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ORIGINAL PAPER

Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and a cold (Hornsund) Spitsbergen fjord in mid-summer 2002

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Abstract Kongsfjorden and Hornsund are two glacial fjords without sills on the West Spitsbergen coast. Both sites are under the influence of relatively warm Atlantic-derived water, although Hornsund is more influenced by cold water from the Barents Sea. In this study, we compared the impacts of cold Arctic and warmer Atlantic waters on the pelagic ecosystems of Kongsfjorden and Hornsund. Both fjords were strongly influenced by Atlantic-derived waters during summer (2002). Diatoms were the most substantial contributors to phytoplankton biomass, especially in outer basins of both fjords, whereas the second most important contributors were autotrophic dinoflagellates in Kongsfjorden and nanoflagellates in Hornsund. Total phytoplankton biomass was highest in Hornsund. Primary production rates were an order of magnitude lower in Kongsfjorden than in Hornsund, and increased from inner to outer fjord (from 2.47 to 4.48 mg C m^{-2} h^{-1} in Kongsfjorden and from 14.00 to 86.65 mg C m^{-2} h^{-1} in Hornsund). Chlorophyll-*a* concentration was also substantially lower in Kongsfjorden. Zooplankton was dominated by omnivorous species in Kongsfjorden and herbivorous in Hornsund. Observed differences between the fjords may originate from (1) advection of different waters into the fjords; (2) differences in freshwater runoff and turbidity, and (3) timing of the phytoplankton bloom. Climate warming will likely increase the Atlantic water influence, and result in reduced production of diatoms and increase in flagellates.

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Introduction

The Svalbard archipelago (Norway, 74–81°N; 10–35°E) is surrounded by two distinct water masses: warm Atlantic-derived water with summer temperatures around 4–6°C on the western coast, and a cold (<0°C) Arctic water mass from the Barents Sea on the eastern coast (Svendsen et al. 2002; Fig. 1a). The Atlantic water, flowing northwards as the West Spitsbergen Current, warms the archipelago and influences the temperature of the fjords of the largest island of the archipelago—Spitsbergen; e.g. Kongsfjorden. On the other hand, cold water from the Barents Sea, flowing in the South Cape Current, might enter the southernmost fjord—Hornsund (Swerpel 1985). In summer, inner reaches of both fjords are under the influence of melting glaciers. The runoff of fresh water from the glaciers creates very strong salinity stratification of the water column (Svendsen et al. 2002). Surface water salinity can be reduced to less than 28 PSU in the inner part of Kongsfjorden; Weslawski et al. (1991) reported that up to 12% of the water mass in the main basin of Hornsund may originate from glacier freshwater runoff. Presently, when the glacier runoff is elevated due to rising temperatures (Palli et al. 2003), the proportion of freshwater in the fjord might be even higher. Together with freshwater, large amounts of mineral particles enter the fjords, which reduce the thickness of the euphotic layer (Urbański et al. 1980; Svendsen et al. 2002). Simultaneous inflow of Atlantic waters from the mouth of the fjord and runoff of fresh and turbid water from the glaciers result in steep horizontal gradients in temperature, salinity and light regime along the fjord's axis, which impact phytoplankton

assemblages (Keck et al. 1999). The complex dynamics of the fjord's water masses are regarded as major driving forces for the observed zooplankton variability (Basedow et al. 2004; Walkusz et al. 2007).

