Phytoplankton biomass, production and potential export in the North Water

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Abstract

The seasonal patterns of phytoplankton biomass and production were determined in the North Water, located between Greenland and Ellesmere Island (Canadian Arctic), in August 1997, April–July 1998, and August–September 1999. The patterns differed among the four defined regions of this large polynya, i.e. North (≥77.5°N), East (≥75°W), West (<75°W), and South (<76°N). Phytoplankton biomass and production were low during April throughout the North Water. Biomass first increased in the East during April. From there, the biomass spread north- and westwards during May–June, when the bloom culminated (chlorophyll a concentrations up to 19.8 mg m⁻³). The large-sized (>5 mm) fraction dominated the biomass and production during the bloom. During July, August, and September, biomass and production decreased over the whole region, with the highest biomass, dominated by large cells, occurring in the North. The annual particulate and dissolved phytoplankton production were the highest ever reported for the high Arctic, reaching maximum values of 254 and 123 g C m⁻² yr⁻¹, respectively, in the East. Rates in the North and West were considerably lower than in the East (ca. two- and three-fold, respectively). The f-ratios (i.e. ratio of new to total production), derived from the size structure of phytoplankton, were high north of 76°N (0.4–0.7). Regionally, this indicated a high potential export of particulate organic carbon (EPOC) from the phytoplankton community to other trophic compartments and/or downwards in the East (155 g C m⁻² yr⁻¹), with lower values in the North and West (i.e. 77 and 42 g C m⁻² yr⁻¹, respectively). The seasonal and spatial patterns of EPOC were consistent with independent

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estimates of potential carbon export. Phytoplankton biomass and production were generally dominated by the large size fraction, whereas EPOC seemed to be dominated by the large size fraction early in the season and by the small size fraction (<5 μm) from June until the end of the growing season.

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1. Introduction

The North Water is one of the largest polynyas in the Northern Hemisphere, encompassing Smith Sound (northern extent) and the northern part of Baffin Bay between Greenland and Ellesmere Island (Canadian Arctic). The limited data available suggested that the marine ecosystem of the North Water is more productive than that of other polynyas in the Canadian Arctic (e.g. Stirling, 1997), but substantive biological oceanographic data for this area had been scarce until now. Polynyas may be as productive as the ice-edge zone, of which they may be regarded as a special case (Sakshaug and Skjoldal, 1989). The winter concentration of nutrients generally determines the upper limit of phytoplankton production and biomass in these regions (Sakshaug and Skjoldal, 1989). Lewis et al. (1996) conducted a 48-h survey in the North Water during mid-May 1991, and found that phytoplankton biomass (integrated to 30-m depth) decreased from east to west from 506 to 50 mg chlorophyll a m$^{-2}$. They concluded that a diatom bloom was initiated by the melting of sea ice due to the upward input of sensible heat and that the bloom moved westwards, progressively exhausting the nutrients. However, there had heretofore been no phytoplankton production data published for the North Water.

The objectives of this study were two-fold: (1) to describe the seasonal cycle of size-fractionated phytoplankton biomass and production in the North Water; and (2) to use these data to compute potential carbon export from the phytoplankton community in the euphotic zone towards other trophic compartments and/or downwards that could be compared with independently derived export estimates.

2. Materials and methods

Three expeditions were conducted in the North Water (Fig. 1) during August 1997, on board the CCGS Louis S. St. Laurent, and during April–July 1998 and August–September 1999, on board the CCGS Pierre Radisson. Phytoplankton biomass

![Fig. 1. Map of the North Water, located between Greenland and Ellesmere Island (Canadian Arctic), showing all stations sampled at least once during cruises in 1997, 1998, and 1999 (Table 1) and station groupings into North, East, West and South regions.](image-url)
was determined at “basic” stations, whereas at “full” stations (ca. 30% of all stations) both phytoplankton biomass and production were measured (Table 1). Water samples were collected in 1997 and 1999 (basic stations) at fixed depths (0, 5, 10, 25, 50, and 100 m) and, in 1997, also at 15, 20, 30, and 40 m and in 1998 (basic and full stations) and 1999 (full stations) at seven photic depths (100%, 45%, 30%, 20%, 10%, 1%, and 0.1% incident photosynthetically available radiation (PAR) corresponding to irradiance available in our incubators) and two metric depths below 0.1% PAR. Sampling was accomplished with a rosette system (General Oceanics Inc.) equipped with 10-l bottles (Brooke Ocean Technology Limited, Dartmouth, Nova Scotia) and a CTD (ICTD, Falmouth Scientific Inc.). Samples were prefiltered during May–July through a 300- or 500-μm Nitex screen to remove large grazers. Subsamples for the determination of phytoplankton biomass (chlorophyll a (chl a)), using a fluorometer (Turner Designs, Model 10), were filtered through Whatman GF/F (total chl a, B_T) and 5-μm polycarbonate filters (Poretics; large-sized chl a > 5 μm, B_L). Small-sized chl a (<5 μm) was obtained by difference (B_S = B_T - B_L).

