Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton

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ABSTRACT: Plankton community structure in Disko Bay, West Greenland, was examined during late summer 1994. Sampling with high temporal and vertical resolution was conducted at a 250 m deep station from mid-July to mid-September. The water column was strongly stratified and the phytoplankton community in the surface layer was nitrate and silicate depleted. A prominent feature was the occurrence of enhanced phytoplankton biomass in association with the pycnocline where nitrate became detectable. Three distinct blooms ($\text{chl } a > 8 \mu\text{g l}^{-1}$) were observed in the pycnocline, the first dominated by haptophyte flagellates and subsequently by diatoms. Bacterial biomass mirrored the vertical and temporal distribution pattern of the phytoplankton. Comparison between primary production and bacterial production showed that pelagic bacterioplankton were important in this high latitude ecosystem, as documented for low latitude ecosystems. The most important bacterivores, the heterotrophic nanoflagellates, had the potential of clearing the daily bacterial production. It is concluded that future studies of Arctic pelagic ecology should consider the plankton community in the subsurface layer if carbon flow in the pelagic food web is to be fully understood.

KEY WORDS: Arctic pelagic food web · Nutrient dynamics · Phytoplankton · Bacterioplankton · Subsurface blooms

INTRODUCTION

Until the late 1970s marine pelagic ecology was dominated by studies of the fate of large primary producers (diatoms) through a simple linear food chain. This view has been more persistent in Arctic research than at lower latitudes where the view on the pelagic food web has changed dramatically during the last decades (Pomeroy 1974, Sorokin 1977, Azam et al. 1983). Accordingly the biology of large Arctic phytoplankton and copepods has been intensively studied during the past century (Gran 1902, Jespersen 1934, Grøntved & Seidenfaden 1938, Ussing 1938, Smidt

1979). The state of the art is that much of the basic biology such as biomass contribution, species composition and role in energy transfer of the smaller components of the pelagic food web has been largely ignored.

It is now documented that the previous view on the Arctic pelagic food web structure was too simple. The taxonomic composition of Arctic phytoplankton is highly diverse (e.g. Thomsen 1982, Booth & Smith 1997) and a significant fraction of the primary production also at these latitudes is due to small celled species ($< 5 \mu\text{m}$) occurring outside the main bloom (Legendre et al. 1993). The size composition of the primary producers is of great importance for the structure of the succeeding links in the food web, e.g. small cells lose a larger fraction of their stored DOM than does a community dominated by larger cells (Bjørnsen 1988, Kiør-

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boe 1993). Consequently a community dominated by small cells will leak a larger fraction of its production to the bacterioplankton. Information on bacterioplankton in Arctic pelagic ecosystems is limited, probably because they were assumed to be insignificant compared with low latitude ecosystems (Pomeroy & Deibel 1986, Pomeroy et al. 1990). However, during and after the spring bloom in Disko Bay, Western Greenland, Nielsen & Hansen (1995) reported that the bacterioplankton was active and had a prominent role in the pelagic food web. This observation is supported by a recent review by Rivkin et al. (1996), who suggest that growth rates of cold-water bacterioplankton are similar to those observed from temperate waters.

At present few investigations that consider the importance of both the microbial and mesozooplankton part of the arctic food web are available. This study describes both components of the pelagic food web during the stratified summer-autumn period after the main spring diatom bloom. Since the dominating large copepods (*Calanus* spp.) start to hibernate before the breakdown of the summer stratification this investigation gave us the opportunity to evaluate the role of the succeeding smaller copepods and the microbial community with a reduced top-down control.

The present paper reports on hydrography, water chemistry, phytoplankton and the bacterioplankton while a companion paper, Levinsen et al. (1999, in this issue), addresses the composition, the growth and the role of ciliates and heterotrophic dinoflagellates. A second companion paper, Hansen et al. (1999, in this issue), discusses the role of copepods and meroplankton, and the overall pelagic carbon budget for the entire stratified summer-autumn period.

MATERIALS AND METHODS

Study site. This investigation was conducted from July 17 to September 17, 1994, approximately 1 nautical mile offshore from Qeqertarsuaq (Godhavn) (69° 15' N, 53° 33' W) at a 250 m deep station in Disko Bay, West Greenland (Fig. 1).

Sampling. The present investigation is based on 18 visits to the station with the RV 'Porsild' (Arctic Station, University of Copenhagen). From July 17 to August 23 the biological investigations were limited to assessments of standing stocks. After August 23 the sampling frequency was intensified and growth rate measurements included in the investigation (this part of the investigation will be referred to as the second part).

Data on wind speed and direction originates from a meteorological station at Arctic Station in Qeqertarsuaq (Nielsen et al. 1995).

Sampling was conducted around local noon. Vertical profiles of salinity, temperature and fluorescence were obtained from the surface to 30 m. Temperature and salinity were recorded using a WTW-probe, and chlorophyll *a* (chl *a*) fluorescence was measured with a Hardt fluorometer. The salinity probe was calibrated against a Gulidline Portosal salinometer using water from various depths in order to cover the salinity range. The *in situ* fluorometer measurements were calibrated against the spectrophotometrically determined chlorophyll content in the water samples, and a linear regression was conducted ($r^2 = 0.70$, $n = 56$). Light attenuation was measured in the upper 35 m with a Licor Quantum Photometer (model Li-192 SA equipped with a spherical sensor). Based on the vertical distribution of temperature, salinity and fluorescence, 5 or 6 depths in the upper 30 m were selected for chemical and biological measurements.