Kongsfjorden (79°N) is a small fjord with a wide opening to the open ocean via Kongsfjordrenna. A sill in the middle of the fjord divides it in an outer part, strongly influenced by West Spitsbergen Current, and an inner part that is under impact of glaciers: Kronebreen, Kongsvegen, Conwaybreen and Blomstrandbreen (Svendsen et al. 2002). Kongsfjorden's marine ecosystem has been extensively investigated for many years (Digby 1961; Svendsen et al. 2002; Hop et al. 2002; Willis et al. 2006; Hop et al. 2006; Walkusz and Rolbiecki 2007; Steen et al. 2007). This cannot be said about the southernmost Hornsund (77°N), which is geologically similar to the Kongsfjorden. The most recent publications concerning phytoplankton and primary production in Hornsund are from the late 1980s (Gorlich et al. 1987; Weslawski et al. 1988; Eilertsen et al. 1989). Eilertsen et al. (1989) showed that, albeit in close geographical proximity and influenced by the same water masses, phytoplankton assemblages and primary production may differ significantly between the fjords of West Spitsbergen.

In this study we compare phytoplankton assemblages, primary productivity and zooplankton composition in two fjords of West Spitsbergen: Kongsfjorden that is strongly influenced by Atlantic derived waters, and Hornsund, more influenced by waters derived from the Barents Sea. So far such comparative studies have been performed for hydrology and zooplankton (Weslawski et al. 1991; Walkusz 2006) and benthic fauna (Wlodarska-Kowalczuk et al. 1998). In addition, for the first time in almost 20 years, we present data on phytoplankton and primary production for Hornsund.

Materials and methods

Sampling was undertaken in Kongsfjorden and Hornsund in July 2002 during a cruise of R/V *Oceania* (Institute of Oceanology, Polish Academy of Sciences). Samples were collected at periods between 29 and 30 of July and between 23 and 27 of July in Kongsfjorden and Hornsund, respectively (Fig. 1b).

Vertical temperature and salinity profiles along the fjords were acquired with a Sea Bird 911 plus CTD probe. Underwater photosynthetically active radiation (PAR) was measured only in Hornsund, by means of a LI—193. Underwater Spherical Sensor (LiCor Biosciences) deployed from the ship.

Qualitative and quantitative samples for phytoplankton analyses were collected with 5-l Niskin bottle from arbitrarily chosen depths in Kongsfjorden; and from the depths of 100, 40, 25, 15, 10, 4, 2 and <1% sub-surface incident PAR in Hornsund (Fig. 1b). Sub-samples for taxonomical composition and abundance were immediately fixed with 2% formalin buffered with borax and kept in the dark until processed in the laboratory. The samples were counted according to the procedure described by Utermöhl (1958). At least 300 individual cells were counted using an inverted microscope (Nikon TM 300) equipped with phase contrast and differential interference contrast. Diatoms and dinoflagellates were identified to the lowest possible taxonomical level, whereas most nanoflagellates generally remained unidentified except for cryptophytes (at class level), colonial

