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Synthesis of particulate and extracellular carbon by phytoplankton at the marginal ice zone in the Barents Sea

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Abstract. Large phytoplankton biomass accumulates during ice-edge blooms in Arctic waters, where taxa such as diatoms or the prymnesiophyte *Phaeocystis pouchetii* usually dominate. Based on characteristics from temperate phytoplankton, we hypothesized that in Barents Sea waters, a larger fraction of primary production would be extracellular (for synthesis of colonial mucilage) during periods of dominance by *P. pouchetii* as opposed to periods when diatoms dominated. This alternation of *P. pouchetii* and diatoms would affect the relationship between the particulate and dissolved carbon pools in the upper water column of the marginal ice zone (MIZ). Results presented in this paper do not support this hypothesis. Although *P. pouchetii* contributed strongly to the extracellular carbon pool (mucilage and dissolved organic carbon, DOC) during an ice-edge bloom in May 1993, arctic diatoms contributed an equal amount of exuded carbon. Three process stations visited along a north-south transect in the MIZ in the Barents Sea, presented between 36% and 55% of the primary production as extracellular carbon, defined as labeled organic matter which passes through a Whatman GF/C filter. No difference in the carbon allocation between diatom- and *P. pouchetii*-rich phytoplankton was observed in these stations. In contrast, the station located in ice-free waters had 18% of primary production in the extracellular fraction. These results (1) highlight similar carbon allocation for diatom- and *P. pouchetii*-dominated phytoplankton in surface waters of the Barents Sea during the spring and/or ice-edge bloom at the MIZ and (2) suggest that polar phytoplankton may be stronger producers of extracellular carbon, and possibly DOC, than previously thought.

1. Introduction

Large phytoplankton biomass accumulates during blooms in the Arctic ice edge [*Barnard et al.*, 1984; *Wassmann et al.*, 1990] with rates of primary production from 1 to 3 g C m^{-2} d^{-1} [*Rey*, 1991; *Smith et al.*, 1991]. A few phytoplankton species dominate in these blooms, mainly diatoms or the colonial form of the prymnesiophyte *Phaeocystis pouchetii*. While diatoms are often found in sediment traps and are believed to be a major component of the sedimenting particulate organic carbon [*Smetacek*, 1985, *Wassmann*, 1989], there is conflicting evidence about the fate of *P. pouchetii* blooms [*Wassmann*, 1994]. One of the main differences between these two phytoplankton taxa is the formation of the mucilaginous matrix in *Phaeocystis* spp. [*Lancelot and Mathot*, 1985; *Veldhuis and Admiraal*, 1985] and the question concerning the fate of the carbon fixed by photosynthesis [*Thingstad and Billen*, 1994]. This difference led us to hypothesize that a large fraction of the primary production during *P. pouchetii* blooms in the Barents Sea would be used to synthesize the colonial mucilage, and the difference in phytoplankton community composition would affect the particulate and extracellular carbon pools in ice-edge blooms and, ultimately, carbon sedimentation.

Photosynthetic rates of polar phytoplankton are dependent on temperature, irradiance and nutrients. Maximum assimilation numbers remain generally low, at about 1-3 mg C (mg chl *a*)$^{-1}$ h^{-1} [*Holm-Hansen et al.*, 1977; *Platt et al.*, 1982; *Gallegos et al.*, 1983; *Sakshaug and Holm-Hansen*, 1984, 1986; *Holm-Hansen and Vernet*, 1990; *Sakshaug and Slagstad*, 1991]. Maximum photosynthetic rates (P_{max}) values of 12-15 mg C (mg chl *a*)$^{-1}$ h^{-1} have been cited for *Phaeocystis pouchetii* [*Cota et al.*, 1994]. There are at least two possible interpretations for these high rates: (1) *P. pouchetii* can adapt to low temperatures and photosynthesize to levels comparable to tropical waters [*Laws et al.*, 1988]; or (2) part of the ^{14}C incorporated is not associated with particulate carbon but is in the mucilage and can be considered extracellular carbon [*Lancelot and Mathot*, 1985; *Veldhuis and Admiraal*, 1985]. Studies in the North Sea

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suggest that this extracellular carbon may be reutilized by the alga at night as indicated by ^{14}C incorporation into protein [*Lancelot and Mathot*, 1985] or, alternatively, enter the microbial loop [*Lancelot and Billen*, 1984; *Martinussen et al.*, 1990]. Photosynthesis versus irradiance (P versus I) curves of cultures and natural populations of the colonial stage of polar *Phaeocystis* spp. showed that this genus can produce up to 47% of the primary production as extracellular carbon (defined as the carbon not retained on a Whatman GF/C glass-fiber filter and includes carbon in the mucilage and dissolved organic carbon [*Matrai et al.*, 1995]).

The amount of extracellular carbon produced by phytoplankton has been a controversial subject for several decades [*Sharp*, 1977; *Fogg*, 1983; *Bjørnsen*, 1988; *Wood et al.*, 1992]. Excretion of carbon by photosynthetic organisms is a widespread process associated with photosynthesis [*Mague et al.*, 1980]. On average, phytoplankton excretes 5-25% of the carbon incorporated in particulate matter, both in monospecific cultures and in natural populations [*Fogg et al.*, 1965; *Mague et al.*, 1980] and the amount excreted is a constant proportion of photosynthetic rates. Several studies have indicated that a large proportion of photosynthetic carbon goes through a DOC phase [*Azam et al.*, 1983] for at least short periods of time [*Kirchman et al.*, 1991]. During spring bloom events, between 20 and 60% of photosynthate must go into the DOC pool to explain the DOC changes observed in the North Atlantic [*Kirchman et al.*, 1991]. Additional organic carbon excretion in phytoplankton seems associated with physiological imbalance due to events such as nitrogen limitation [*Hellebust*, 1965; *Myklestad et al.*, 1989; *Norrman et al.*, 1995], in particular under high-irradiance conditions [*Hellebust*, 1965]. In the field, the transfer of cells to higher irradiance might produce excess photosynthate [*Mague et al.*, 1980; *Wood et al.*, 1992]. Nutrient limitation is observed during late growth stages in batch cultures [*Myklestad*, 1974] or at the end of the spring bloom. High DOC concentrations have also been observed after *Phaeocystis* spp. blooms [*Veldhuis and Admiraal*, 1985; *Davidson and Marchant*, 1992]. This excess carbon excreted might be also associated with increased intracellular carbohydrate in diatoms [*Myklestad and Haug*, 1972; *Richardson and Cullen*, 1995] but this phenomenon was not observed in dinoflagellates [*Sakshaug et al.*, 1973].

In this study we present estimates of phytoplankton primary production at the marginal ice zone (MIZ) in the Barents Sea in May 1993. Rates of primary production into two fractions, particulate and extracellular, were measured in situ in four process stations. The sampling was designed to test the hypothesis that a larger fraction of primary production would be extracellular (mainly for the synthesis of colonial mucilage) during dominance by *P. pouchetii* as opposed to areas dominated by diatoms.

2. Materials and Methods

The central Barents Sea was sampled from the R/V *Jan Mayen* of the University of Tromsø from May 13 to 29, 1993. Sampling along a transect from 72°45.017'N, 30°21.014'E to 76°32.165'N, 32°55.526'E covered 17 stations, from station 534 on May 17 to station 551 on May 18. Stations along the transect were sampled at 6 depths corresponding to surface, 50%, 30%, 10%, 1%, and 0.1% surface irradiance. From May 18 to 27 we revisited four stations (station I to IV) along the transect for 36 hours each where in situ experiments on drifting buoys were performed (Table 1). The station locations were selected to sample the gradient from ice-free to ice-covered waters at the MIZ (Figure 1 and Table 1) and to represent phytoplankton populations dominated by either diatoms or the prymnesiophyte *Phaeocystis pouchetii* during different stages of the bloom. While drifting, we took vertical profiles every 6 hours or less. Data presented per station are averages of all the casts taken while drifting with the in situ moorings (n = 6-9), unless otherwise noted.