Nutrients. Samples for the determination of nutrient concentration (NO_2^- , NO_3^- , PO_4^{3-} , SiO_4^{3-}) were frozen on board the ship. Measurements were carried out at the National Environmental Research Institute (NERI) on an automatic nutrient analyzer (Dansk havteknik) following Grashoff (1976). All nutrient samples were analysed in duplicate with a precision of 0.06, 0.09 and 0.12 μM for nitrate, phosphorus and silicate respectively.

Chl *a* and phytoplankton. Samples (1 to 2 l) intended for chl *a* measurements were placed in the dark and filtered at the land based laboratory within 3 h after collection onto GF/F filters, extracted in 96% ethanol (Jespersen & Christoffersen 1987) and measured spectrophotometrically (Strickland & Parsons 1972). The chl *a* fraction <11 μm was measured as the concentration of chl *a* after gentle filtration through 11 μm Nitex screen, the fraction >11 μm was then calculated as total chl *a* – chl *a* <11 μm . In addition to absorption measurements for chl *a* (665 nm), absorption was also measured at 480 nm (carotenoids). Carotenoid concentration in phytoplankton is largely independent of the ambient nutrient concentrations, while the chl *a* declines as the phytoplankton become nitrogen depleted. Changes in the ratio (480/665 nm) of absorption thus indicate nutritional status of the phytoplankton. Values above 2 indicate that the phytoplankton is nitrogen limited (Heath et al. 1990). The abundance and biomass of the dominating phytoplankton taxa were determined by epifluorescence microscopy of filters stained by proflavine (Haas 1982). Biomass was calculated from volume and a carbon conversion factor of 0.12 $\text{pg C } \mu\text{m}^{-3}$ (Edler 1979). The mean carbon/chl *a* ratio was calculated from a linear regression of corresponding values of phytoplankton biomass and chl *a*.

Primary production. Primary production was measured *in situ* with the ^{14}C method (Steemann-Nielsen 1952). Water samples from each of the selected depths

Fig. 1. Map showing location of Disko Bay and approximate position of the station investigated

were incubated for 2 h around noon in 2 light and 1 dark Jena bottle (100 ml) with 4 $\mu\text{Ci H}^{14}\text{CO}_3^-$ (International Agency for ^{14}C Determination) added to each bottle. After incubation, bottles were kept dark, and filtered within 1 h. The entire content of each bottle was vacuum-filtered (<100 mm of Hg) through 25 mm GF/F filters. Filters were placed in scintillation vials, and inorganic ^{14}C removed through addition of 200 μl of 1 N HCl. The samples were kept frozen until counting at NERI. In preparation for counting the open vials were placed under a hood for 24 h, allowing the excess inorganic ^{14}C to evaporate. Prior to liquid scintillation counting, 10 ml Filtercount was added and the sample was mixed with a Vibrofix VF1 electronic mixer.

Total CO_2 was assumed to be 2.1 mM (Richardson 1991). Daily primary production was calculated by multiplying with a light factor: total daily insolation divided by insolation during the incubation period (e.g.

Vadstein et al. 1989). Automatic light measurements were made every 30 min with a Solar Radiation Sensor 2770 at 300 to 2500 nm (Aanderaa Instr. Bergen, Norway) as part of the Arctic Station environmental monitoring programme. Carbon fixation is presented after subtracting dark fixation, and without subtracting respiration. The daily primary production per m^2 was calculated by trapezoidal integration down to 30 m (Nielsen & Bresta 1984).

Bacteria. Bacteria were counted using the acridine orange technique (Hobbie et al. 1977). At least 400 cells were enumerated on each filter using an Olympus BH-2 epifluorescence microscope. Cell volume was estimated from length and width measurements of 50 cells per filter and converted to carbon using a conversion factor of 0.35 $\text{pg C } \mu\text{m}^{-3}$ (Bjørnsen 1986). Bacterial production was measured by incorporation of ^3H -thymidine (Fuhrman & Azam 1980). Immediately after sam-

Fig. 2. (A) Running mean of cubed wind velocity, and vertical distribution of (B) temperature ($^{\circ}\text{C}$), (C) salinity (‰), and (D) phytoplankton expressed as chl *a* ($\mu\text{g chl } a \text{ l}^{-1}$). Dots indicate the resolution of measurements

pling triplicate samples (10 ml) were incubated with 5 nM methyl- ^3H -thymidine ($20 \mu\text{Ci nmol}^{-1}$, New England Nuclear) for 1 h at *in situ* temperature. Blanks were prepared by addition of formalin prior to addition of isotope. The incubations were stopped by adding buffered formalin (1% final concentration). Samples were subsequently filtered onto $0.2 \mu\text{m}$ cellulose nitrate filters, washed 10 times with 5% ice cold TCA and counted using liquid scintillation counting. The incorporated ^3H -thymidine was converted to cell production using a factor of 1.1×10^{18} cells mol^{-1} thymidine incorporated (Riemann et al. 1987). To test whether the incubation time was appropriate, we incubated triplicate samples from the same station for 0.5, 1, 2, 3 and 4 h; the incorporation in each sample was the same, showing isotope saturation. To check that the bacterial uptake sites were saturated with thymidine an experiment with addition of 2.5, 5, 7.5, 10 and 20 nM was conducted, showing that the incubation was saturated by addition of 5 nM.