Size-fractionated phytoplankton production (P) was estimated at full stations in 1998 and 1999 using the 14C uptake method. Samples were incubated in 0.6-l polycarbonate bottles (one light and one dark with DCMU [3-(3,4-dichlorophenyl)-1,1-dimethyl urea], inoculated with 10 or 20 μCi [1998] or 35 μCi [1999] NaH14CO3) under simulated in situ conditions in deck incubators with running surface seawater and incident irradiances adjusted with neutral density filters. At the end of the 24-h incubations, subsamples (up to 250 ml) were filtered as above (i.e. for total phytoplankton production, P_T, large-sized production, P_L, and small-sized production, P_S). Filters were rinsed with non-radioactive filtered seawater. The 14C that was not incorporated by phytoplankton was removed by addition of 200 μl of 0.5 N HCl. Upon evaporation of the acid, scintillation liquid (Ecolume, ICN) was added and activity determined using a Packard Tri-Carb 2100 TR (1998) or Beckman LS 6500 (1999) liquid scintillation counter. Furthermore, a small subsample was used for the determination of total phytoplankton production (PP; cf. Lewis and Smith, 1983) using the method of Gosselin et al. (1997), i.e. particulate plus released dissolved compounds (P_DOC, where P_DOC = PP - P_T). Dark values were not subtracted; they were generally ≤5% of the light values. Incubations were initiated when possible early in the morning (minimal PAR) or at dawn, depending on transits and overall sampling logistics, in order to reduce variability in 14C accumulation (Mingelbier et al., 1994). Phytoplankton production estimates were corrected for ice cover (see below). Ambient dissolved inorganic carbon (DIC) concentrations (see Miller et al., 2002) were used to calculate production rates. Depth of the euphotic zone (1% surface PAR) was determined at full stations from in situ PAR profiles obtained with a Satlantic SPMR (see Mei et al., 2002) or PNF-300 or PUV-542 (both Biospherical Instruments Inc.) or a Secchi disk (cf. Parsons et al., 1984). Because PAR profiles could not always be obtained before sampling, euphotic-zone depths were verified a posteriori using in situ PAR profiles or the relationship between euphotic depth and average B_T in the euphotic zone (see Mei et al., 2002). Euphotic-zone depths ranged from 12 to >60 m (Mei et al., 2002). Methods for determination of phytoplankton biomass and production followed the JGOFS core measurements protocols (Knap et al., 1996), with all modifications specified above.

Table 1
Sampling period, dates and number of basic and full stations sampled during each period. Phytoplankton biomass was determined at basic stations, whereas phytoplankton biomass and production were measured at full stations (Fig. 1).

<table>
<thead>
<tr>
<th>Period</th>
<th>Dates</th>
<th>Basic stations</th>
<th>Full stations</th>
</tr>
</thead>
<tbody>
<tr>
<td>April 98</td>
<td>4 April–4 May 98</td>
<td>27</td>
<td>9</td>
</tr>
<tr>
<td>May 98</td>
<td>7–31 May 98</td>
<td>19</td>
<td>7</td>
</tr>
<tr>
<td>June 98</td>
<td>4–27 June 98</td>
<td>23</td>
<td>12</td>
</tr>
<tr>
<td>July 98</td>
<td>1–21 July 98</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>August 97</td>
<td>19–26 August 97</td>
<td>14</td>
<td>0</td>
</tr>
<tr>
<td>August–</td>
<td>27 August–10</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>September 99</td>
<td>September 99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>September 99</td>
<td>11 September–11 October 99</td>
<td>17</td>
<td>10</td>
</tr>
</tbody>
</table>
The simulated light conditions in deck incubators used for the estimation of phytoplankton production could not account for the ice cover, which might have biased our results, since the relationship between irradiance and photosynthesis is non-linear. Like other polar researchers, we corrected the simulated in situ estimates posteriori in an attempt to compensate for the inability of such incubations to accurately simulate the in situ irradiance field (Smith, 1995). This potential bias is inherent to the simulated in situ technique, one used generally in ice-covered waters (e.g., Smith, 1995; Pesant et al., 1996; Gosselin et al., 1997). The ice-cover correction of phytoplankton production estimates in 1998, described in detail by Mei et al. (2002), was a modified version of the correction described by Gosselin et al. (1997). Gosselin et al. (1997) used percentages of ice cover and open water (OW) (like Smith, 1995) and measured transmission of light through the snow, ice, and ice algae. Mei et al. (2002) used different ice categories, each with a different thickness and light attenuation by snow, ice, and ice algae. Briefly, for the 1998 cruise, ice-cover data were obtained from RADARSAT (see Mundy, 2000, and Mundy and Barber, 2001) for the sampling day and the two preceding days, when possible, using a resolution of 10 × 10 km², i.e. the average of 25 grid cells (2 × 2 km²) with the sampling station in the center cell. If no satellite data were available for these days, then ice-cover data as close to the sampling date as possible were used. The ice cover during the 2d before the sampling date was included, because the light history of algal cells is influenced by changes in ice cover. In April and May 1998, there were eight ice categories, ranging from OW to multi-year ice (> 200-cm thick). After 31 May (average date of melt onset), the classification scheme was no longer valid and only OW and ice-covered waters could be distinguished (Mundy, 2000). The ice thickness used for computing % PAR penetration after 31 May was 1.2 m. The average ice cover and ice thickness of the 3-d period for each ice category were used for calculating the penetration of light (PAR) through the snow, ice, and ice-bottom biota into the water column. The attenuation of PAR by sea ice was determined in April–June 1998 at several ice stations (see Mei et al., 2002). The sum of % light reaching the water column through each ice category was used for linear correction of the phytoplankton production estimates.

In August and September 1999, when detailed RADARSAT data were not available, ice-cover estimates were obtained visually from the ship. The ice at that time of the year was thick multi-year ice advected from the Arctic Ocean through Kane Basin. Phytoplankton production estimates were corrected for ice cover according to Smith (1995) using only % OW. Because there was no new (i.e. thin) ice formation during our study (see Mundy, 2000), only thick multi-year ice, and the amount of light reaching the under-ice water column is very close to 0% when the ice is > 1 m thick; the correction factors obtained with this method were similar to those using RADARSAT data.