At each experimental station we deployed a Neil Brown Mark III conductivity-temperature-depth (CTD) profiler, which also had connected a SeaTech fluorometer (25-cm pathlength) and a Biospherical Instruments QSP-200L underwater sensor. Water samples were taken from 10 10-L

Table 1. Physical, Chemical, and Optical Properties at the Four Experimental Stations Visited in May 1993 for a 36-Hour Period

	Station			
	I	II	III	IV
Latitude	76° 22.9'N	75° 49.2'N	74° 59.2'N	73° 44.1'N
Longitude	32° 43.9'E	32° 30.5'E	31° 40.5'E	31° 00.4'E
Surface salinity, ‰	34.373	34.489	34.991	34.939
Surface temperature, °C	-1.835	0.815	2.832	3.674
Surface nitrate, μM	0.8	3.9	7.4	3.8
Surface silicic acid, μM	0.1	2.6	3.4	0.9
Mixed layer depth, m	36	14	65	61
Euphotic zone, m	15	26	35	38
Average surface PAR, μmol quanta m^{-2} s^{-1}	557	283	32	147
Daily incident PAR irradiance, mol m^{-2} d^{-1}	70.5	53.3	24.4	38.7
Ice cover, %	55	20-40	0-10	0
Water mass	Arctic Water	Polar Front	Atlantic Water	Atlantic Water

Mixed layer depth based on the salinity profile. Ice coverage at each station changed during the in situ deployments and it is shown as the range of values observed while on station. Water masses defined as in the work by *Loeng* [1991]. PAR denotes photosynthetically available radiation.

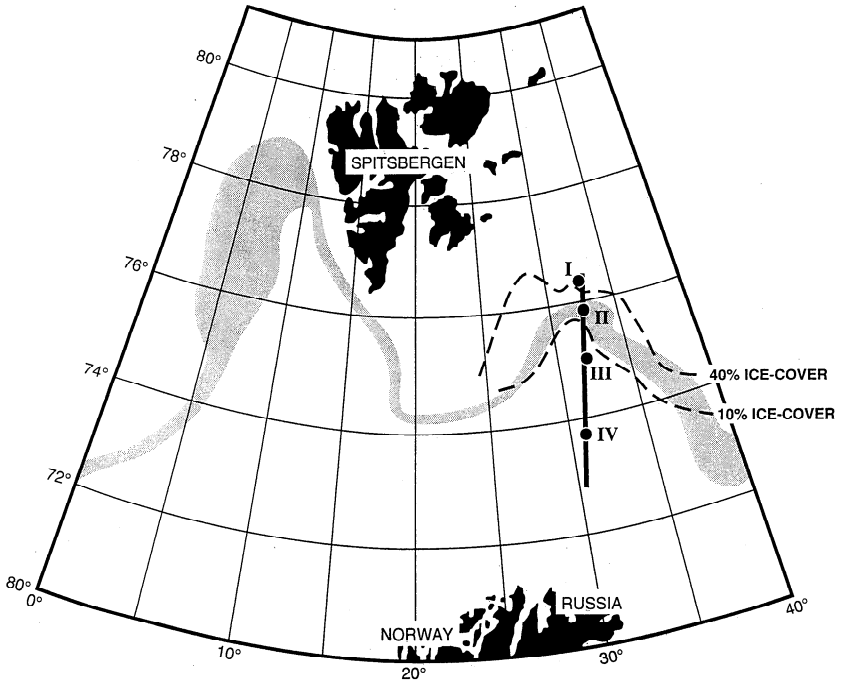

Figure 1. Map of the western Barents Sea describing the transect (solid line) and the four experimental stations (circles) visited in May 1993 (see Table 1 for locations). Ice cover is shown by the dashed line (40% and 10%). The Polar Front is shown by the shaded area.

Niskin bottles placed on a rosette, each fitted with teflon coated stainless steel closing springs. Surface photosynthetically active radiation (PAR) was measured continuously with a Biospherical Instrument QSR-240 scalar sensor mounted high on the ship's superstructure.

Phytoplankton taxa were identified and cellular volume determined from preserved samples under an inverted microscope. Twenty-five milliliter samples preserved in a mixture of glutaraldehyde and lugol [*Rousseau et al.*, 1990] were sedimented for 24 hours before analysis and examined in a Leitz DM IL inverted microscope. A minimum of 50-100 cells of the dominant phytoplankton species were counted. Cellular carbon for diatoms, flagellates and dinoflagellates was calculated following *Strathman*'s [1967] equations for diatoms and other phytoplankton. Cell volume was calculated to the closest stereometric shape for each taxon. Cell and colonial carbon calculations for *Phaeocystis pouchetii* followed *Rousseau et al.* [1990] for *Phaeocystis* sp. For diatoms, no colony estimates are available, only total cell number of free and colonial (e.g., *Chaetoceros socialis*) cells.

Chlorophyll *a* (chl *a*) and phaeopigments were measured with a Turner Designs AU-10. One hundred milliliters of each sample were filtered through a 25-mm Whatman GF/C filter and extracted with 10 mL of 90% aqueous acetone for 24 hours at 4°C in the dark. The samples were subsequently centrifuged and immediately analyzed following *Holm-Hansen et al.* [1965]. Calibration was done with pure chl *a* from SIGMA Chemical Co. In order to evaluate any loss of phytoplankton in the primary production incubations, the performance of the Whatman GF/C filter was compared to a 25-mm Whatman GF/F filter (nominal pore size of 0.7 μm) in retaining chl *a*. This comparison was carried out at all depths on the transect and at least once per station in stations I to IV. In addition, one profile of chl *a* in the <20 μm fraction (nanoplankton) was measured at each of the experimental stations by prefiltering the sample through a 20 μm Nytex mesh.

Inorganic nutrients (nitrate, nitrite, silicic acid and orthophosphate) were analyzed by a Technicon autoanalyzer following the methods of *Strickland and Parsons* [1968]. Samples were filtered through a 1 μm Nuclepore filter and stored at -20°C on board ship. Upon return to Tromsø the samples were shipped to the Institute of Marine Resources, Bergen and analyzed within one month.

Primary production was measured with 24-hour in situ incubations. Samples from the Niskin bottles were used to fill 125-mL screw-capped borosilicate glass bottles which were immediately injected with 5 μCi of ^{14}C-labeled sodium bicarbonate (ICN Corporation). The bottles were gently shaken and hung from a polycarbonate line at the same depth from which they were sampled. The line was attached to a free-drifting float in ice-free waters and to an ice floe in all other places. All samples were incubated for approximately 24 hours, starting between midnight and 0200 hours. The incubations were terminated by lifting the mooring and transporting the samples to the lab in the dark. Primary production was measured as the difference in incorporation of ^{14}C between two light and one dark bottles incubated at each depth; the dark bottle was kept in a refrigerator at 4°C during the incubation. Three samples were taken from each bottle: (1) 0.1 mL sample was added before the incubation to 0.25 mL of ethanolamine in a 20-mL scintillation vial for estimation of radiocarbon specific activity; after the incubation, (2) 3 mL of sample were pipetted into a 20-mL scintillation vial to measure radiocarbon assimilation to particulate and extracellular carbon; and (3) 100 mL of sample were

concentrated onto a 25-mm Whatmann GF/C filter at 15 mm Hg which collects the cells and lets through the mucilage from phytoplankton [*Gieskes and van Bennekom*, 1973; *Matrai et al.*, 1995]. This last step measured radiocarbon assimilated only into particulate carbon. The vials with the 3 mL sample and the filter were acidified for 24 hours with 0.25 mL of 10% HCl. After completing acidification, 3 mL of distilled water were added to the vials prepared in steps 1 and 3 to bring the same water content to all vials. Subsequently, 7 mL of Universol ES (ICN Biomedicals, Inc.) were added to all samples. Radioactivity in the samples was counted on a Beckman liquid scintillation counter at the University of Tromsø upon return from the cruise (June 1 to 3, 1993). All counts were corrected using an external quenching curve. In this way, carbon assimilated into particulate matter was measured from the radiocarbon activity retained in the Whatman GF/C filters (vial 3) and extracellular carbon (carbon assimilated to the mucilage and dissolved organic matter) was calculated from the difference between vials 2 (total primary production) and 3 (particulate primary production).

Production / biomass (P/B) was calculated as the ratio of primary production and chl *a* concentration at the same depth, in units of mg C (mg chl *a*)$^{-1}$ h^{-1} [*Falkowski*, 1981] where the daily production obtained from the 24-hours in situ incubations was divided by the effective light period, 18 hours. The average daily irradiance at depth was calculated from the measured incident radiation and the extinction coefficients at depth. The hourly average irradiance was then calculated by dividing the daily irradiance by 24 hours.

Phytoplankton carbon-specific growth rates (μ) were calculated according to *Eppley* [1980], $\mu = P_Z$ (C:chl)$^{-1}$, where P_Z is production per unit chl *a* at depth (mg C (mg chl *a*)$^{-1}$ d^{-1}), and C:chl is the carbon to chl ratio (mg C (mg chl *a*)$^{-1}$). P_Z is based on the in situ 24-hour incubations and C:chl ratios were based on values by *Rey* [1991] as presented in *Sakshaug and Slagstad* [1991], who calculated them from POC:chl ratios, by depth intervals, from an average of five cruises to the Barents Sea. Average carbon-specific growth rate values for the euphotic zone were estimated by calculating the integrated value by the trapezoid method and divided by the depth range.