Nanoflagellates. The abundance of heterotrophic nanoflagellates was determined by epifluorescence microscopy of filters stained by proflavine (Haas 1982). Discrimination between autotrophic and heterotrophic flagellates was carried out by switching between blue and green excitation. Samples were fixed in 1% glutaraldehyde. The diameter of 100 randomly selected cells per filter was measured, and the corresponding biomass calculated assuming a spherical shape and a conversion factor of $0.12 \mu\text{g C } \mu\text{m}^{-3}$ (Edler 1979). Clearance rates were estimated as 10^5 body volume h^{-1} (Fenchel 1982). The assumption of maximal clearance is reasonable since the bacterial biomass (15 to $45 \mu\text{g C l}^{-1}$) during this investigation was far below the K_m ($2 \text{ ppm} \approx 240 \mu\text{g C l}^{-1}$) reported for heterotrophic nanoflagellates (Hansen et al. 1997). The clearance was converted to *in situ* temperature by a Q_{10} of 2.8 (Hansen et al. 1997).

RESULTS

Hydrography and vertical distribution of nutrients

The mixing potential of wind on the water column is illustrated as a running mean of the cubed wind velocity ($\text{m}^3 \text{s}^{-3}$). The running mean was made by parzen filtering excluding events shorter than 1 d (Fig. 2A). The investigation was characterised by 4 relatively long periods of strong wind including episodes of wind velocities up to $10\text{--}15 \text{ m s}^{-1}$. These events had a pronounced effect on the water column structure, as revealed by a deepening of the mixed surface layer (Fig. 2B,C). Throughout summer the upper part of the water column was vertically stratified due to temperature and salinity differences (Fig. 2B,C). A layer with salinities less than 33.3‰ and temperatures above 5°C formed the upper 10 to 20 m of the water column. The thermal stratification was still developing during the first part of the study, when surface temperature increased from 3.8 to 6°C between the first and second sampling. The maximum surface temperature recorded (7.4°C) was reached on August 18 whereafter the temperature decreased as a result of autumn cooling (Fig. 2B). Furthermore, the decreasing solar radiation affected stratification by reducing freshwater input to the bay. On September 17, the temperature was uniform down to $>15 \text{ m}$, the salinity stratification was less pronounced, and the water column was beginning to destabilise.

In general phytoplankton biomass was low ($<0.5 \mu\text{g chl } a \text{ l}^{-1}$) above the pycnocline (Fig. 2D). However after the strong wind event in the beginning of August the chl *a* in the upper 10 m of the water column increased from 0.4 to $0.9 \mu\text{g l}^{-1}$ (Fig. 2D). All chlorophyll fluores-

Fig. 3. Size distribution of the phytoplankton community during the second part of the investigation at (A) the surface 2.5 m and (B) the depth of maximum fluorescence

cence profiles showed a subsurface maximum located between 10 and 30 m. Three distinct blooms with chl *a* concentrations above $8 \mu\text{g l}^{-1}$ occurred in mid-July and the beginning and middle of August, respectively (Fig. 2D). Microscopic examination showed that the phytoplankton was dominated by nanoplankton during most of the study. This finding was supported by fractionated chl *a* samples from the second part of the investigation where the $<11 \mu\text{m}$ fraction dominated both the surface and the subsurface community with 70 and 87% of the chl *a* respectively (Fig. 3). Three pronounced subsurface blooms were observed. The first bloom was composed of haptophyte flagellates and included *Chrysochromulina* spp. and single celled *Phaeocystis* sp. (Fig. 4C). Subsequent blooms were dominated by diatoms: one by *Chaetoceros* spp. and *Thalassiosira* spp., the other by *Pseudonitzschia* sp., *Chaetoceros* spp. and *Thalassiosira* spp. (Fig. 4A). A linear regression of the phytoplankton biomass based on microscopic examination versus chl *a* measurements gave a carbon:chl *a* ratio of 43, $r^2 = 0.44$, $n = 66$.

The vertical distribution of nutrients closely mirrored the structure of the water column and the distribution of phytoplankton (Fig. 5). The nutrient uptake capacity of the phytoplankton community and the well established pycnocline effectively sealed the nutrients in the

Fig. 4. Vertical distribution of the biomass ($\mu\text{g C l}^{-1}$) of the dominating phytoplankton groups, (A) diatoms, (B) autotrophic dinoflagellates and (C) autotrophic nanoflagellates

deep water. The surface and pycnocline concentration of phosphorus was above detection level (0.07 to $0.1 \mu\text{M}$) throughout the investigation (Fig. 5A), while nitrate and silicate were below detection limit most of the summer (Fig. 5B,C). The vertical distribution of nitrite in the euphotic zone followed that of nitrate but with a concentration of $<5\%$ of the nitrate concentration. Elevated concentrations of phosphorus, nitrate and silicate were measured below the maximum phytoplankton biomass at the bottom of the euphotic zone, increasing to maximum values just above the seafloor (250 m, Table 1).