All phytoplankton biomass and production data were integrated over the euphotic zone and presented as a multi-year composite of the April–September cycle (see also below). This period corresponded to the growth period of phytoplankton in the North Water. Data were grouped by regions: North, East, West, and South (Fig. 1; > 77.5°N, 76–77.5°N and < 75°W, 76–77.5°N and > 75°W, and < 76°N, respectively). These regions approximated the horizontal distribution of different water masses in June 1998, i.e. Smith Sound, Central Northern Baffin Bay, Carey Islands, and West Greenland Current, respectively (Bâcle, 2000; Bâcle et al., 2002). The southern region could not be subdivided because of insufficient sampling. The boundaries among the four regions were neither sharp nor stationary (e.g. Tremblay et al., 2002b); stations close to the boundaries could have been in one water mass on one sampling date and in the other water mass on the next date. The use of fixed boundaries was primarily for convenience. When the phytoplankton production data were aggregated into geographic regions, the number of observations was small (generally n = 1–3; cf. Table 1, full stations), precluding the calculation of variances and covariances on regional f-ratios and annual production.
3. Results

3.1. Phytoplankton biomass integrated over the euphotic zone

The combined data from all stations, representing a composite April–September cycle from the different-year cruises (Table 1), showed a clear seasonal cycle (Table 2). Mean chl a (BT) was low during April and followed by maximum chl a values during May and June (ca. 110 mg m\(^{-2}\)), which then decreased to rather constant concentrations during the remainder of the growing season. Small phytoplankton (BS) showed the same seasonal cycle as BL; although BS values were low (<34 mg m\(^{-2}\)) throughout the year (Fig. 2).

There were differences in the stocks and responses of phytoplankton among the four regions. Phytoplankton growth started in the East, where the highest chl a occurred during May and June (up to 210 mg m\(^{-2}\), corresponding to ca. 10 mg chl a m\(^{-3}\)), followed by a decrease. In the North, maximum biomass was lower than that in the East and occurred 1 month later, but the decrease during summer was less marked. Maximum chl a in the West was somewhat lower than in the North and occurred in June. Values in the South were always low (no data for April and May due to heavy ice cover) and, unlike other regions, BS sometimes exceeded BL.

3.2. Phytoplankton production

Seasonal changes in mean total phytoplankton production (PP) for the whole polynya (Table 3) were similar to those of chl a. Production was low during April, followed by a large increase during May–June due mainly to large phytoplankton (Fig. 3). During August–September, production was high with P\(_{DOC}\) accounting for nearly 50% of total production. During September, production returned to low levels similar to those in April. Throughout the sampling period, P\(_{DOC}\) accounted for 15–82% (average of 44%) of the total production at individual stations and did not appear related to season or ice cover (not shown).

There were striking differences in production among regions. Highest production was in the East, during May (up to 5270 mg C m\(^{-2}\)d\(^{-1}\)), where it was mainly associated with large-sized phytoplankton, whereas during June, total production was ca. half of that during May (Fig. 3). Maximum production was lower in the North (June) and still lower in the West. The few data from the South (no data for April and May 1998 due to heavy ice cover and no production measurements in June 1998 and August 1997) showed low production (<570 mg C m\(^{-2}\)d\(^{-1}\)). In the East and the North, a second increase in production occurred during August–September.

In general, the two size fractions showed similar phytoplankton production/biomass ratios (P/B; not shown). The exception was during September, when the P/B of the small size fraction was up to four times greater than that of the large size fraction, especially in the North and the East.

3.3. f-Ratios estimated from P\(_L\)/P\(_T\) and B\(_L\)/B\(_T\)

The f-ratios (i.e. ratio of new to total production) are generally estimated from the uptake rates of major N sources by phytoplankton, i.e. f-ratio = uptake of NO\(_3^-\)/uptake of total N nutrients
(generally NO$_3^-$ plus NH$_4^+$ and sometimes urea). Tremblay et al. (1997) showed that $f$-ratios could be estimated from the size structure of the phytoplankton community:

$$f = 0.04 + 0.74(P_L/P_T), \quad r^2 = 0.80$$

or

$$f = 0.08 + 0.53(B_L/B_T), \quad r^2 = 0.43.$$

Values obtained for the North Water with the two models were generally similar (Fig. 4). The production-based $f$-ratios were generally higher than...
the biomass-based ratios from April to July and lower in August–September. The f-ratios were generally high (range of 0.4–0.7), except in the South where values ranged from 0.2 to 0.4 from June to August. The four regions and the whole polynya showed a similar pattern of increase of the f-ratio from April to May–June, followed by a decrease and then second increase in autumn. Assuming steady-state assumption (see below), high f-ratios indicate that a large fraction of the particulate phytoplankton production can be exported.

### 3.4. Potential POC export from the euphotic zone

The f-ratios can be used to estimate phytoplankton new production ($P_{\text{NEW}}$; Dugdale and Goering, 1967):

$$P_{\text{NEW}} = P_T \times f\text{-ratio}.$$ 

According to Eppley and Peterson (1979), $P_{\text{NEW}}$ is the maximum potential export of particulate organic carbon from the euphotic zone ($E_{\text{POC}}$):

$$E_{\text{POC}} = P_{\text{NEW}}.$$ 

Over the whole polynya, $E_{\text{POC}}$ was highest in May and June, when it reached ca. 1000 mg C m$^{-2}$ d$^{-1}$ (Fig. 5). Large differences in new production were observed among regions, as for phytoplankton production. The highest $E_{\text{POC}}$ values were in the East during May, reaching 2765 or 2184 mg C m$^{-2}$ d$^{-1}$, depending on whether the f-ratios were estimated from $P_L/P_T$ or $B_L/B_T$, respectively. $E_{\text{POC}}$ during June was ca. one-third of that in May. In the North, the maximum $E_{\text{POC}}$ was in June, reaching ca. 1400 mg C m$^{-2}$ d$^{-1}$.

In the West, the maximum $E_{\text{POC}}$ was <500 mg C m$^{-2}$ d$^{-1}$, similar to values in the East and North for the remainder of the year. The few data from the South were low.