3. Results

3.1. Transect

The transect started in ice-free waters of the central Barents Sea. It covered stations through the ice edge and into the pack ice (Figure 1). The ice edge (defined as the 40% ice coverage) followed the Polar Front. Surface temperatures in the transect varied from 3.6°C to -1.8°C and surface salinities from 34.9‰ to 34.3‰ (Table 1). According to *Loeng* [1991], the temperature-salinity diagrams at the surface corresponded to Atlantic waters (>3°C and >35‰), Polar Front (-0.5° to 2.0°C and 34.8‰ to 35.0‰), and Arctic Water (<0.0°C and 34.3‰ to 34.8‰). Stations for experiments were thus located in Arctic waters (station I), Polar Front (station II), MIZ in Atlantic waters (station III), and ice-free Atlantic waters (station IV).

No loss of chl-containing particles was observed when comparing chl *a* concentrations in samples collected both with Whatman GF/F and GF/C filters (Figure 2). Whatman GF/F filters are known to retain all chl *a* associated with phytoplankton [*Chavez et al.*, 1995]. Similar results had been obtained previously with *Phaeocystis pouchetii* cultures [*Matrai et al.*, 1995]. After this test, all samples, both for chl *a* and primary production measured on particles, were collected on Whatman GF/C filter at a differential pressure of 15 mm Hg. The GF/C filter collects all chl *a*-containing particles but allows the mucilage associated with the cells to pass through the filter [*Gieskes and van Bennekom*, 1973; *Matrai et al.*, 1995].

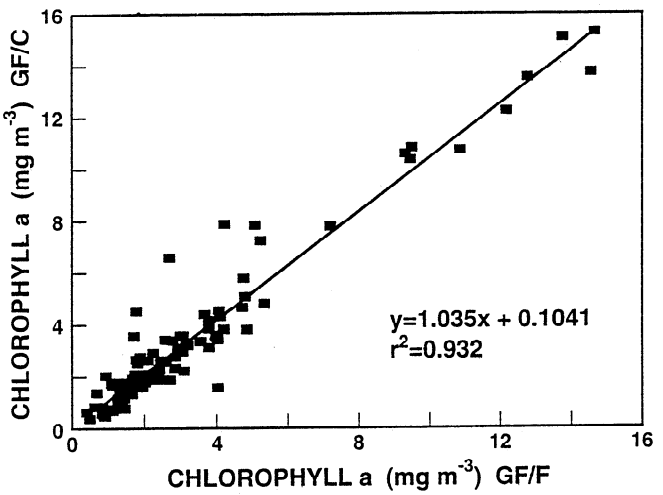

Figure 2. Correlation of chl *a* estimates based on filtration onto Whatman GF/C (*y* axis) and Whatman GF/F (*x* axis) filters. Data collected on 18 stations along the transect (see Figure 1), from surface to the depth of 0.1% surface irradiance.

The chl *a* concentration from surface to 100 m depth along the transect remained between 0 and 3 mg m^{-3} up to 76° N where a phytoplankton bloom was encountered in Arctic Waters with concentrations in the upper 40 m of up to 14 mg m^{-3} (Figure 3a). The integrated chl *a* concentration in the euphotic zone, defined in this study as the depth of 1% light transmission, increased with latitude, from 30 to 341 mg chl *a* m^{-2}. Light transmission in the water column decreased steadily from south to north, following the chl *a* distribution (Figure 3b). The depth of the euphotic zone, decreased from 50 m in the south (Atlantic water) to < 20 m in the north (Arctic water).

3.2. Experimental Stations

The four experimental stations visited on the transect while steaming south are indicated in Figure 1 and Table 1. The phytoplankton community at station I was dominated by diatoms with an average number of diatoms in the euphotic zone of 4.3×10^6 - 7.3×10^6 cells L^{-1} (Table 2). The phytoplankton community was characterized by pennate, chain-forming species (*Fragilariopsis* sp. and *Navicula* spp.), *Chaetoceros* spp. and *Thalassiosira* spp. *Fragilariopsis* sp. and *Chaetoceros socialis* were the most abundant species in terms of biomass. Only a few colonies of *Phaeocystis pouchetii* were found in the water column (5.6×10^2 - 1.5×10^3 colonies L^{-1}). *Phaeocystis* was identified as *P. pouchetii* based on colony morphology, distribution of cells within the colony, and temperature tolerance [*Baumann et al.*, 1994].

The phytoplankton community at station II consisted of both diatoms and *Phaeocystis pouchetii*. Diatoms dominated

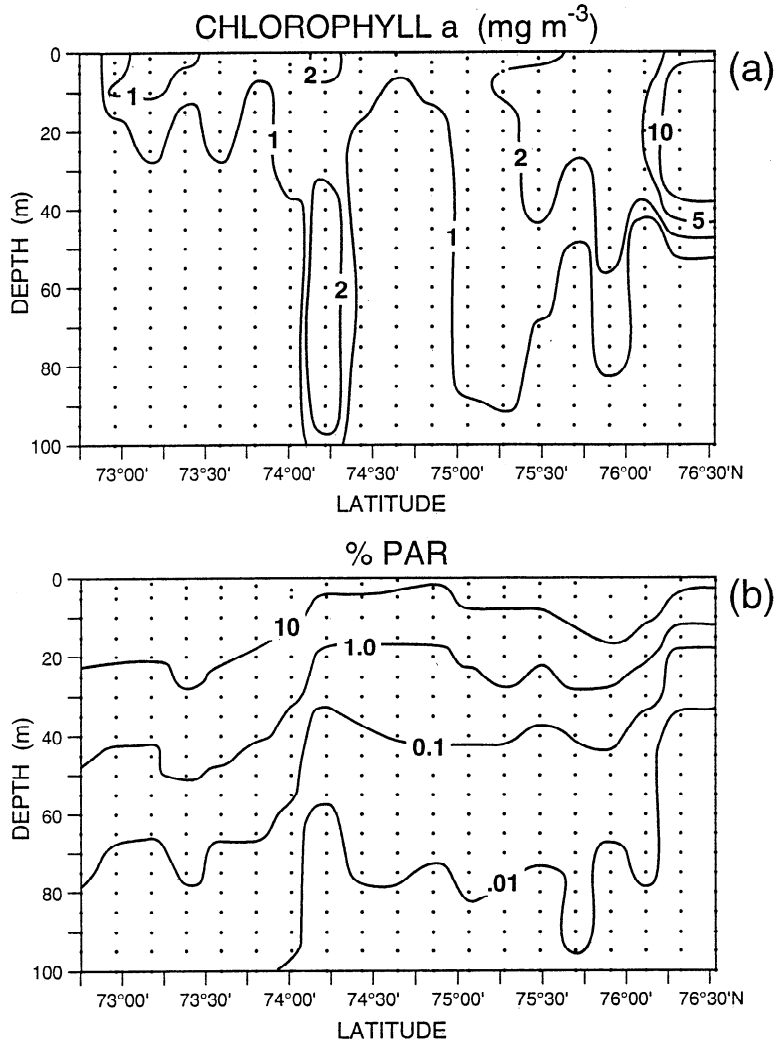

Figure 3. Distribution of (a) chl *a* concentration and (b) attenuation of light in the water column expressed as percent of incident irradiance during a transect from 72°45.017'N, 30°21.014'E to 76°32.165'N, 32°55.526'E during May 16 to 18, 1993.

the surface water due to a high abundance of *Thalassiosira* spp. and *Chaetoceros socialis* (average abundance of 3.3×10^4 and 1.5×10^6 cells L^{-1}, respectively). *C. socialis* was not abundant below 10 m where *P. pouchetii* colonies dominated. *Chaetoceros* spp. and *Thalassiosira* spp. were the dominant diatoms below 10 m.

At station III, *Phaeocystis pouchetii* colonies dominated at the surface (>60% of phytoplankton carbon). The abundance of *P. pouchetii* colonies decreased below 8 m and *Thalassiosira* spp. (2.6×10^4 - 2.9×10^4 cells L^{-1}) became the dominant group of the phytoplankton community in terms of carbon. *Chaetoceros socialis* was abundant throughout the euphotic zone (3.3×10^5 - 9.6×10^5 cells L^{-1}).

The phytoplankton community at station IV was dominated by large cells of *Chaetoceros* spp. with concentrations up to 2.5×10^5 cells L^{-1}. *Phaeocystis pouchetii* was present but was not abundant. The distribution of phytoplankton was even throughout the water column down to 38 m. Autotrophic and heterotrophic ciliates were also present (B. Hansen, University of Roskilde, personal communication, 1996).