The potential nutrient deprivation of the phytoplankton community in the surface layer was also reflected in the changes in vertical distribution of the absorption ratio at $480/665 \text{ nm}$. Values above 2, indicating that phytoplankton were more nitrogen limited, were only recorded in the surface layer above the pycnocline (Fig. 5D).

Comparison of the 3 major nutrient species (Fig. 6A,B) suggests nitrogen and/or silicate limitation of the primary production in the surface water. Phosphorus was always present in excess compared with the Redfield ratio (Fig. 6A). The present investigation demonstrates that both nitrate and silicate became exhausted from the surface layer after the establishment of stratification. However, the predominance of points with a low nitrate:silicate ratio in the surface

Fig. 5. Vertical distribution of (A) phosphate (μM), (B) nitrate (μM), (C) silicate (μM) and (D) the absorption ratio at 480/665 nm at the Disko Bay station during the investigation. Dots indicate sampling depths

layer, on the left side of Fig. 6B, supports the idea of a primarily nitrate-limited phytoplankton population.

Euphotic zone depth (depth of 1% light penetration) was stable (33.5 ± 1.8 m, $n = 8$) through the second part of the investigation period where measurements of primary production were made (Fig. 7A). This is supported by measurements of Secchi depth (data not shown) which varied between 10 and 15 m (13 ± 2 m, mean (SD)). Hereafter the term euphotic zone will refer to the upper 30 m of the water column. The euphotic zone covered the pycnocline layer where the highest phytoplankton biomass was located. Compared with

Fig. 6. Relationship between (A) phosphorus and nitrate and (B) silicate and nitrate. Lines indicate Redfield ratios of the nutrients in consideration

July and August, the vertical distribution of phytoplankton during the second part of the investigation was the same, with the highest biomass located in and around the pycnocline. The absolute phytoplankton biomass was, however, relatively low and constant (Fig. 7B). Primary production reflected the light regime with the highest primary production (1.5 to $2 \mu\text{g C l}^{-1} \text{ h}^{-1}$) occurring in the upper 5 to 10 m of the water column (Fig. 7C) except on the second sampling day when the relatively high subsurface biomass below 15

Table 1. Salinity and water chemistry below the euphotic zone, mean $\pm$ SD. Numbers of measurements in parentheses

Depth (m)	Salinity (‰)	PO_4^{3-} (μM)	NO_3^- (μM)	NO_2^- (μM)	NH_4 (μM)	SiO_2 (μM)
50	33.4 ± 0.2 (6)	0.61 ± 0.17 (28)	4.58 ± 2.34 (28)	0.11 ± 0.06 (28)	1.27 ± 0.61 (28)	2.27 ± 1.36 (28)
100	33.6 ± 0.1 (4)	0.98 ± 0.14 (16)	9.75 ± 1.37 (16)	0.13 ± 0.04 (16)	0.89 ± 0.57 (16)	8.66 ± 3.05 (16)
150	33.8 ± 0.1 (3)	1.13 ± 0.06 (10)	11.60 ± 1.38 (10)	0.08 ± 0.02 (10)	0.44 ± 0.34 (10)	10.48 ± 2.17 (10)
250	34.0 ± 0.2 (4)	1.14 ± 0.09 (10)	12.08 ± 1.83 (10)	0.04 ± 0.02 (10)	0.18 ± 0.11 (10)	13.30 ± 2.43 (10)

and introduction of nutrient- and phytoplankton-rich water to the surface layer (Fig. 8B). Bacterial production was only measured during the last part of the investigation together with primary production. In general the highest bacterial production was measured above the pycnocline, where the highest primary production was also measured (Fig. 8C), and bacterial production at this depth reached 1 to 2 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. Below the pycnocline bacterial production varied between 0.1 and 0.3 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. Depth integrated bacterial production varied between 8 and 33 $\text{mg C m}^{-2} \text{ d}^{-1}$ (Table 3).

Bacterivorous protists were dominated by heterotrophic nanoflagellates (HNF) and small ciliates, and on the last visit a sarcodine amoeba reminiscent of *Vanella* spp. was abundant. The HNF were the most abundant (10 to 300 cells ml^{-1}) followed by sarcodines (20 to 25 cells ml^{-1}), choanoflagellates (10 to 20 cells ml^{-1}) and ciliates (0.5 to 3.2 cells ml^{-1}). The mean cell volume of the nanoflagellates, the choanoflagellates, *Vanella* spp. and the ciliates was 74, 34, 268 and 900 μm^3 respectively. The vertical distribution of HNF biomass was relatively patchy (Fig. 8D), with the highest abundance observed below the subsurface bloom, where the highest bacterial biomass was also recorded.

The potentially bacterivorous ciliates were dominated by *Strombidium* spp. and *Lohmaniella* spp. The structure and role of the ciliate community is thoroughly discussed in Levinson et al. (1999) and only addressed here to provide estimates of potential grazing pressure on bacteria.