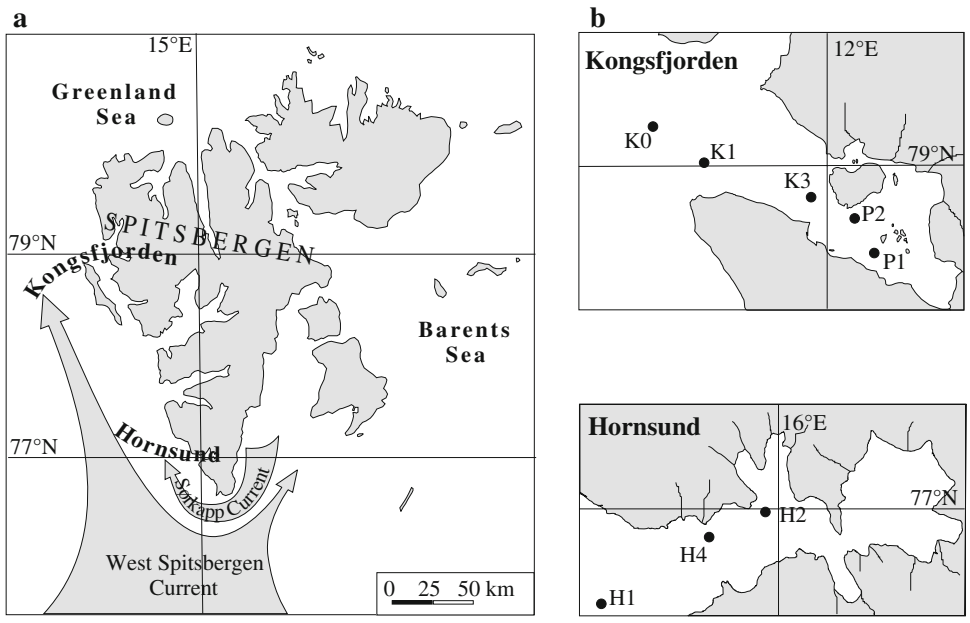

Fig. 1 The Svalbard Archipelago with location of the investigated fjords (**a**) and the location of the sampling stations in the fjords (**b**). Phytoplankton and zooplankton stations were generally the same, except for the station K3, where only zooplankton was collected, and the stations P1 and P2, where only phytoplankton was sampled

stages of *Phaeocystis pouchetti* and few larger genera of minor importance (e.g. *Eutreptiella* sp., *Pachysphaera* sp.). The complete list of identified organisms has been published elsewhere (Wiktor and Wojciechowska 2005). The biomass of most abundant taxa was estimated from cell volume measurements (at least ten cells measured) (Edler 1979) using conversion factors for carbon content according to Menden-Deuer and Lessard (2000). Values of carbon content per single cell given in the Biological Atlas of the Arctic Seas (Matishov et al. 2000) were used in case of less abundant or rare taxa.

Samples for chlorophyll-*a* and primary production analyses were collected at stations P2 and P1 in Kongsfjorden and H1, H4 and H2 in Hornsund (Fig. 1b). Sub-samples for chlorophyll-*a* concentration were filtered through Whatman GF/F glass fibre filters and frozen at −20°C until analysed at the onshore laboratory. Chlorophyll-*a* was extracted in 96 % ethanol in the dark for 24 h, determined spectrophotometrically (Beckman DU 68) and concentrations were calculated according to the equation of Jeffrey and Humphrey (1975). Phytoplankton primary production was measured with the ^{14}C method (Strickland and Parsons 1972; Nielsen and Bresta 1984). Water samples, 100 ml each, for primary production, were inoculated with $Na^{14}CO_3$ to obtain final radioactivity of 8 μCi per sample and incubated in transparent glass bottles in situ for 6–9 h at mid-day. The same procedure was used for measurements of the dark fixation of carbon, but the dark bottles were incubated in surface waters and the deepest layers only. After the incubation, samples were filtered through 0.45 μm cellulose nitrite ester filters (Sartorius, Germany) with applied pressure <0.4 atm. To remove extracellular ^{14}C exudates, filters were exposed to vapours of fuming HCl in a desiccator for 5 min. Filters were dissolved in Ready Value Light Scintillation Cocktail for Aqueous Samples (Beckman, USA) and stored in the dark at 4°C until further analysis on BETA scintillation counter (Beckman LS 6000IC, USA) to determine radioactivity in the samples. All handling, prior to and after the incubation, was performed in dimmed light and bottles were stored in dark. The fixation rate of carbon was calculated according to equation of Strickland and Parsons (1972).

Mesozooplankton samples were collected at stations K0, K1 and K3 in Kongsfjorden (Fig. 1a) and H1, H4 and H2 in Hornsund (Fig. 1b) with multi plankton sampler (MPS; HydroBios, Kiel; 0.25 m^2 opening) with a 180-μm mesh net from the uppermost layer, which extended from the surface to a maximum of 40 m (Table 1 and 2). Filtrated water volumes were measured by means of digital flowmeter (HydroBios). The samples were fixed in a 4% borax buffered formaldehyde salt water solution. All organisms in the samples were identified to the lowest possible taxonomic level. For this purpose, the procedures given by Harris et al. (2000) were applied, while guidelines of Kwasniewski et al. (2003) were used for the *Calanus* species identification. Discrimination of species as herbivorous and omnivorous was done according to Blachowiak-Samolyk et al. (2007).