3.2.1. Phytoplankton carbon. Cellular carbon from diatoms dominated the euphotic zone at stations I and IV (74% and 75%, respectively) while *Phaeocystis pouchetii* cell+colony carbon dominated at stations II and III, respectively, contributing 42% and 48% (Table 2). Dinoflagellates were always present and were the second dominant group at station I, with 23% of the cell carbon. Carbon from flagellates represented, on the average, the lowest contribution (1% - 5% of cell carbon; see also I. Andreassen and P. Wassmann, Vertical flux of phytoplankton and particulate biogenic matter in the Marginal Ice Zone of the Barents Sea, submitted to *Marine Ecology Progress Series*, 1997).

3.2.2. Chlorophyll distribution. High chl *a* concentrations between 7 and14 mg m^{-3} were observed from surface to 25 m depth at station I (Table 2), with more than 85% of the chl *a* in cells, chains or colonies larger than 20 µm (Figure 4a). At station II, chl *a* concentrations were intermediate and showed a subsurface maximum at 10-20 m (Figure 4b). Similar to station I, 85% of the chl *a* was in cells, chains, or colonies larger than 20 µm. Chl *a* concentrations continued to decrease further south. station III had 1.2 to 2 mg chl *a* m^{-3} in the upper 30-m depth and then remained at about 1 mg chl *a* m^{-3} down to a depth of 80 m (Figure 4c). Nanoplankton

Table 2. Cell Abundance, Presented as Average Concentration in the Euphotic Zone, Carbon, and Surface Chl *a* at the Four Experimental Stations

	Station			
	I	II	III	IV
Diatom concentration, 10^6 cells l^{-1}	5.15	1.19	0.49	0.12
Phaeocystis colonies, # l^{-1}	1,040	11,152	1,026	68
Diatom cell C	2,124 (74%)	647 (35%)	266 (39%)	1,365 (75%)
P. pouchetii cell+colony C	55.6 (2%)	796 (42 %)	334 (48%)	31 (2%)
Dinoflagellate C	663.7 (23%)	381 (20%)	65 (9%)	179 (10%)
Flagellate C	30.2 (1%)	47 (2.5%)	24 (3%)	82 (5%)
Total carbon	2,873	1,872	688	1,812
Surface chl *a*, mg m^{-3}	14.29	2.44	1.47	1.98
Integrated chl *a*, mg m^{-2}	172	63	30	74
POC:chl [*Rey*, 1991]	67	59	55	65

Integrated values (carbon and chl *a*) for the euphotic zone in units of mg m^{-2}. Cellular carbon was estimated following *Strathman* [1967] for diatoms, dinoflagellates and flagellates and *Rousseau et al.* [1990] for *Phaeocystis* sp. cells and colonies. Cell volume was calculated based on the closest stereometric shape for each taxon. No colonial carbon for diatoms, similar to *Phaeocystis* sp. colonies, is available from the literature.

dominated at this station, with an average 37% of the chl *a* associated with cells, chains or colonies > 20 μm in the euphotic zone (indicated by a white arrow in Figure 4). At station IV, a subsurface chl *a* maximum of 2.5 mg m^{-3} was observed at 10 m, with values around 1.5 mg chl *a* m^{-3} for the rest of the euphotic zone (10-38 m layer) (Figure 4d). Similar to stations I and II, between 66% and 87% of the cells in station IV were > 20 μm at all depths except at 60 m. On the average, a larger proportion of smaller cells was found at depth, below the euphotic zone. Large cells or net plankton dominated in surface waters, with the exception of station III.

3.2.3. Inorganic nutrients. Inorganic nutrients were measured at selected casts during the 24-hour drifting with the in situ moorings. Here we present profiles for casts 555, 570, 591, and 609, corresponding to stations I, II, III, and IV, respectively. Nitrate concentrations in the euphotic zone (indicated by a white arrow in Figure 5) decreased across the Polar Front, toward the north. Minimum nitrate concentrations were found at station I (Figure 5a), coinciding with maximum chl *a* concentrations (up to 14 mg m^{-3}; Figure 4a). Station II had low nitrate concentrations (2 to 4 μ*M*; Figure 5b) from surface to 14 m depth, with higher values below the mixed layer (indicated by a black arrow in Figure 5). station III had the highest nitrate concentration near the surface (Figure 5c), with values around 8 μ*M* and increasing slightly with depth. station IV had intermediate nitrate values in the euphotic zone, between 4 and 6 μ*M*, and increasing toward the bottom of the mixed layer (Figure 5d). In general, silicic acid profiles were similar to those of nitrate, although the ratio of the two at any given depth was not constant and will be discussed with more detail below.

3.2.4. Chlorophyll:nitrate ratios. As expected, chl *a* concentrations in the euphotic zone did not show a linear relationship with nitrate concentrations (Figure 6a). At station I, a wide range of chl *a* concentrations (4 -14 mg chl *a* m^{-3}) was observed for constant and low nitrate concentrations (0.8 -3 μ*M*). The other three process stations showed the opposite pattern: low and more constant chl *a* concentrations (0.3 - 5 mg chl *a* m^{-3}) in a wider range of nitrate concentrations (2 - 11 μ*M*). The high chl *a* and low nitrate values at station I suggest uptake of recycled N compounds (not measured) if we assume 1 μg chl *a* produced per 1 μ*M* nitrate in the water column. In comparison to nutrient concentrations at depth, station II had about 30% of nitrate left in the mixed layer (2 - 4 μ*M* nitrate; Figure 5b) while stations III and IV had more than 50% nitrate left in the mixed layer (3 to 8 μ*M*; see also Figures 5c and 5d). These nitrate concentrations associated with a relatively lower chl *a* biomass suggest more nitrate-based phytoplankton production can be maintained at the south of the Polar Front. This is consistent with the notion that the phytoplankton spring bloom was still occurring in this region at the time of our sampling.

3.2.5. Silicic acid:nitrate ratios. As shown before, the two phytoplankton groups dominating at the MIZ bloom in the Barents Sea in May 1993 were diatoms and prymnesiophytes. While diatoms require both nitrate and silicic acid, prymnesiophytes depend mainly on nitrate for growth. By plotting silicic acid versus nitrate concentrations we observed two groups of samples (Figure 6b). One group of samples corresponded to a silicic acid:nitrate ratio close to 1:2 (higher line), and a second group of samples had a silicic acid:nitrate ratio of approximately 1:6 (lower line). The samples on either of the lines were further classified in corresponding to within (solid symbols) and below (open symbols) the mixed layer at each station (Table 1). Samples with low silicic acid:nitrate ratio were found within the mixed layer at stations I and IV and below the mixed layer (14 m; Table 1) at station II. Samples with high silicic acid:nitrate ratio were found below the mixed layer at stations I and IV, at the mixed layer at station II, and all samples at station III. As expected, the lower silicic acid:nitrate ratio was associated with the samples dominated by diatoms while *Phaeocystis*