In order to evaluate the relationship between bacterioplankton and their most important predators the samples were divided into 3 groups according to water column characteristics, i.e. surface samples taken in the upper mixed part of the water column (0 to 10 m), samples from the pycnocline (11 to 20 m) and samples from

the deep part of the euphotic zone (>20 m). The temporal biomass succession in bacterioplankton, heterotrophic nanoflagellates and oligotrichous ciliates, and the potential clearance capacity (% of the water column d^{-1}) of bacterivorous protists from the surface, pycnocline and deep euphotic zone layers are shown in Fig. 9. Oscillations in bacterial biomass were observed in all 3 water strata investigated. Oscillations of biomass peaks of bacteria and bacterivorous protists were out of phase with each other. In general a decrease in the bacterioplankton biomass was observed when the clearance capacity of protists peaked. Heterotrophic nanoflagellates contributed most to potential bacterial grazing. Calculations show that the combined population of bacterivorous protists had the potential to clear 0.5 to 3% of the water column bacteria d^{-1} (Fig. 9).

DISCUSSION

The hydrography and current pattern of Disko Bay are complicated due to a heterogeneous bottom topography with many ridges, banks and sills. In summer the surface layer is influenced by both melting of sea ice and land runoff, creating a thin layer with low salinity in the euphotic zone. Stratification is strengthened by heat trapped in the surface layer during summer. This surface layer is also influenced by the West Greenland Current that enters the southern part of the Bay and after a cyclonic circulation leaves the area through Vaigat and the northern part of the Bay just off Godhavn (Kiilerich 1939, Andersen 1981a). Water column structure at our permanent sampling station is thus strongly influenced by advection of surface water leaving Disko Bay. However, for the purpose of this discussion we assume that the overall succession pattern in plankton observed from the uppermost 50 m is representative of what happens during the summer

months on a larger scale in the Bay proper. This assumption is supported by observations during horizontal surveys in Disko Bay in June-July 1996 and June 1997 (Munk et al. unpubl. data). During both years pronounced subsurface blooms were observed in the pycnocline at all stations visited, and the permanent station was representative of the plankton in the bay.

Regulation of the phytoplankton biomass

The large freshwater input mediates the establishment of a pycnocline in early

Table 3. Integrated biomass (mg C m^{-2}) and production ($\text{mg C m}^{-2} \text{ d}^{-1}$) of the phyto- (PB and PP, respectively) and bacterioplankton (BB and BP, respectively) and the bacterial biomass and bacterial production expressed as percentage of phytoplankton biomass (BB/PB) and primary production (BP/PP). Calculations are based on values integrated over the euphotic zone (upper 30 m)

	August		September					
	27	29	1	4	6	8	13	17
PB	761	1625	1195	851	718	912	1530	1290
PP	115	210	125	266	50	122	161	180
BB	433	416	394	369	416	395	781	356
BP	31	16	9	33	11	24	17	8
BB/PB	57	26	33	43	58	43	51	28
BP/PP	27	8	7	13	21	20	11	4

Fig. 9. Biomass of (A) bacterioplankton, (B) heterotrophic nanoflagellates, (C) small oligotrichous ciliates and (D) potential clearance capacity of the bacterivorous protist community (% of water column d^{-1}) in the mixed surface layer (0–10 m), the pycnocline (10–20 m) and the deeper part of the water column (> 20 m)

summer and favourable light conditions in the surface layer trigger the development of a diatom bloom which rapidly depletes the surface layer of nutrients and sinks out of the euphotic zone (Andersen 1981b, Nielsen & Hansen 1995). Normally this spring bloom is considered the single main bloom of the season in Arctic areas (Smith & Sakshaug 1990). During this investigation, however, several blooms developed in the pycnocline, where reverse gradients of light and nutrients create favourable conditions for the phytoplankton community. The present study was conducted in the period after the spring bloom, when both nitrate and silicate were depleted from the euphotic zone and the surface phytoplankton community was dominated by small flagellates dependent on regenerated nutrients. Since light penetration was high, with $\geq 1\%$ of incident light at 30 m depth, the subsurface population, in contrast to the phytoplankton in the surface, probably relied on new nutrients supplied from nutrient-rich water below the pycnocline (Fig. 5). Unfortunately these major blooms occurred before the primary production measurements were initiated, but undoubt-

edly the frequency and duration of such blooms determine the magnitude of the annual primary production in Disko Bay.

Compared with primary production measurements following the spring bloom in late June 1992, $300 \pm 30 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Nielsen & Hansen 1995), depth integrated primary production during this investigation, $154 \pm 66 \text{ mg C m}^{-2} \text{ d}^{-1}$, clearly reflects the shorter day length in August–September. The surface irradiance is reduced by 50% in September compared with June (Andersen 1981b). The integrated annual pelagic primary production in Disko Bay is highly dependent on the overall weather conditions of a particular year. Crucial factors for the magnitude of the annual primary production are the timing of the ice break-up (April to June), the establishment of the pycnocline, the incidence of fog and clouds, and the wind regime. The 2 patches of diatoms could represent a response to wind generated intrusion of nutrient-rich bottom water to the surface layer and/or advection of new water masses to the sampling station (Fig. 2A,D).