Table 1 Densities of zooplankton taxa (ind. m^{-3}) in Kongsfjorden

Station	K0	K1	K3
Layer (m)	20–0	40–0	30–0
Herbivorous taxa			
Calanus hyperboreus	2	2	1
C. glacialis	166	125	424
C. finmarchicus	338	283	1,158
Pseudocalanus spp.	630	356	1,233
Calanoida nauplii	1,154	339	3,121
Limacina helicina	100	367	362
Fritillaria borealis	1,280	206	1,344
∑ herbivorous	3,671	1,679	7,642
Omnivorous taxa			
Acartia longiremis	13	24	21
Oithona similis	4,431	4,496	10,563
O. atlantica	0	4	21
Triconia borealis	83	64	164
Bivalvia veliger	113	94	227
Echinodermata larvae	3,416	5,962	11,669
Polychaeta larvae	93	0	1
∑ omnivorous	8,149	10,645	22,667
Others	38	17	32
Total	11,858	12,341	30,340

Results

Oceanography

Both fjords were under the influence of warm Atlantic-derived waters, although water temperature and salinity were slightly higher in Kongsfjorden (Fig. 2). A surface layer of freshened and cooled water spread above the transformed Atlantic water, indicating effects of precipitation and runoff from the glaciers. This influence of runoff decreased towards the mouth of both fjords (stations K0 and K1 in Kongsfjorden and H1 in Hornsund), where surface water temperatures reached 6 and 5°C in Kongsfjorden and Hornsund, respectively. Salinity in this layer in both fjords was still lower compared to deeper layers. In the middle basins (stations P2 and P1 in Kongsfjorden and H4 and H2 in Hornsund), the water column was less homogenous in respect to vertical changes in temperature and salinity (Fig. 2).

Table 2 Densities of zooplankton taxa (ind. m^{-3}) in Hornsund

Station	H1	H4	H2
Layer (m)	10–0	20–0	10–0
Herbivorous taxa			
Calanus hyperboreus	0	0	17
C. glacialis	229	680	114
C. finmarchicus	123	333	131
Pseudocalanus spp.	446	465	1,105
Copepoda nauplii	122	93	278
Oikopleura spp.	6	5	0
∑ herbivorous	929	1,578	1,649
Omnivorous taxa			
Microcalanus spp.	11	3	6
Metridia longa	1	7	0
Acartia longiremis	0	7	28
Oithona similis	1,063	533	403
O. atlantica	11	13	51
Triconia borealis	27	20	11
Harpacticoida n. det.	4	4	2
Cirripedia cypris	4	13	136
Polychaeta larvae	1	1	11
Bivalvia veliger	42	60	17
Echinodermata larvae	4	7	2
∑ omnivorous	1,167	668	668
Others	42	41	36
Total	2,134	2,286	2,349

Phytoplankton assemblages

In both fjords, we observed a steep decrease in depth-integrated phytoplankton biomass towards the inner reaches of the fjords (Fig. 3). The decrease was from 2,770 mg C m^{-2} at the mouth of Kongsfjorden (station K0) to 254 mg C m^{-2} at innermost station P2, and from 2,100 mg C m^{-2} at the mouth of Hornsund (station H1) to 608 mg C m^{-2} at innermost station H2. Major biomass contributors at the mouth of both fjords were diatoms (>40% of total phytoplankton biomass). Dinoflagellates and cryptophytes were also quite important in terms of biomass in Kongsfjorden (~20%), whereas cryptophytes and unidentified nanoflagellates contributed importantly in Hornsund (Fig. 3).