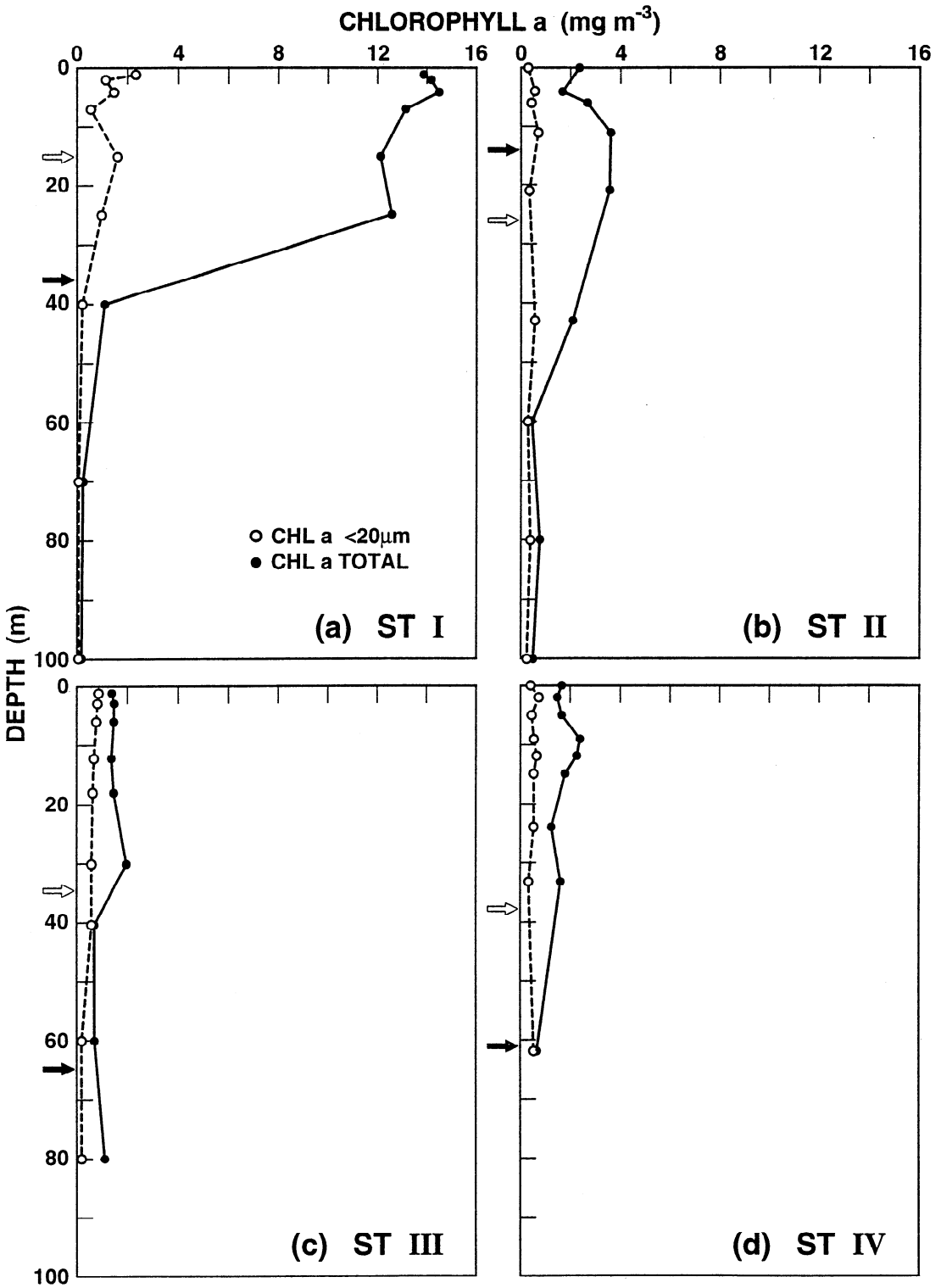

Figure 4. Depth distribution of chl *a* in the four experimental stations, with total chl *a* (solid curve) and chl *a* associated with particles < 20 µm (dashed curve). The depth of the euphotic zone or 1% surface irradiance (white arrow) and the mixed layer depth (black arrow) are shown on the *y* axis.

pouchetii and other flagellates dominated the samples with higher silicic acid:nitrate ratio [*Stefansson and Olafsson*, 1991]. Samples taken below the mixed layer had a higher nutrient ratio, with the exception of the samples from the station II which did not fall clearly on any line.

3.2.6. Primary production. Total primary production and the proportion of primary production allocated to particulate and extracellular carbon in phytoplankton are shown in Figure 7 and Table 3. Total primary production varied from 1.3 to 1.8 g C m^{-2} d^{-1}, integrated within the euphotic zone. These

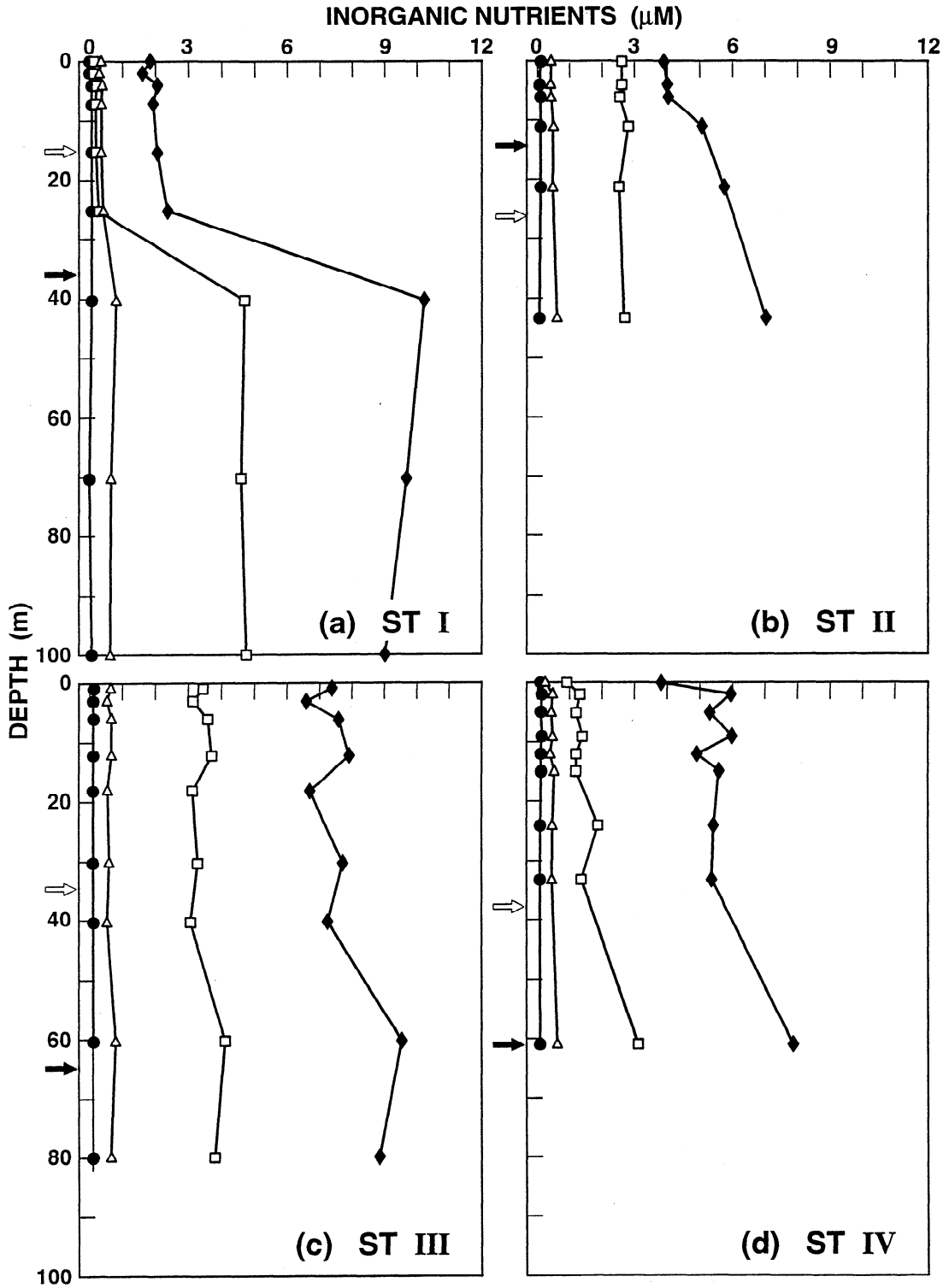

Figure 5. Depth distribution of inorganic nutrients at each of the four experimental stations, (based on one station during the 24-hour period of the primary production mooring), with nitrate (diamonds), silicic acid (squares), orthophosphate (triangles), and nitrite (circles) concentrations (μM). The depth of the euphotic zone and the mixed layer depth are shown as in Figure 4.

values are intermediate for this time of the year at the ice edge in the Barents Sea [*Rey*, 1991]. Most of the primary production occurred down to the 1% irradiance level, indicated by the white arrow in Figure 7, with <3% of the primary production occurring between 1% and 0.1% irradiance level.

In all stations, between 18% and 55% of the primary production was associated with extracellular carbon, with maxi-