The large annual variation in sea ice coverage and overall weather conditions complicates a direct comparison with previous primary production estimates from the area. However, our estimated values fall within the range previously reported from Disko Bay (Steemann-Nielsen 1958, Petersen 1964, Andersen 1981b) as well as from the same latitude in an East Greenland fjord (Rysgaard et al. 1996). If the annual primary production and the basis for the pelagic food chain are to be thoroughly investigated it is essential to take into account the primary production of the ice algae. Andersen (1977) concluded that the primary production occurring in association with the ice in Disko Bay off Qeqertarsuaq contributed only slightly to the annual primary production. Our unpublished results, however, indicate that the phytoplankton layer in the ice-water interface had very high rates of production. In April 1996 the diatoms dominating the algal community in the ice-water interface reached a biomass of $300 \mu\text{g chl a l}^{-1}$. The contribution of this key component of the primary producers needs further investigation if the total annual primary production in Disko Bay is to be calculated.

Role of the bacterioplankton

The magnitude of bacterioplankton abundance and production is primarily regulated by temperature, substrate supply and mortality. Pomeroy & Deibel (1986) questioned the importance of bacteria in cold-water ecosystems since their results showed that low temperature suppressed bacterial growth to a greater degree than that of phytoplankton. This suggests that a larger fraction of the primary production would be available to the metazooplankton and benthos. Recently, however, Rivkin et al. (1996) reviewed the literature and concluded that cold-water bacterioplankton had growth rates similar to temperate-region bacterioplankton populations at their ambient temperatures. The potential role of the Disko Bay bacterioplankton can be evaluated from the ratio of bacterial and phytoplankton biomass and production (Table 3). The ratios of bacterial to phytoplankton biomass from this and a previous study in the area (Nielsen & Hansen 1995), 40 and 57% respectively, are within the range of ratios reported from temperate latitudes, e.g. the North Sea and the North Atlantic Ocean (Nielsen & Richardson 1989, Ducklow et al. 1993, Nielsen et al. 1993). The ratios of bacterial to phytoplankton biomass from Disko Bay also fall within the range reported from temperate and subtropical marine ecosystems compiled by Simon et al. (1992). The bacterial production rate measured in the euphotic zone during this and a previous investigation in the area is similar to those reported

from the North Sea and the North Atlantic Ocean (Nielsen & Richardson 1989, Ducklow et al. 1993, Nielsen et al. 1993). However, the turnover rate of the Disko Bay bacterioplankton is relatively low, 2 to 9% d^{-1} (Table 3), compared with the North Sea and North Atlantic studies cited above. The ratio of bacterial production to primary production varies from 4 to 27%, with a mean of 14% (Table 3). This is comparable to ratios measured at similar temperatures before and during the spring bloom in the North Sea (10 to 30%, Nielsen & Richardson 1989). Assuming a growth efficiency of 50% (Cole 1982) our measurements fall within the range of 20 to 60% of the primary production that fluxes through the bacterioplankton reported by Cole et al. (1988) for temperate and tropical ecosystems. We found $28 \pm 6\%$ in the present investigation and 7 ± 2 and $48 \pm 13\%$ during and after a diatom bloom in June 1992 (Nielsen & Hansen 1995). This corroborates the conclusion by Rivkin et al. (1996) regarding the pivotal role of the bacterioplankton in the trophic pathways of Arctic ecosystems, particularly after the main bloom period when the dominating phytoplankters are too small to be grazed efficiently by the *Calanus*-dominated copepod community.

Regulation of the bacterioplankton

The enhanced bacterial biomass observed in the patches of diatoms was probably stimulated by the grazing activity of the high biomass of large heterotrophic dinoflagellates (Levinsen et al. 1999) and the *Calanus* spp. population which was present in the euphotic zone until mid-August (Hansen et al. 1999). The smallest heterotrophic protists, i.e. some nanoflagellates and the smallest ciliates (Fig. 9), were the most prominent bacterial grazers during the present investigation, as documented for other marine pelagic ecosystems (Fenchel 1982, Sherr et al. 1986). The other potentially important bacterivores, the appendicularians, which are known to play a key role as bacterial grazers in other ecosystems (Deibel & Lee 1992), were not particularly abundant during this study. The average abundance during the summer in the upper 50 m was only 30 ind. m^{-3} (data not shown). During our investigation indications of oscillations between the bacterial biomass and their potential grazers were observed, as documented from temperate ecosystems (Fenchel 1982, Bjørnsen et al. 1988, Wikner & Hagström 1991). A rough calculation shows that, during their abundance peaks, bacterivorous protists had the capacity to clear the daily bacterial production (Table 3, Fig. 9). This calculation, however, only included the obligate heterotrophic forms. Several mixotrophic nanoflagellates (*Chrysochromulina* spp.,

Dinobryon spp.) were abundant but not included in the clearance calculation.