The vertical and horizontal distribution of total phytoplankton biomass varied between the two fjords (Fig. 4). The highest phytoplankton biomass (>100 mg C m^{-3}) in Kongsfjorden was in the deeper layers at the mouth of the fjord (stations K0 and K1), and decreased to almost 0 mg C m^{-3} in surface layers of the middle basin (stations P2 and P1). Biomass in water column did not exceed 32 mg C m^{-3} in the middle part of the fjord. In contrast, phytoplankton biomass was concentrated in the surface layers (>15 m) of Hornsund, reaching almost 100 mg C m^{-3} at 5 m at station H4. Phytoplankton biomass was consistently <40 mg C m^{-3} at depths below 20 m in Hornsund (Fig. 4).

Diatoms were the major contributor to total phytoplankton biomass, especially at sampling depths below 30 m

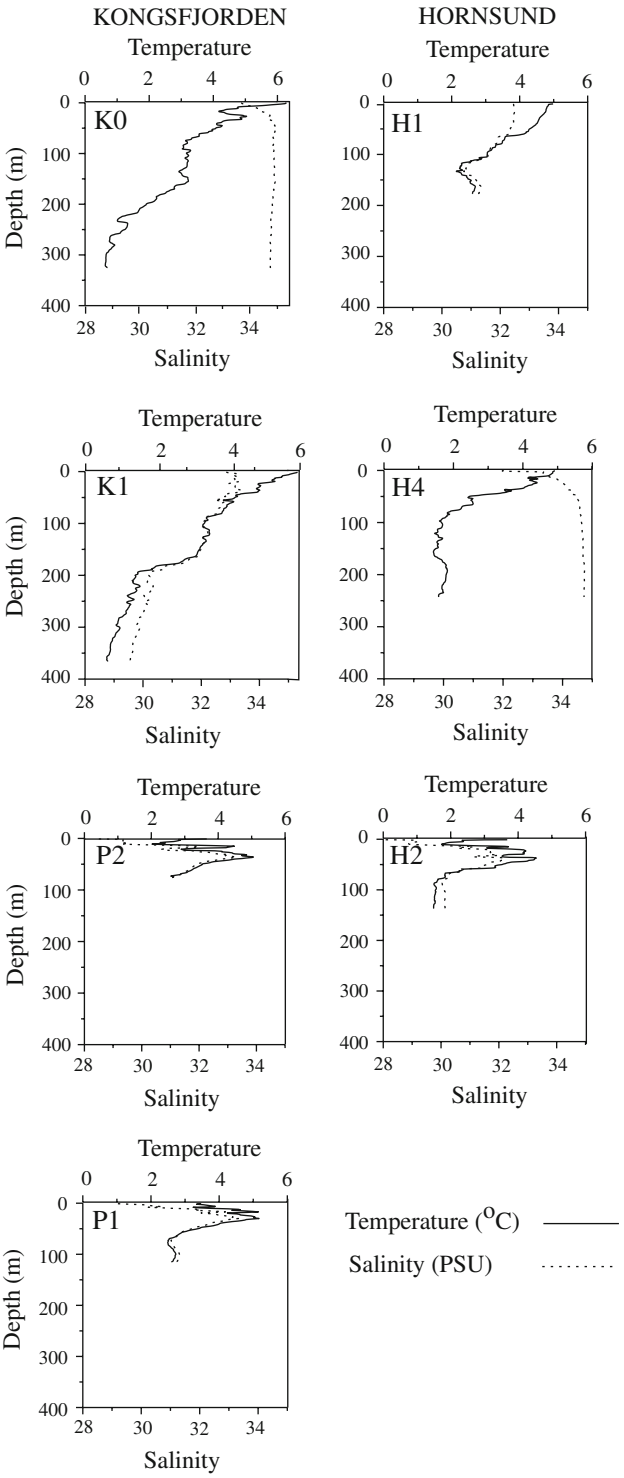

Fig. 2 Vertical profiles of temperature and salinity in Kongsfjorden and Hornsund