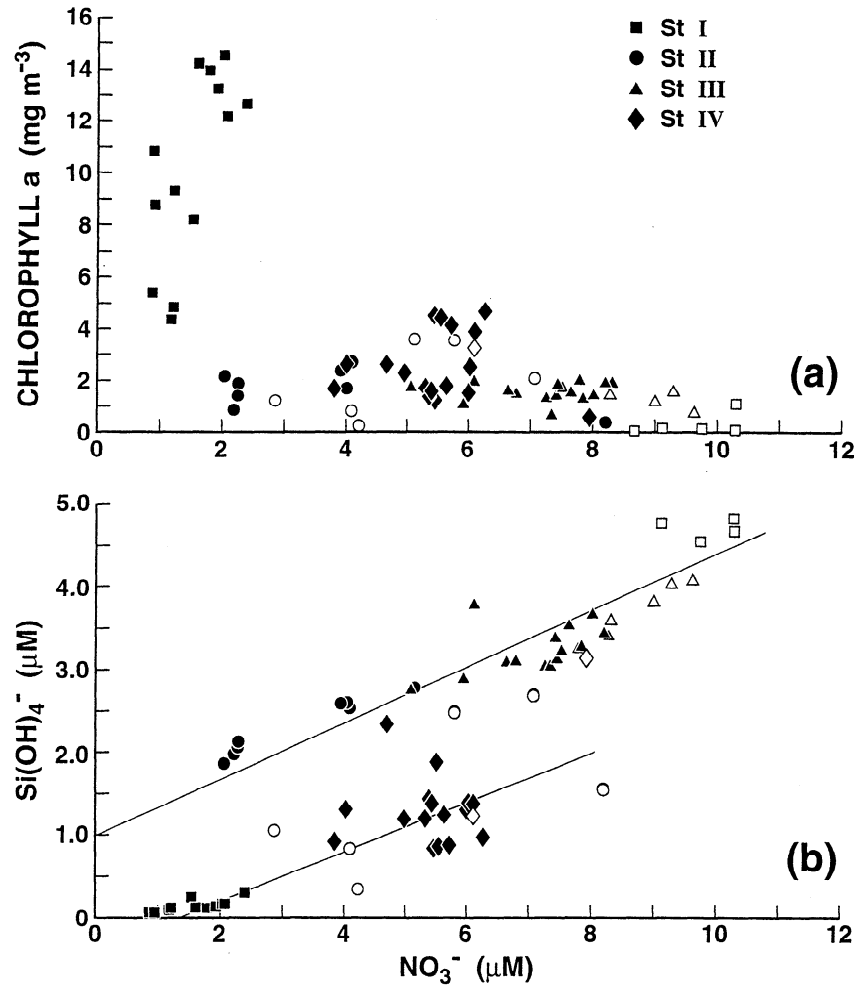

Figure 6. Relationship between (a) chl *a* and nitrate concentration and (b) silicic acid and nitrate concentration at all depths sampled in each station.

mum values at the ice edge (station III) and minimum values in ice-free waters (station IV). The stations influenced by ice (stations I - III) had an average 43% of the primary production as extracellular carbon. In general, the depth profile of primary production as extracellular material (dotted line in Figure 7) had a similar shape to the profile of primary production as particulate carbon, with values lower than particulate primary production at each depth. The exception was station III where the extracellular fraction showed a broad subsurface maximum from 5 to 17 m with values of extracellular primary production in that depth range higher than for particulate primary production (Figure 7c).

3.2.7. Production / biomass. Total primary production normalized to chl *a* concentration varied from 2.52 to 7.41 mg C (mg chl *a*)$^{-1}$ h^{-1} (Table 3). The change of P/B with irradiance (Figure 8) was similar to the change of primary production with depth (Figure 7). Maximum P/B values were observed near the surface at station I and at 13, 15, and at 30 m at stations II, III and IV, respectively, corresponding to average irradiance of 557, 283, 32, and 147 µmol quanta m^{-2} s^{-1} (Table 1).

3.2.8. Phytoplankton carbon-specific growth rates. Estimates of phytoplankton carbon-specific growth rates for the four experimental stations, averaged over the euphotic zone, varied from 0.30 to 0.54 d^{-1} (Table 3). These estimates are based on particulate primary production measurements presented in Table 3 and Figure 7. In general, carbon-specific growth values were high for the ambient temperature, lower at station I (0.3 d^{-1}) and higher and constant elsewhere (0.5 d^{-1}).

4. Discussion

Estimates of integrated total primary production from surface to 1% irradiance varied from 1.3 to 1.8 g C m^{-2} d^{-1} (Table 3). Our estimates are within the upper range of primary production estimates in the Arctic [i.e., *Smith et al.*, 1991] and the Antarctic [i.e., *Holm-Hansen and Mitchell*, 1991; *Smith et al.*, 1996] while average values for spring and summer are about an order of magnitude lower for the eastern Canadian Arctic [e.g., 0.29 g C m^{-2} d^{-1}, *Harrison and Cota*, 1991] and the Greenland Sea (0.21 g C m^{-2} d^{-1}) [*Smith*, 1995].

An average of 37% (range of 18% to 55%) of the total primary production was extracellular, as calculated by the difference between total and particulate primary production (Table 3; Figure 7). As defined in this study, extracellular carbon includes any carbon exuded by phytoplankton as mucilage to form colonies, such as in *Phaeocystis pouchetii* and *Chaetoceros socialis*, dissolved organic carbon (DOC), and

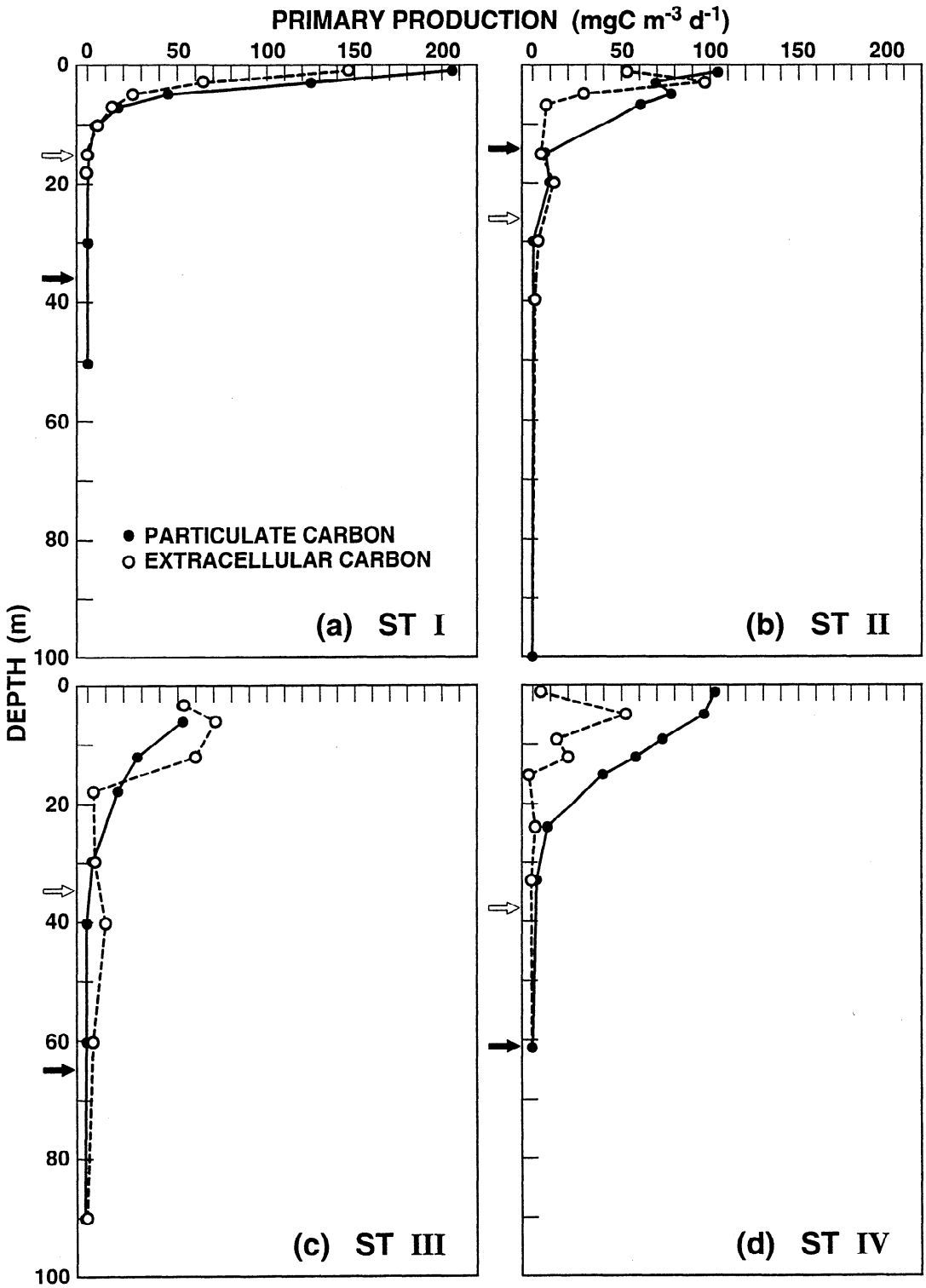

Figure 7. Depth distribution of primary production (mg C m^{-2} d^{-1}) by particulates (solid curve) and extracellularly (dashed curve), measured in situ during 24-hour incubations starting around midnight. The depth of the euphotic zone and the mixed layer depth are shown as in Figure 4.

bacterial carbon [*Matrai et al.*, 1995]. The latter should be considered in future experiments for more accurate measurements.