### 3.5. Potential particulate export from the phytoplankton community

Tremblay and Legendre (1994) proposed an approach to estimate the potential particulate export from the phytoplankton community to other trophic compartments or downwards. Their approach is based on $P/B$ diagrams, where the two axes are $P_L/P_T$ and $B_L/B_T$. An index combining the $P_L/P_T$ and $B_L/B_T$ information into a single value was developed by Tamigneaux et al. (1999):

$$P\% - B\% = (P_L/P_T - B_L/B_T)100.$$ 

According to these authors, the $P\% - B\%$ index can be interpreted as follows: $P\% - B\% = 0$ corresponds to a dynamic balance between the production and export of large and small phytoplankton; $P\% - B\% > 0$ indicates that the export of large relative to total phytoplankton is higher than their proportional contribution to the phytoplankton production, which can also be interpreted as retention or accumulation of small phytoplankton in the euphotic zone; and $P\% - B\% < 0$ means that the export of large relative to total phytoplankton is lower than their share of the phytoplankton production, which can also be interpreted as retention or accumulation of large phytoplankton in the euphotic zone.

In the North Water, a significant change in $P\% - B\%$ occurred over the season (Fig. 6). In the

<table>
<thead>
<tr>
<th>Region</th>
<th>April 98</th>
<th>May 98</th>
<th>June 98</th>
<th>July 98</th>
<th>Aug–Sept 99</th>
<th>Sept 99</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole polynya</td>
<td>650 (84)</td>
<td>2100 (118)</td>
<td>2468 (72)</td>
<td>907 (110)</td>
<td>1719 (98)</td>
<td>550 (77)</td>
</tr>
<tr>
<td>North</td>
<td>10 (37)</td>
<td>261 (25)</td>
<td>3291 (59)</td>
<td>931 (49)</td>
<td>1587 (74)</td>
<td>628 (65)</td>
</tr>
<tr>
<td>East</td>
<td>803 (61)</td>
<td>5268 (14)</td>
<td>2382 (85)</td>
<td>976 (102)</td>
<td>1951 (102)</td>
<td>733 (115)</td>
</tr>
<tr>
<td>West</td>
<td>37</td>
<td>771 (31)</td>
<td>1514 (58)</td>
<td>1174</td>
<td>587</td>
<td>193 (139)</td>
</tr>
<tr>
<td>South</td>
<td>nd</td>
<td>nd</td>
<td>nd</td>
<td>269</td>
<td>nd</td>
<td>571 (1)</td>
</tr>
</tbody>
</table>

The mean phytoplankton production ($PP_i$, i.e. $P_T + P_{\text{DOC}}$, mg C m$^{-2}$ d$^{-1}$), integrated over the euphotic zone for the whole polynya and the four regions during the sampling periods (Table 1), and the coefficient of variation (%), between brackets; nd, no data). For the North in April, $P_T$ is given, since no estimates of $P_{\text{DOC}}$ were made.
whole polynya and in the East and the North, $P_\% - B_\%$ was $>0$ in April, close to 0 in May and $<0$ during the remainder of the growing season. In the West, the shift from $>0$ to $<0$ took place a few weeks later. In all regions, the largest negative values occurred in September. The shift in $P_\% - B_\%$ from $>0$ to $<0$ suggests that most of the $E_{POC}$ from the phytoplankton community consisted of large cells in April, the two size fractions contributed equally to export during May, and export consisted mostly of small phytoplankton during the remainder of the growing period. The dominance of export by the small size fraction was highest during September.

Fig. 3. Mean phytoplankton production (mg C m$^{-2}$ d$^{-1}$) for the whole polynya area and the four regions (Fig. 1). The April–September cycle is a composite of data obtained during cruises in 1997, 1998, and 1999 (Table 1). $P_L$ indicates large-sized (>5 $\mu$m) production; $P_S$, small-sized (<5 $\mu$m) production; $P_{DOC}$, released DOC; and nd, no data.
3.6. Annual production and export

Total annual production and potential export for the whole polynya and the different regions can be estimated for the April–early October period, which corresponds to the phytoplankton growing season in the region. Estimates were obtained by integrating the production and export over the observational periods, i.e. $4 \times 1$ month and $3 \times 3$ weeks (Table 1). Because there were no production/export data for August, the mean value of the periods July and August–September was used for August.

Fig. 4. Mean $f$-ratios estimated from $P_L/P_T$ and $B_L/B_T$ for the whole polynya area and the four regions (Fig. 1). The April–September cycle is a composite of data obtained during cruises in 1997, 1998, and 1999 (Table 1); nd indicates no data.
Total annual production of particulate organic matter ($P_T$) reached ca. 250, 125 and 75 g C m$^{-2}$ yr$^{-1}$ in the East, North, and West, respectively (Table 4). The total annual release of DOC also showed an East > North > West pattern and accounted for 33–47% of the total annual phytoplankton production ($PP = P_T + P_{DOC}$).

The high $f$-ratios in the three northern regions (range of 0.4–0.7) resulted in high potential annual export from the phytoplankton community in the euphotic zone (up to 155 g C m$^{-2}$ yr$^{-1}$ in the East). $E_{POC}$ showed the same East > North > West pattern as $PP$ and $P_T$.

4. Discussion

The data in this study, collected during cruises conducted over a 3-yr period (Table 1), are
presented here as a seasonal composite of an April–September cycle. We recognize that interannual and spatial variations of physical conditions, e.g., ice cover and wind, did influence the precise timing, distribution and intensity of the phytoplankton bloom. Arguments are presented below to support our opinion that patterns emerging from composites of mean values for the large areas examined are a reasonable representation of the general temporal and spatial trends and regional variations in the North Water.