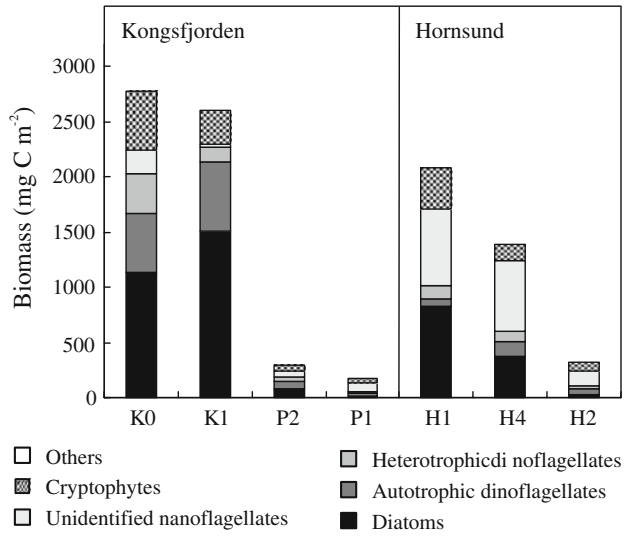

Fig. 3 Relative abundance (%) of main phytoplankton groups in integrated biomass in Kongsfjorden and Hornsund

(Fig. 5). The most important diatom species were *Pseudonitzschia seriata* (Cleve) H. Peragallo and M. Peragallo, 1900, in Kongsfjorden and *Chaetoceros socialis* Lauder, 1864, in Hornsund. Diatoms at these depths below 30 m were in rather poor condition, with bleached chloroplasts and plasmolysed cytoplasm. Spores of *Chaetoceros* sp. and *Thalassiosira* sp. contributed almost 6% to phytoplankton abundance in Hornsund, but they were not included in biomass calculation. The deep peak of phytoplankton biomass in the outer basin of Kongsfjorden (30 m depth) was additionally supported by the presence of heterotrophic dinoflagellates (*Cochlodinium* sp.). In Hornsund, heterotrophic dinoflagellates had highest biomass in shallow layers at the innermost station (H2).

The second most important contributor to total phytoplankton biomass in Kongsfjorden, were autotrophic dinoflagellates, e.g. *Scrippsiella trochoidea* (Stein) Loeblich III, 1976; *Ceratium arcticum* (Ehrenberg) Cleve, 1901. They contributed >60% of the biomass in subsurface layers (10–15 m). Autotrophic dinoflagellates (*Gymnodinium arcticum* Wulff, 1919) were also important at the innermost station (P1) in the surface layers (>80% at 0 m). They were of lesser importance in terms of total phytoplankton biomass in Hornsund, and their biomass contribution did not exceed 22%.