An increasing proportion of primary production as extracellular carbon (39% to 55% of the primary production) was observed from north to south within the MIZ (stations I to station III). No such consistency was observed in phytoplankton composition. Station I was dominated by diatoms (74% of the cell carbon) with less that 2% of cell carbon from *Phaeocystis pouchetii*. Stations II and III, in contrast, had 42%-48% as *P. pouchetii* cell carbon and 35%-39% of diatom cell carbon (Table 2). Similarly, stations I and IV were

Table 3. In situ Primary Production for the Four Experimental Stations

	Station			
	I	II	III	IV
	Primary Production, mg C m^{-2} d^{-1}			
Particulate	814 (61%)	903 (64%)	804 (45%)	1476 (82%)
Extracellular	530 (39%)	502 (36%)	1004 (55%)	312 (18%)
Total	1344	1405	1808	1788
	Production / Biomass, mg C (mg chl a)$^{-1}$ h^{-1}			
Particulate	1.57 (58%)	3.07 (41%)	2.28 (40%)	2.36 (94%)
Extracellular	1.12 (42%)	4.34 (59%)	3.35 (60%)	0.16 (6%)
Total	2.69	7.41	5.63	2.52
Carbon-specific growth rates, d^{-1}	0.30	0.50	0.51	0.54

Integrated values to the depth of 1% surface irradiance (euphotic zone). Values in parenthesis indicate percent particulate and extracellular primary production with respect to the total primary production.

dominated by diatoms (74% and 75%, respectively) but had different amounts of primary production allocated as extracellular (38% and 18%, respectively). From these results we reject the hypothesis that phytoplankton composition (diatoms versus *P. pouchetii*) is the dominant factor in explaining carbon allocation between particulate and extracellular fractions in the Barents Sea.

The production / biomass ratio based on total primary production (Table 3; Figure 8), was higher than expected for phytoplankton at the MIZ (stations II and III). When considering only particulate primary production, the ratios varied from 3.07 mg C (mg chl *a*)$^{-1}$ h^{-1} in station II to 2.28 mg C (mg chl *a*)$^{-1}$ h^{-1} in station III (Table 3), and are within Arctic averages [*Harrison and Cota*, 1991; *Platt et al.*, 1982]. However, if we add the fraction of primary production measured as extracellular, P/B increases to 7.41 and 5.63 mg C (mg chl *a*)$^{-1}$ h^{-1} at stations II and III, respectively. These values of P/B are high for the measured ambient surface temperature (0.8° C and 2.8° C; Table 1) and coincide with values of maximum photosynthetic rates for short-term incubations reported for a bloom of Antarctic *Phaeocystis sp.* under the ice [*Palmisano et al.*, 1986]. Our field measurements of P/B are about half the photosynthetic rates measured by *Cota et al.* [1994] in the Fram Strait and similar to those based on short-term incubations in the laboratory [*Matrai et al.*, 1995]. Although *Palmisano et al.* [1986] and *Cota et al.* [1994] used the *Lewis and Smith* [1983] method which includes extracellular carbon in its primary production estimates, the comparison between our field estimates (based on 24-hour incubations in situ) and the P versus I curves (based on 1-2 hours incubations in the laboratory) is made with caution.

These results support the hypothesis that *Phaeocystis pouchetii* has a higher efficiency of carbon assimilation per unit chl *a* than diatoms, as found in other field [*Cota et al.*, 1994] and laboratory [*Verity et al.*, 1991] studies. *P. pouchetii* contributed from 42% to 48% of the biomass at stations II and III while it was a minor component (<2% of phytoplankton biomass) at stations I and IV (Table 2) where P/B based on total primary production was lower (2.69 and 2.52 mg C (mg chl *a*)$^{-1}$ h^{-1}, respectively; Table 3). High production per chl *a* might be balanced by a higher C:chl ratio in *P. pouchetii* than in diatoms, as found in laboratory cultures, by a factor of approximately 2 [*Verity et al.*, 1991]. Carbon-specific growth rates calculated in this study, based on the calculations and assumptions described in the methods section and using previous average C:chl ratios for the area (Table 2), were similar for the three southern stations (Table 3), and were not related to the dominant phytoplankter.

Although an unknown proportion of the extracellular carbon becomes part of the dissolved organic carbon pool (DOC), previous studies with cultures have shown the ability of cells to form high-molecular weight carbohydrates in the form of mucilage [*Janse et al.*, 1996]. Several species found in our study area, in particular the diatoms *Thalassiosira antarctica*, *Chaetoceros socialis*, and the prymnesiophyte *Phaeocystis pouchetii*, produce large amounts of mucilage which remains associated with the cells as part of the colony or chain [*Lancelot and Rousseau*, 1994; M. Sieracki, Bigelow Laboratory for Ocean Sciences, personal communication, 1996]. The mucilage is composed mostly of carbohydrates and is exuded from the cells as part of their metabolism [*Myklestad*, 1974; *Lancelot and Mathot*, 1985]. Studies have concentrated on the total amount of mucilage produced and the conditions under which it is excreted. Strains of diatoms maintained in culture have shown increased exudation under conditions of nutrient limitation as it occurs at the end of the exponential phase in a batch culture [*Myklestad and Haug*, 1972; *Myklestad*, 1974; *Myklestad et al.*, 1989]. In our field study, the amount of extracellular carbon produced (Figure 7; Table 3) seems to be related primarily to the presence of mucilage-producing species (e.g., *Chaetoceros socialis* and *P. pouchetii*) and to a lesser extent to low nitrate concentration (Figure 5). In station I, dominated by *Chaetoceros socialis* and *Fragilariopsis* sp., 39% of the primary production was allocated extracellularly under low silicic acid (<0.2 μ*M*) and low, but measurable, nitrate concentrations (0.5-2.5 μ*M*). Similar proportions were found in a mixture of *C. socialis* and *P. pouchetii* in station II with higher nitrate and silicic acid concentrations (Figure 5). The largest amount of extracellular carbon, both in absolute and relative numbers, was found at station III under conditions of moderate to high nitrate

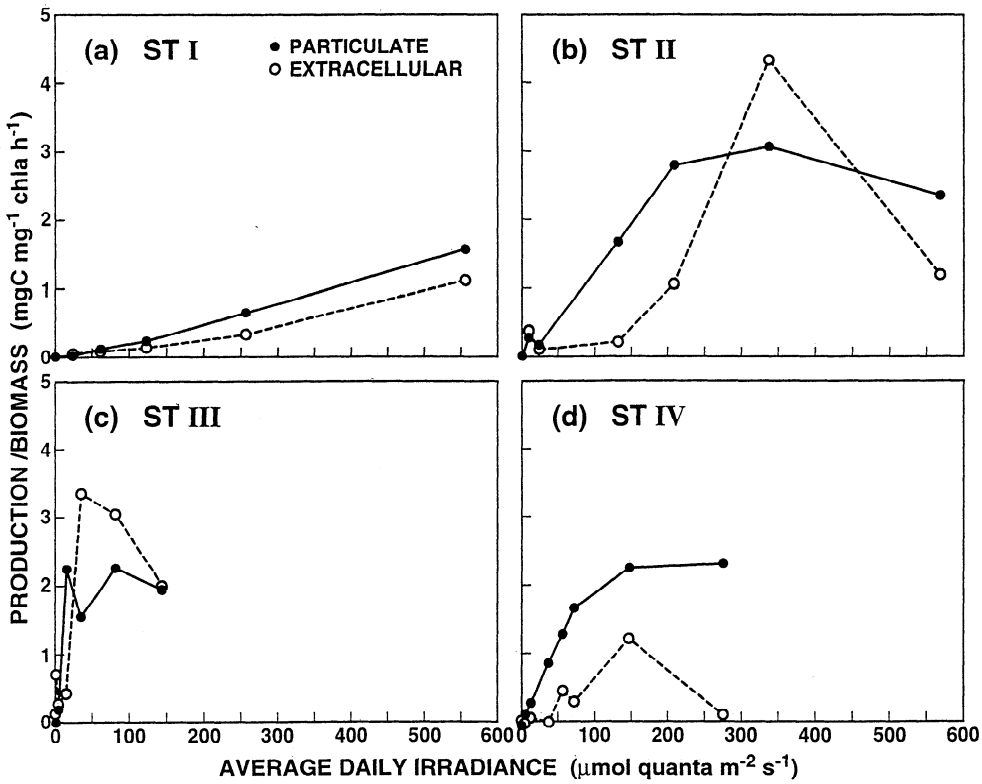

Figure 8. Production / biomass (mg C (mg chl *a*)$^{-1}$ h^{-1}) of particulate (solid curve) and extracellular (dashed curve) matter as a function of average irradiance at the depth of incubation during the four experimental stations.

concentrations (6 -10 µ*M*). These results suggest that species composition, in terms of solitary versus colonial life-forms, may control extracellular carbon production in the field to a larger extent than nutrients. As shown in this study, *P. pouchetii* and diatoms from the Barents Sea can maintain a high capacity to form mucilage in a broad range of nutrient conditions in the field.

