treatment. Both studies (see Lovejoy et al. 2002c) were conducted at 1 irradiance level and using 1 loss rate, but under different starting conditions. Further studies using semi-continuous culture techniques but differing loss and irradiance levels may find similarly surprising results. Under the irradiance levels used here, the importance of advective versus recycled conditions was evident; under low irradiance this was not a major factor in determining species outcome (C. Lovejoy et al. unpubl. data).

In contrast to our initial prediction that simulated stratified conditions (our REC treatment) would result in nutrient drawdown, we found that advective conditions (our NEW treatment) resulted in greater consumption of nutrients and lower final nutrient concentrations than non-advective (REC) conditions. Heterotrophic protist, bacteria and virus net production rates were similar under both sets of conditions, whereas a persistent diatom bloom occurred under the advective regime. Consistent with the results of the current study and of Lovejoy et al. (2002c), Booth et al. (2002) and Tremblay et al. (2002) speculated that periodic advective nutrient inflows of Arctic waters into the western and central parts of the NOW could be responsible for ongoing diatom production. As Tremblay et al. (2002) pointed out, climatic changes due to global warming may have non-intuitive impacts on the structure and functioning of this currently productive ecosystem. Rather than increased production due to a longer ice-free season, increasing temperatures and early stratification in the NOW polynya would probably lead to lower overall production. Our results are consistent with this conclusion and further suggest that

the initial diatom bloom could be replaced by other protist species, potentially reducing the food availability to higher trophic levels, in addition to having an impact on carbon and nutrient cycling.

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