Conclusion

Historically the primary productivity in Arctic seas is characterised by having a single spring bloom of phytoplankton that depletes the surface layer of nutrients (Smith & Sakshaug 1990). However, the measurement of fluorescence profiles, rather than chl *a* at discrete depths, has, in this investigation, demonstrated the occurrence of subsurface blooms in the pycnocline throughout the summer, as observed during the summer in temperate waters (Richardson & Christoffersen 1991). Unfortunately the contribution of the subsurface blooms to the annual production was not assessed, but this phytoplankton population likely contributes substantially to the productivity in the area. The species and size compositions of these blooms are important for the fate of the productivity. The fuelling of the bacterioplankton by exudates from phytoplankton is considered to be most important in situations where the phytoplankton is dominated by pico- and nanoplankton (Kiørboe 1993). The contribution of dissolved organic matter from zooplankton feeding activity is expected to be most important during blooms when the food is available to the copepods (Jumars et al. 1989). The presence of a subsurface population in the pycnocline is of major importance for the vertical distribution of the succeeding heterotrophic links in the food chain. Patches of high biomass of bacteria, nanoflagellates and protozooplankton (Levinsen et al. 1999) were concurrently observed here. Since these patches of high phytoplankton biomass/production provide a potential shelter from e.g. copepod or fish larvae predation and/or better food availability compared with the nutrient depleted surface water, it is important that the subsurface phytoplankton community is included in future studies of Arctic carbon cycling.

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LITERATURE CITED

- Andersen OGN (1977) Primary production associated with sea ice at Godhavn, Disko, West Greenland. *Ophelia* 16(2):205–220
- Andersen OGN (1981a) The annual cycle of temperature, salinity, currents and water masses in Disko Bugt and adjacent waters, West Greenland. *Medd Grønland Biosci* 5:1–33
- Andersen OGN (1981b) The annual cycle of phytoplankton primary production and hydrography in the Disko Bugt area, West Greenland. *Medd Grønland Biosci* 6
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263
- Bjørnsen PK (1986) Automatized determination of bacterioplankton biomass by image analysis. *Appl Environ Microbiol* 51:1199–1204
- Bjørnsen PK (1988) Phytoplankton release of organic matter: why do healthy cells do it? *Limnol Oceanogr* 33:151–154
- Bjørnsen PK, Riemann B, Horsted SJ, Nielsen TG, Pock-Steen J (1988) Trophic interactions between heterotrophic nanoflagellates and bacterioplankton in manipulated seawater enclosures. *Limnol Oceanogr* 33(3):409–420
- Booth BC, Smith WO Jr (1997) Autotrophic flagellates and diatoms in the Northeast Water Polynya, Greenland: summer 1993. *J Mar Syst* 10:241–261
- Cole JJ (1982) Interaction between bacteria and algae in aquatic ecosystems. *Annu Rev Ecol Syst* 13:291–314
- Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems; a cross-system overview. *Mar Ecol Prog Ser* 43:1–10
- Deibel D, Lee SH (1992) Retention efficiency of sub-micrometer particles by the pharyngeal filter of the pelagic tunicate *Oikopleura vanhoffeni*. *Mar Ecol Prog Ser* 81:25–30
- Ducklow HW, Kirchman DL, Quinby HL, Carlson, CA, Dam HG (1993) Stocks and dynamics of bacterioplankton carbon during the spring bloom in eastern North Atlantic Ocean. *Deep-Sea Res II* 40:245–263
- Edler L (1979) Recommendations for marine biological studies in the Baltic sea. *Baltic Mar Biol Publ* 5:1–38
- Fenchel T (1982) Ecology of heterotrophic microflagellates IV. Quantitative occurrence and importance as bacterial consumers. *Mar Ecol Prog Ser* 8:35–42
- Fuhrman J, Azam F (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. *Appl Environ Microbiol* 39(6):1085–1095
- Gran HH (1902) Das Plankton des Norwegischen Nordmeeres. *Rep Norw Fish Mar Invest II*(5)
- Grashoff K (1976) Methods for sea water analysis. Weinheim, New York
- Grøntved J, Seidenfaden G (1938) The phytoplankton of the waters west of Greenland, the Godthaab expedition 1928. *Medd Grønland* 82(5)
- Haas LW (1982) Improved epifluorescence microscopy for observing planktonic microorganism. *Annls Inst Océanogr* 58:261–266
- Hansen BW, Nielsen TG, Levinsen H (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. III. Mesozooplankton. *Aquat Microb Ecol* 16:233–249
- Hansen PJ, Bjørnsen PK, Hansen B (1997) Zooplankton grazing and growth: scaling within the 2–2,000 μ m body size range. *Limnol Oceanogr* 42(4):687–704
- Heath M, Richardson K, Kiørboe T (1990) Optical assessment of phytoplankton nutrient depletion. *J Plankton Res* 12(2):381–396