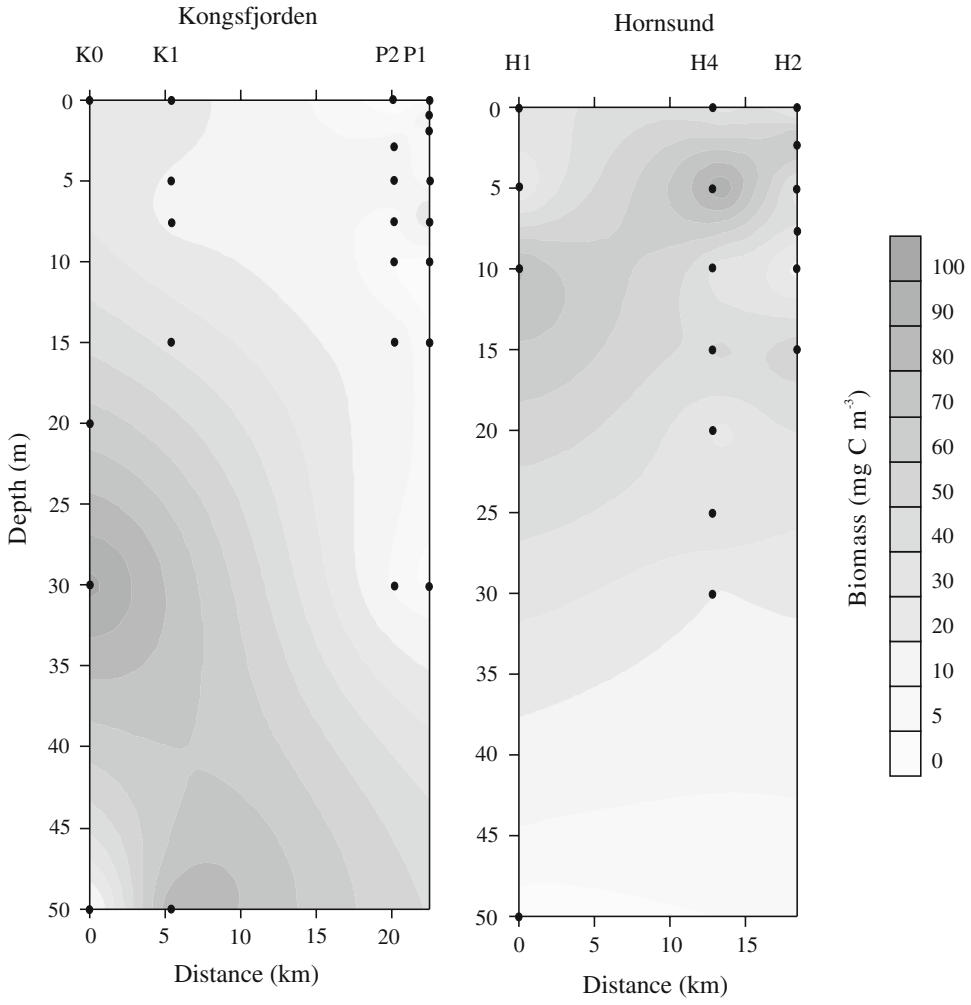

Fig. 4 Distribution of phytoplankton biomass in Kongsfjorden and Hornsund

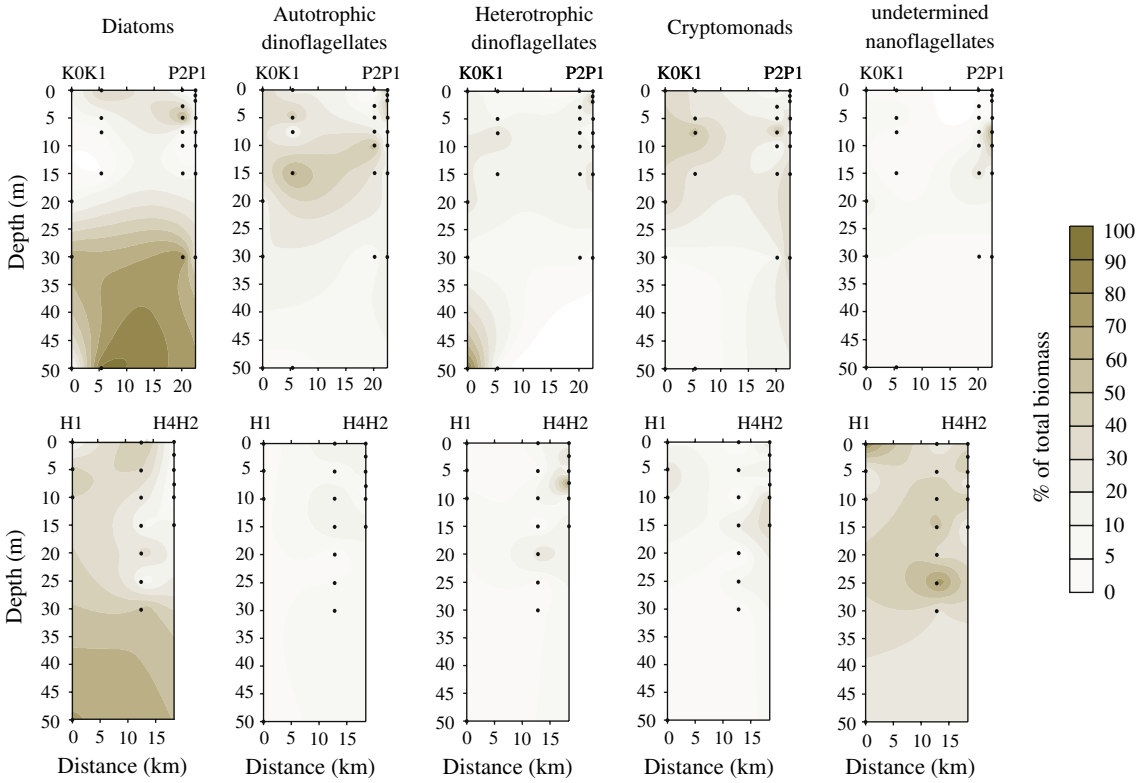

Fig. 5 Phytoplankton composition in percentage of total biomass in Kongsfjorden (*upper panel*) and Hornsund (*bottom panel*)

Cryptomonads were quite important in both fjords. Their biomass was mainly concentrated in upper layers. Contribution to the phytoplankton biomass was >50% in Kongsfjorden, and up to 40% at the innermost station of Hornsund. Other nanoflagellates generally contributed <15% in Kongsfjorden, except for the station P1 at 7 m, where they made up >75% of total phytoplankton biomass. This is in contrast to Hornsund, where the nanoflagellates were the second most important contributor to phytoplankton biomass. They contributed >80% in surface layers at the mouth of the fjord and were also important in deeper layers along the investigated basins. Their contribution was always >20% of total phytoplankton biomass.

Primary production and chlorophyll-*a*

Primary production integrated over the entire sampling depth in Kongsfjorden was 4.84 mg C m^{-2} h^{-1} at station P2 and 2.47 mg C m^{-2} h^{-1} at station P1. Steep decreases in integrated primary production towards the inner reaches of the fjord were observed in Hornsund. It was 86.65 mg C m^{-2} h^{-1} at station H1, 55.54 mg C m^{-2} h^{-1} at station H4 and 14.00 mg C m^{-2} h^{-1} at the innermost station H2.