4.1. Phytoplankton biomass

Biomasses presented here are average values for large regions (see Mei et al. (2002), for more
detailed distributions of the size-fractionated phytoplankton biomass in April–July 1998). The highest chl $a$ concentration observed in the euphotic zone at an individual station in the North Water in 1998 (19.8 mg m$^{-3}$) is similar to the maximum value reported by Lewis et al. (1996) in the upper 30 m in 1991 (19.5 mg m$^{-3}$). The maximum areal chl $a$ (integrated over the euphotic zone) for an individual station was 300 mg m$^{-2}$ in 1998, the same as that reported by Mei et al. (2002) but lower than the maximum value reported by Lewis et al. (1996; 506 mg chl $a$ m$^{-2}$ in the upper 30 m). The latter difference is because the depth of the euphotic zone was only 16–25 m at stations with average chl $a$ concentration $>6$ mg m$^{-3}$ in the euphotic zone (Mei et al., 2002) versus the 30-m depth used by Lewis et al. (1996). The similarity in the range of chl $a$ concentrations observed in this study and in 1991 by Lewis et al. (1996) suggests that the intensity of the spring phytoplankton bloom in the North Water is a recurrent feature, related to the concentrations of wintertime nutrients (Lewis et al., 1996; Tremblay et al., 2002b; Mei et al., 2002).

Weekly composite SeaWiFS images are available for early May–early September 1998 and 1999. The distributions of chl $a$ (SeaWiFS-ocean color) in spring 1998 and August–early September 1999 agree well with the field observations (Fig. 2; Bélanger, 2000; Bélanger et al., 2002). No SeaWiFS images are available for the period corresponding to the field sampling of August 1997, but chl $a$ values in 1997 (Fig. 2) fall in the same range as those obtained with SeaWiFS in August 1998 and 1999, with the difference that in 1999, the highest biomass was observed in the West instead of the North. Furthermore, the phytoplankton species composition in August 1997 and 1999 is similar enough to suggest a single temporal pattern (Booth et al., 2002). The SeaWiFS images reveal some interannual variations in the spatial and temporal patterns of phytoplankton biomass (Bélanger, 2000; Bélanger et al., 2002). In 1999, the bloom developed about 2 weeks later than in 1998, culminated a few weeks later and lasted until mid-July, whereas chl $a$ decreased considerably at the beginning of July 1998. The total duration of the bloom in 1999, which was mainly located between Smith Sound and the Carey Islands on the Greenland side (i.e. regions East and North), was about 3 weeks longer than in 1998.

Phytoplankton biomass in the North Water was high, but comparable to concentrations observed in other Arctic environments (e.g., Bering Strait, Arctic ice edges after depletion of winter nutrients in the upper layer, St. Lawrence Island Polynya; Table 5). Higher concentrations were observed in the Bering Sea, related to higher concentrations of winter nutrients than in the North Water, and much lower ones in the Northeast Water Polynya. A difference between the North Water and other Arctic high-chl $a$ environments is the very large horizontal extent and long duration of the phytoplankton bloom in the North Water. Furthermore, the other Arctic high-chl $a$ environments mentioned above (except for the Northeast Water) are all situated ca. 10° south of the North Water.

### 4.2. Phytoplankton production

Our phytoplankton production data are the first to be published for the North Water. Some values were very high, reaching 4.4 and 5.3 g C m$^{-2}$ d$^{-1}$ in the East during May (mean $P_T$ and PP, respectively). Similarly high rates (> 5 g C m$^{-2}$ d$^{-1}$) were observed during June in the North and East. Despite the persistence of high phytoplankton biomass, production declined in the East in June, likely due to nitrate exhaustion (Tremblay et al., 2002b). In August–September there was also one
observation of $\text{PP} > 5 \text{g C m}^{-2} \text{d}^{-1}$ in the East, probably after replenishment of nutrients.

New production was estimated in 1998 by Tremblay et al. (2002a) from in vitro measurements of nitrate uptake and mesoscale temporal changes in dissolved nitrate inventories. Their estimates for April, May and July fall between our $P_T$ and PP estimates (Table 6), confirming the magnitude of our results. In contrast, their estimate for June is lower than both our $P_T$ and PP values, suggesting that regenerated production can be important in the North Water.

Maximum $P_T$ in the North Water was very high, but similarly high rates of phytoplankton production have been observed in the Western Bering Strait, an advection-upwelling area (Springer et al., 1996) situated ca. 10° south of the North Water (Table 7). Peak values observed in the North Water are ca. 2.5 times higher than the highest $P_T$ observed in the Northeast Water and 1.6 times higher than in the Chukchi Sea. The high average daily production values in the North Water and Bering Strait are comparable to observations in some highly productive, temperate, eutrophic nearshore waters ($P_T$ range of 3–6.5 g C m$^{-2}$ d$^{-1}$, e.g., Dutch Wadden Sea (Cadée, 1986), Gulf of St. Lawrence (de Lafontaine et al., 1991, and references therein), and Chesapeake Bay (Marshall and Nesius, 1996)). Among Arctic polynyas, average daily phytoplankton production is nearly one order of magnitude higher in the North Water than in the Northeast Water. No production data have been published yet for the St. Lawrence Island Polynya, but values there are probably similar to those reported for the surrounding waters of the Bering Sea and Bering Strait (see above).

The DOC released from phytoplankton in the North Water was on average 44% (range = 15–82%) of total production. Wheeler et al. (1996) and Gosselin et al. (1997) found that 0–65% (mean = 25%) of $P_T$ and up to 88% (mean = 34%) of the ice algal production was $P_{\text{DOC}}$ in the Arctic Ocean during summer 1994. The highest DOC release by phytoplankton was under ice cover of $\geq$90%. Vernet et al. (1998) observed that between 36% and 55% of the production was released as DOC in the marginal ice zone and 18% in ice-free waters of the Barents Sea during mid-summer. In contrast, our $P_{\text{DOC}}$ data expressed as %PP did not show any relationship with % ice cover, season or size fractions (either $P_L/P_T$ or $B_L/B_T$; not shown). The $P_{\text{DOC}}$ in the North Water may have been somewhat overestimated due to microzooplankton grazing during the incubations and/or cell lysis during filtration of the water samples. Release of extracellular carbon, however, is a normal process for phytoplankton, with recent studies showing that $P_{\text{DOC}}$ often exceeds $P_T$ (e.g. Søndergaard et al., 2000, and references therein). The DOC release can be high compared to PP, but is normally low when compared to carbon biomass of the phytoplankton. A DOC release of 50% of the total production corresponds to a loss rate of