The role of silicic acid in carbon exudation is not known. If similar to that of nitrate, we can assume that the high extracellular carbon production in station I may be due in part to low silicic acid concentration (Figure 5). Low silicic acid:nitrate ratios (1:2) are characteristic of the Barents Sea and the Nansen Basin [*Harrison and Cota*, 1991], where it has been suggested that silicic acid limits diatom blooms [*Rey and Skjoldal*, 1987]. Other Arctic shelf areas have higher silicic acid concentration, such as the Labrador Sea (1:1 silicic acid:nitrate), the Eastern Canadian Arctic and the Chukchi Sea (2:1), where nitrate limitation is more prominent [*Harrison and Cota*, 1991]. Thus results from the Barents Sea can only be extended to other Arctic shelf areas with caution, in particular, with respect to a possible role of silicic acid in carbon allocation.

Our results highlight that at some time during the spring bloom in the Barents Sea, about 40% of the primary production can be allocated extracellularly, both in colonial mucilage of *Phaeocystis pouchetii* or diatoms in the field (Table 3; Figure 7). However, our cruise did not cover all stages of the bloom to determine the onset of strong extracellular carbon allocation. Based on the data from station IV in ice-free Atlantic waters, where only 18% of the primary production was extracellular, it is clear that phytoplankton in ice-free, nutrient-rich waters and in the absence of *P. pouchetii* and *Chaetoceros socialis*, exude carbon within world averages (10% to 15% carbon excretion) [*Zlotnik and Dubinsky*, 1989]. Thus we might speculate that certain diatoms at the beginning of the bloom at the ice edge have similar low exudation. Other diatoms with a large amount of structural mucilage, such as *C. socialis*, might have a higher proportion of carbon allocated extracellularly throughout their growth cycle. Based on observations from laboratory cultures [*Myklestad*, 1974], we might expect all diatoms to increase the proportion of extracellular carbon release at the end of the exponential growth, during the latter stages of the spring phytoplankton bloom, due to nutrient limitation. The presence and/or dominance of *P. pouchetii* can only increase the extracellular carbon released by diatoms, given the proportion of primary production as extracellular observed in cultures at all growth stages for this genus [*Matrai et al.*, 1995]. Thus a large input of extracellular carbon might be expected to reach the DOC pool following the phytoplankton bloom (Table 3). Indirect evidence, such as large extracellular excretion in the presence of high nitrate concentration at stations II and III and the abundance of diatoms and flagellates as well as *P. pouchetii*, suggest that the proportion of carbon allocated extracellularly during the spring bloom in Arctic shelf waters might be, on the average, higher than in temperate areas (e.g., North Atlantic [*Kirchman et al.*, 1991] and North Sea [*Lancelot*, 1983]) and not limited to the end of the bloom.

Several hypotheses have been suggested for the role of algal exudation which enters the DOM pool. Most of the

carbon entering the microbial loop originates from phytoplankton activity, either directly (from exudation) or indirectly (bacterial hydrolysis, i.e., exoenzymes) [*Smith et al.*, 1995]. As summarized by *Azam and Smith* [1991], the subject is "widely debated" but "there is a lack of consensus on the magnitude and, particularly, on the ecological and evolutionary significance of DOM exudation by phytoplankton". Four major hypotheses include the definition of exudation as a "property tax" or leakage from the cell due to the extreme gradient across the membrane [*Bjørnsen*, 1988]; a strategy to maintain N in the mixed layer [*Williams*, 1990]; a mechanism to promote nutrient remineralization by attached bacteria [*Azam and Ammerman*, 1984; *Azam and Cho*, 1987], or a means to shed bacteria from the cell membrane. For this discussion it is important to differentiate between the polysaccharides which remain bound to the cells or as part of the colony and the exudates which dissolve and rapidly diffuse into seawater. Although ultimately most of the bound polysaccharides may dissolve and become part of the dissolved carbon pool or the microbial loop [*Smith et al.*, 1995] during the bloom demise, it cannot be ruled out that, early on, a large and unknown portion of the carbon might be concentrated on the membrane-bound mucilage during exponential growth, and thus has to be considered particulate carbon.

Between 5% and 50% of the primary production should end in the DOC pool to maintain heterotrophic bacterial production in northern temperate waters [*Azam et al.*, 1983]. This part of the DOC is believed to be remineralized rapidly and, as a result, the concentrations of these reactive substances at any given time are small [*Lee and Wakeham*, 1992]. Given the debate on whether bacterial activity is depressed in polar waters [*Pomeroy and Deibel*, 1986; *Thingstad and Billen*, 1994] and the potential role of substrate on polar bacterial metabolism [*Pomeroy and Wiebe*, 1993], the role of phytoplankton as providers of labile DOC in Barents Sea waters is critical. The degree to which this DOC from algal sources is utilized by bacteria seems to be a function of the source (i.e., algal species [*Malinsky-Rushansky and Legrand*, 1996]). Although, on the average, a large portion of this DOC originating from algal photosynthate is selectively taken up by bacteria [*Norrman et al.*, 1995], a more refractory unreactive part remains in the DOC pool [*Lara and Thomas*, 1995; *Norrman et al.*, 1995]. Either the labile DOC or the unreactive DOC or both are affected by photolysis [*Mopper et al.*, 1991], which is known to facilitate microbial uptake and ultimately DOC degradation [*Bushaw et al.*, 1996]. Polysaccharides, a major component of algal excretion [*Myklestad*, 1974; *Janse et al.*, 1996], are considered a major component of DOC in surface waters [*Benner et al.*, 1992; *McCarthy et al.*, 1997]. Thus we speculate that the large fraction of primary production measured as extracellular carbon in May 1993 in the MIZ of the Barents Sea was mostly polysaccharides, as measured in laboratory cultures, and thus it is expected to be rapidly degraded by heterotrophic activity before or after photolysis [*Putt et al.*, 1994]. Unused labile DOC, either from "unappealing *Phaeocystis* mucus" [*Thingstad and Billen*, 1994] or due to low heterotrophic uptake, and refractive DOC originating in the ice-edge bloom [*Lara and Thomas*, 1995; *Norrman et al.*, 1995] are expected to increase DOM in the Barents Sea, as observed in antarctic coastal waters [*Davidson and Marchant*, 1992], and be subjected to chemical and advective processes.

The role of the mucilage is also of potential importance to the fate of the particulate primary production. The mucilage is believed to act as a floating mechanism for the cells. In the case of diatoms, which are known to sink under conditions of nutrient limitation [*Waite et al.*, 1992], increased exudation can prevent cells from sinking out of the euphotic zone. On the other hand, it has also been suggested that the mucilage can increase coagulation and thus accelerate sedimentation [*Jackson*, 1990]. Experiments with rotating cylinders support the hypothesis that the mucilage, presumably from *Phaeocystis pouchetii*, can agglutinate [*Passow and Wassmann*, 1993] and increase sedimentation of other particles, e.g. diatoms, in the water column [*Passow et al.*, 1994]. Mucilage is also known to dissolve and re-aggregate (transparent exopolymer particles, or TEP), thus affecting particle formation as well as sedimentation of other particles [*Alldredge et al.*, 1993; *Riebesell et al.*, 1995].

Loss of DOC from surface waters can occur with potential downward flux of DOM to deep waters. Recently, such process has been invoked in other parts of the ocean to model successfully the nutrient distributions in open waters [*Bacastow and Maier-Reimer*, 1991; *Najjar et al.*, 1992]. DOC distribution in continental shelves can be explained by water mixing and resultant DOC fluxes can be comparable to those of POC processes [*Guo et al.*, 1995]. In addition, lateral advection along sloping isopycnals is a mechanism involved in transport from shelf to slope waters in continental margins and in the formation of Arctic Intermediate water at the Polar Front of the Barents Sea [*Steele et al.*, 1995]. The extent to which this loss term is of consequence in the Barents Sea remains to be quantified. The measured organic carbon excretion is a potential source of DOC that merits further study given its implication on the Barents Sea carbon cycle and potentially other polar areas.

5. Conclusions

Results presented in this paper do not support the hypothesis that the alternation of *Phaeocystis pouchetii* and diatoms during the spring bloom in the Barents Sea affects the relationship between the particulate and extracellular carbon pools in the upper water column of the MIZ. Although *P. pouchetii* contributed strongly to the extracellular carbon pool (mucilage and DOC) during an ice-edge bloom in May 1993, arctic diatoms contributed an equal amount of exuded carbon. From three experimental stations visited at the MIZ, between 36% and 55% of the primary production was measured as extracellular carbon, defined as labeled organic matter which passes through a Whatman GF/C filter. No difference in the carbon allocation between diatom- and *P. pouchetii*-rich phytoplankton was observed in these stations. In contrast, the station situated in ice-free waters had 18% of primary production in the extracellular fraction, well within world averages. These results (1) highlight similar carbon allocation for diatom- and *P. pouchetii*-dominated phytoplankton in surface waters of the Barents Sea during the spring and/or ice edge bloom at the MIZ and (2) suggest that polar phytoplankton may be stronger producers of extracellular carbon, and possibly DOC, than previously thought.

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