- Hobbie JE, Daley RJ, Jaspers S (1977) Use of nucleopore filters for counting bacteria by epifluorescence. *Appl Environ Microbiol* 33:1255–1228
- Jespersen AM, Christoffersen K (1987) Measurements of chlorophyll *a* from phytoplankton using ethanol as extraction solvent. *Arch Hydrobiol* 109:445–454
- Jespersen P (1934) Copepoda. The Godthaab Expedition 1928. *Medd Grønl* 79(19):1–166
- Jumars PA, Penry DL, Baross JA, Perry MJ, Frost BW (1989) Closing the microbial loop: dissolved carbon pathway to heterotrophic from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res* 36:483–495
- Kiilerich A (1939) The Godthaab expedition 1928. A theoretical treatment of the hydrographical observation material. *Medd Grønl* 78(5)
- Kjørboe T (1993) Turbulence, phytoplankton cell size and the structure of pelagic food webs. *Adv Mar Biol* 29:1–62
- Legendre L, Gosselin M, Hirche HJ, Kattner G, Rosenberg G (1993) Environmental control and potential fate of size-fractionated phytoplankton production in the Greenland Sea (75°N). *Mar Ecol Prog Ser* 98:297–313
- Levinsen H, Nielsen TG, Hansen B (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. II. Heterotrophic dinoflagellates and ciliates. *Aquat Microb Ecol* 16:217–232
- Nielsen GÆ, Bresta AM (1984) Guidelines for measurements of phytoplankton primary production. *Baltic Mar Biol Publ* 1:1–23
- Nielsen N, Hansen BU, Humlum O, Rasch M (1995) Meteorological observations at Arctic Station, Qaqqarsuaq (Godhavn), Western Central Greenland. *Dan J Geogr* 95
- Nielsen TG, Hansen B (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Mar Ecol Prog Ser* 125:239–257
- Nielsen TG, Richardson K (1989) Food chain structure of the North Sea plankton communities: seasonal variation in the role of the microbial loop. *Mar Ecol Prog Ser* 56:75–87
- Nielsen TG, Løkkegård B, Richardson K, Pedersen FB, Hansen L (1993) The structure of the plankton communities in the Dogger Bank area (North Sea) during a stratified situation. *Mar Ecol Prog Ser* 95:115–131
- Petersen GH (1964) The hydrography, primary production, bathymetry and 'Tarsaq' of Disko Bugt. *Medd Grønl* 159(10)
- Pomeroy LR (1974) The ocean's food web, a changing paradigm. *BioSci* 24:499–504
- Pomeroy LR, Deibel D (1986) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science* 233:359–361
- Pomeroy LR, Macko SA, Ostrom PH, Dunphy J (1990) The microbial food web in Arctic seawater: concentration of dissolved free amino acids and bacterial abundance and activity in the Arctic Ocean and in Resolute Passage. *Mar Ecol Prog Ser* 61:31–40
- Richardson K (1991) Comparison of ^{14}C primary production determination made by different laboratories. *Mar Ecol Prog Ser* 72:189–201
- Richardson K, Christoffersen A (1991) Seasonal distribution and production of phytoplankton in the southern Kattegat. *Mar Ecol Prog Ser* 78:217–227
- Riemann B, Bjørnsen PK, Newell S, Fallon R (1987) Calculation of cell production of coastal marine bacteria based on measured incorporation of ^3H -thymidine. *Limnol Oceanogr* 32:471–476
- Rivkin RB, Anderson MR, Lajzerowicz C (1996) Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate. *Aquat Microb Ecol* 10:243–254
- Rysgaard S, Finster K, Dahlgård H (1996) Primary production, nutrient dynamic and mineralisation in a northeastern Greenland fjord during the summer thaw. *Polar Biol* 16:497–506
- Sherr BR, Sherr EB, Andrew TL, Fallon RD, Newell SY (1986) Trophic interactions between heterotrophic protozoa and bacterioplankton in estuarine water analyzed with selective metabolic inhibitors. *Mar Ecol Prog Ser* 32:169–179
- Simon M, Cho BC, Azam F (1992) Significance of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and biogeochemical implication. *Mar Ecol Prog Ser* 86:103–110
- Smidt ELB (1979) Annual cycles of primary production and of zooplankton at Southwest Greenland. *Medd Grønl Biosci* 1
- Smith WO Jr, Sakshaug E (1990) Polar phytoplankton. In: Smith WO Jr (ed) *Polar oceanography. Part B. Chemistry, biology and geology*. Academic Press, Inc, San Diego, p 477–525
- Sorokin YI (1977) The heterotrophic phase of plankton succession in the Japan sea. *Mar Biol* 41:107–117
- Steemann-Nielsen E (1952) The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J Cons Int Explor Mer* 18(2):117–140
- Steemann-Nielsen E (1958) A survey of recent Danish measurements of the organic productivity in the sea. *Rapp PV Réun Cons Perm Int Explor Mer* 144:92–95
- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis. *Bull Fish Res Board Can* 167:1–310
- Thomsen HA (1982) Planktonic choanoflagellates from Disko Bugt, West Greenland, with a survey of the marine nanoplankton of the area. *Medd Grønl Biosci* 8:1–35
- Ussing HH (1938) The biology of some important plankton animals in the fjord of East Greenland. *Medd Grønl* 100(7):1–108
- Vadstein O, Harkjær BO, Jensen A (1989) Cycling of organic carbon in the photic zone of a eutrophic lake with special reference to the heterotrophic bacteria. *Limnol Oceanogr* 34:840–855
- Wikner J, Hagström Å (1991) Annual study of bacterioplankton community dynamics. *Limnol Oceanogr* 36(7):1313–1324

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