<table>
<thead>
<tr>
<th>Region</th>
<th>Chl $a$ (mg m$^{-3}$)</th>
<th>References</th>
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<tr>
<td>North Water Polynya</td>
<td>19.8</td>
<td>This study; Mei et al. (2002)</td>
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<td></td>
<td>19.5</td>
<td>Lewis et al. (1996)</td>
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<tr>
<td>Bering Strait</td>
<td>&gt; 200$^b$</td>
<td>Gosselin et al. (1997)</td>
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<tr>
<td>Ice edges</td>
<td>&gt; 300$^b$</td>
<td>Sakshaug and Skjoldal (1989)</td>
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<tr>
<td>St. Lawrence Island Polynya</td>
<td>9.9</td>
<td>Smith et al. (1997)</td>
</tr>
<tr>
<td>Bering Sea</td>
<td>27.5</td>
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<tr>
<td>Northeast Water Polynya</td>
<td>300$^a$</td>
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$^a$Integration depths of 16–25 m (this study, Mei et al., 2002) or 30 m (Lewis et al., 1996).

$^b$Whole water column (<50 m).
about 5% of carbon biomass per day (Bjørnsen, 1988).

4.3. f-Ratios

The f-ratios in this study were estimated from the size structure of the phytoplankton community. Although the general applicability of this method remains to be demonstrated, it seems to be a reasonable proxy for cold waters, since Tremblay et al. (1997) used, in the development of this method, data from the cold-temperate and sub-Arctic waters of the Gulf of St. Lawrence, which are ice-covered during winter. Moreover, our EPOC estimate is similar to the new production values obtained in 1998 by Tremblay et al. (2002a; see below and Table 6). Despite the theoretical constraints that \( P_T \) should be limited by the availability of nitrogen and that the phytoplankton biomass in the euphotic zone should be in steady state over large space and time scales, the f-ratio is frequently used as a proxy to estimate the export of biogenic carbon from the euphotic zone (Eppley and Peterson, 1979) in predictive models and remote sensing applications (Tremblay et al., 1997).

The f-ratios obtained using the size structure of the phytoplankton community were generally high in the North Water (range of 0.4–0.7). The f-ratios could also be computed as new production (\( P_{NEW} \)) divided by \( P_T \). Estimates of \( P_{NEW} \) were derived from a combination of short-term uptake studies using \( ^{15}\)N-nitrate and mesoscale changes in the inventories of nitrate by Tremblay et al. (2002). Because the estimates of polynya-wide \( P_T \) were similar to, but somewhat lower than, those of \( P_{NEW} \), for April, May, and July, the resulting f-ratios ranged between 1.2 and 1.8. The f-ratio calculated for June was <1 (0.8), which is twice as high as the f-ratio obtained using the size structure of the phytoplankton community (0.4). These very high calculated f-ratios confirm that the f-ratio must have been high in spring–early summer 1998 (see below). Since detailed f-ratios based on the uptake of N-nutrients (NO\(_3\), NH\(_4\) and urea) are not yet available, explaining inconsistencies in the results obtained by the two approaches discussed is not yet possible.

The f-ratios obtained in this study, using the size structure of the phytoplankton community, are comparable to those observed in the Northeast Water in 1992 and 1993 (Smith, 1995; Smith et al., 1997) and in the western Bering Strait (Sambrotto et al., 1984), but much higher than the low f-ratios (range of 0.05–0.38) observed in the Chukchi Sea.
in August 1993 (Cota et al., 1996). In addition, the seasonal variation in $f$-ratios in the North Water, with maximum values early in the season and lower values in mid-summer, corresponds to the patterns observed in the Northeast Water during 1993 (Smith et al., 1997). The relatively high $f$-ratios (0.6–0.75, derived from $P_L/P_T$) in the East and West during April–June suggest that intact phytoplankton might have been part of the sinking POC (Eppley and Peterson, 1979), as observed by Booth et al. (2002) and Sampei et al. (2002). Later in the season, when $f$-ratios were lower, sinking of intact cells should have been less common. This pattern was confirmed by microscopic examination of material from moored sediment traps (see Table 2 in Sampei et al., 2002). The much lower $f$-ratios in the South reflect the fact that the composition of the phytoplankton community there differed from that elsewhere in the North Water (Lovejoy et al., 2002) and that both biomass and production were dominated by the small-size fraction, whereas large cells dominated in the northern regions.

4.4. Phytoplankton size fractions and potential export

Both biomass and, to a lesser extent, production ($P_T$) in the North Water were generally dominated by the large size fraction, except in the South (see also Fig. 4 in Mei et al., 2002, and Lovejoy et al., 2002). Tremblay et al. (2002a) estimated that as much as 80% of new production in April–July 1998 was mediated by diatoms >5 µm. Dominance by the large size fraction was also observed in the Northeast Water during bloom situations (regimes 1 and 2, early bloom and a later stage of the bloom, respectively, in Pesant et al., 1996) and in the Chukchi Sea (Gosselin et al., 1997). In the Greenland Sea the biomass was dominated by the small size fraction but the production by large cells (Legendre et al., 1993). Changes in the $P\%-B\%$ index indicate that $E_{POC}$ from the phytoplankton community shifted from large cells in April, to an equal contribution of the two size fractions during May, and to dominance of the small phytoplankton during the remainder of the season. This pattern also can be interpreted as retention or accumulation of small phytoplankton in the euphotic zone during April, with a shift to retention or accumulation of large phytoplankton later in the season. This effect is especially clear in the East, where the biomass in June was only slightly lower than in May, but production decreased two-fold.

Only a few data sets from the Arctic provide both size-fractionated biomass and production measurements. Data for the Northeast Water from the end of May until August (Pesant et al., 1996) and from a transect across the Arctic Ocean (plotting the data from Gosselin et al., 1997, their Fig. 6, in a $P-B$ diagram) show that in those areas, as in the North Water after May, the potential export was dominated by small cells, except at a few stations. This effect is indicated by the position of nearly all of the data points below the main diagonal of the $P-B$ diagram, thus corresponding to a negative $P\%-B\%$ index. The situation was reversed in the Greenland Sea, with nearly all of the data points located above the main diagonal of the $P-B$ diagram (Legendre et al., 1993), corresponding to a positive $P\%-B\%$ index and dominance of the potential export by large cells. Unfortunately, the data sets from the Northeast Water and the Arctic Ocean cannot be plotted as a time series. Pesant et al. (1996), however, suggested that their regime 1 in the Northeast Water corresponded to an early bloom situation ($P\%-B\%$ index near zero) which then shifted to regime 2, a later stage in bloom development (a negative $P\%-B\%$ index). Such a shift suggests that in the Northeast Water, a shift in $E_{POC}$ towards dominance by small cells during the progression of the bloom also may have occurred, as observed in the North Water.

4.5. Annual production and export

Total annual production in the North Water during this study was high. Since the nutrient concentrations in spring 1998 reached their potential upper limit (Tremblay et al., 2002a,b), the annual production estimates presented here may be close to the maximum production possible in the North Water, assuming the region is nutrient-limited rather than light-limited. Total annual
production was two- to three-fold higher in the East than in North and West (Table 4). This difference is somewhat surprising since nutrient concentrations in the North Water in April 1998 did not show large differences among regions (Tremblay et al., 2002b). The latter authors observed that, in May in the East region, nitrate was nearly exhausted in the southern part (76.2°N) and a moderate deficit had developed in the northern part (ca. 77.5°N). Severe nitrate depletion was observed in June as far north as 79°N along the Greenland coast, while little depletion occurred along the coast of Ellesmere Island where the nitrate deficit developed in July. Nitrate concentrations remained slightly elevated in the South. These nutrient data suggest that total production in the East, North and West should have been similar, which was not the case. The high annual values of $P_T$, $P_{DOC}$, PP and $E_{POC}$ in the East compared to the other regions were due not only to the somewhat earlier opening of the polynya but also to high production estimates at individual stations during May (see above) compared to those elsewhere in the polynya. Since these high May estimates, which may correspond to the end of the exponential development of the bloom, were used in the integration through time, our annual production values in the East may be overestimates. Reducing the daily May production values in the East by 50%, however, reduces the annual $P_T$, $P_{DOC}$, PP and $E_{POC}$ only by ca. 20%, leaving them still higher than annual estimates in the North and the West.

The North region of the North Water remained ice-covered until early June (Mundy and Barber, 2001), which limited light penetration and phytoplankton production. There was continuous advection through Kane Basin of Arctic Ocean water, however, which flows southward along the coast of Ellesmere Island (Bacle et al., 2002; Melling et al., 2001). Thus, the general circulation provides an input of nutrient-rich water in the North (Tremblay et al., 2002a), which would support high production until the end of the growing season. From there, the water moves southwestwards, with phytoplankton gradually consuming the nutrients in surface waters, which limits production in the West. Waters in the South remained ice-covered until the beginning of June (Mundy and Barber, 2001), with phytoplankton biomass remaining low throughout the summer (see also Belanger, 2000; Odate et al., 2002).

To our knowledge, this study represents the first time that total annual production, i.e. including $P_{DOC}$, has been estimated for Arctic waters from field measurements. Our annual $P_T$ ranged from 76 to 254 g C m$^{-2}$ yr$^{-1}$ (Table 4). Annual $P_T$ has reached 324 and 170 g C m$^{-2}$ yr$^{-1}$ in the western and southeast Bering Strait, respectively (Sambrocco et al., 1984), and 462 g C m$^{-2}$ yr$^{-1}$ on the northern shelf of the Bering Sea (average of several published data sets; Springer et al., 1996), but these locations are situated ca. 10° south of the North Water. Rysgaard et al. (1999) compiled data from the literature on annual phytoplankton production in Arctic waters and concluded that values in the Bering Sea and Strait are much higher than in other regions because it is a strong advection-upwelling area.

Annual $P_T$ in the Northeast Water, in 1993, was ca. 66 g C m$^{-2}$ yr$^{-1}$, computed as the average daily new production multiplied by time (assuming a productive period of 120 d) and divided by the average $f$-ratio, i.e. 0.361 × 120/0.65 (data from Smith et al., 1997). This rate is probably an upper estimate because there were no data for September. This $P_T$ is in the same range as our North Water estimate for the West. The annual production in the Northeast Water was estimated incorrectly by Rysgaard et al. (1999) to be only 18–27 g C m$^{-2}$ yr$^{-1}$. They did not take into account the fact that the data presented by Smith et al. (1997) were new production values (i.e. not $P_T$) and that the productive period was longer than the 2.7-month sampling period. This error, however, does not influence their conclusion that the overall relationship between annual $P_T$ and duration of the OW production period for the Arctic is linear (Rysgaard et al., 1999). Our annual $P_T$ for the West (Table 4) and an OW period of about 4 months is consistent with the data set of Rysgaard et al. (1999). Our $P_T$ estimates for the East and the North (254 and 127 g C m$^{-2}$ yr$^{-1}$, respectively) are, like the Bering Sea values, out of range, probably because of the advection of nutrient-rich water in the North. Presently, no robust physical explanation exists for
the high values in the East, i.e. Melling et al. (2001) have shown that the upwelling of West Greenland Current water (WGCW) does not reach the upper mixed layer. Tidal mixing over the Carey shallow, however, could entrain some WGCW into the upper mixed layer, but this is still under investigation (Y. Gratton, unpublished).

Estimating potential POC export using f-ratios is normally only valid for large temporal and spatial scales and applies to steady-state systems, which was certainly not the case in the North Water. As indicated above, no f-ratios estimated from the uptake of N-nutrients are available, but Tremblay et al. (2002) present estimates of \( P_{\text{NEW}} \).

Our \( E_{\text{POC}} \) estimates for the whole polynya for April–July 1998 (when comparable data are available; Table 6) are lower, but of the same order of magnitude as their \( P_{\text{NEW}} \). This similarity lends support to our approach of estimating \( E_{\text{POC}} \) using f-ratios based on the size structure of the phytoplankton community (see also above).

The annual potential POC export in the North Water by our methods ranged from 42 g C m\(^{-2}\) yr\(^{-1}\) in the West to 155 g C m\(^{-2}\) yr\(^{-1}\) in the East, with an average value of 92 g C m\(^{-2}\) yr\(^{-1}\) for the whole polynya (Table 4). Only a few annual POC export estimates are available for the Arctic for comparison. New production (annual \( P_T f \)-ratio) has reached 178 and 68 g C m\(^{-2}\) yr\(^{-1}\) in the western and southeastern Bering Strait, respectively (Sambrotto et al., 1984). These values are similar to our estimates in the East and North, respectively. In the Northeast Water, total new production was 43 g C m\(^{-2}\) yr\(^{-1}\) (assuming a production period of 120 d; Smith et al., 1997), which corresponds to our estimate for the West. A large part of the potential POC export in the North Water was probably retained in the upper part of the water column (see also below). Tremblay et al. (2002a) estimated that, during 1998 in regions dominated by Baffin Bay Water, as much as 94% of the autotrophic matter produced during the bloom may have remained suspended until early June, which is consistent with calculations by Hargrave et al. (2002) that only 0.4–2.4% of our \( P_T \) estimates in the East reached moored sediment traps at >200 m. Furthermore, values of chl a integrated to 100-m depth declined more rapidly than the integrated POC in June–July (not shown). These results suggest an increasing abundance of heterotrophic organisms, as demonstrated for bacterioplankton (Huston and Deming, 2002), and/or detritus as the season progressed.

The \( E_{\text{POC}} \) pattern with highest values in the East, followed by the North and finally the West, differs slightly from that obtained by Miller et al. (2002) using changes in surface carbon budgets from April until October (i.e. highest values in the North, followed by the West and finally the East). This difference among regions is probably due to advection (see also Tremblay et al., 2002a). The 6-month budget values of Miller et al. (2002) for the growing season are ca. 75% of our annual \( E_{\text{POC}} \) (based on the same period).

The polynya-wide \( E_{\text{POC}} \) estimates from April to July 1998 reveal a seasonal trend similar to that of the \( P_{\text{NEW}} \) estimates of Tremblay et al. (2002a; see Table 6), even though \( E_{\text{POC}} \) were slightly lower than \( P_{\text{NEW}} \) (range of 28–74%). All three export estimates obtained from samples collected simultaneously in the water column, i.e. \( E_{\text{POC}} \), \( P_{\text{NEW}} \) (Tremblay et al., 2002a) and changes in surface carbon budgets (Miller et al., 2002), appear to be internally consistent. Furthermore, for the period of July 1998, two other polynya-wide estimates of carbon export are available for comparison, one based on \(^{234}\text{Th} \) deficits (Amiel et al., 2002) and the other on floating sediment-trap collections (Huston and Deming, 2002). These estimates are also similar to our \( E_{\text{POC}} \) values (330, 174 and 196 mg C m\(^{-2}\) d\(^{-1}\), respectively). Amiel et al. (2002) report a POC flux for August 1999, which is less than a third of our \( E_{\text{POC}} \), while Huston and Deming (2002) report an even lower fraction of our estimate for May 1998. The latter authors, however, qualified their May estimate as unrepresentative of the whole polynya, due to insufficient sample size. Overall, our \( E_{\text{POC}} \) data are remarkably coherent with the biogenic carbon export estimates obtained in the upper water column using a variety of different techniques.

Regionally, our results show that \( E_{\text{POC}} \) in the East was much higher than in the West, whereas particle fluxes (of organic C and chloropigments) observed in deep long-term sediment traps (moored at ca. 200-m depth and 50 m above the
bottom; Hargrave et al., 2002) show the opposite trend, with highest sedimentation in the West. Furthermore, two distinct seasonal peaks were observed in the deep particle flux in the North Water, i.e. a small spring–early summer peak (April–June) followed by a larger late summer–autumn peak (July–early October; Hargrave et al., 2002), whereas our data show that $E_{\text{POC}}$ was highest in May–June. These differences reflect a temporal disconnection between both PP and $E_{\text{POC}}$ near the surface and particle fluxes deeper in the water column. Our measurements were instantaneous, reflecting what was happening in the euphotic zone on the sampling day (phytoplankton production and potential effects on the pelagic food web) and the resultant potential downward export from the euphotic zone in the near future. In contrast, deeper particle fluxes integrate the whole water column above the sediment trap over a longer period of time. The disconnection in time also led to a spatial disconnection, since a substantial part of the $E_{\text{POC}}$ appeared to remain for some time in the upper water column, where it was likely retained in different compartments of the planktonic food web and even recycled several times before reaching the sediment traps at ca. 200-m depth. Considerable East–West advection of particulate material must have occurred, as also evidenced and discussed by Sampei et al. (2002). Deep sedimentation in the North Water started earlier in the East than in the West, with the chlorophyll content of the settling particles being higher in the East than in the West (Hargrave et al., 2002). These results are consistent with our observations that $E_{\text{POC}}$ starts earlier and is higher in the East than in the West. Particles reaching the sediment traps early in the season indeed included intact phytoplankton cells (Booth et al., 2002; Sampei et al., 2002), which must have had high sinking velocities in order to escape advection or mid-water grazing.

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