The maximum primary production rates (>0.55 mg C m^{-3} h^{-1}) at station P2 were in surface layers: at 0 and at 3 m (Fig. 6). They gradually decreased with depth, reaching 0.13 mg C m^{-3} h^{-1} at 10 m, and were negligible deeper in the water column. Closer to the glaciers, at station P1, maximum primary production rates were found just below the surface layer (1–2 m) and were higher (>0.65 mg C m^{-3} h^{-1}) than maximum rates at station P2. In surface layer (0 m) at station P1, primary production rates were almost three times lower than at 1–2 m depth. After the peak at 2 m (0.73 mg C m^{-3} h^{-1}), primary production steeply decreased and the productive zone extended to only 5 m.

Primary production rates in the water column were much higher in Hornsund than in Kongsfjorden (Fig. 6). At all stations, maximum primary production was found in subsurface layers (3–7 m), while at the surface (0 m) it was usually approximately three times lower, except for the innermost station H2. At the outermost station H1, the highest primary production rate in the water column was 6.44 mg C m^{-3} h^{-1} at 5-m depth, and remained >2 mg C m^{-3} h^{-1} until 17-m depth. At station H4, highest primary production rate (6.27 mg C m^{-3} h^{-1}) was at 7 m, but the productive zone extended below 30 m. At the innermost station H2, the maximal primary production rate was already two times lower than at station H4, and it was only 2.99 mg C m^{-3} h^{1} at 3 m. At this innermost station, the productive zone was very shallow extending to about 10 m.

The vertical distribution of chlorophyll-*a* was highly variable in both fjords, but in Hornsund chlorophyll-*a*

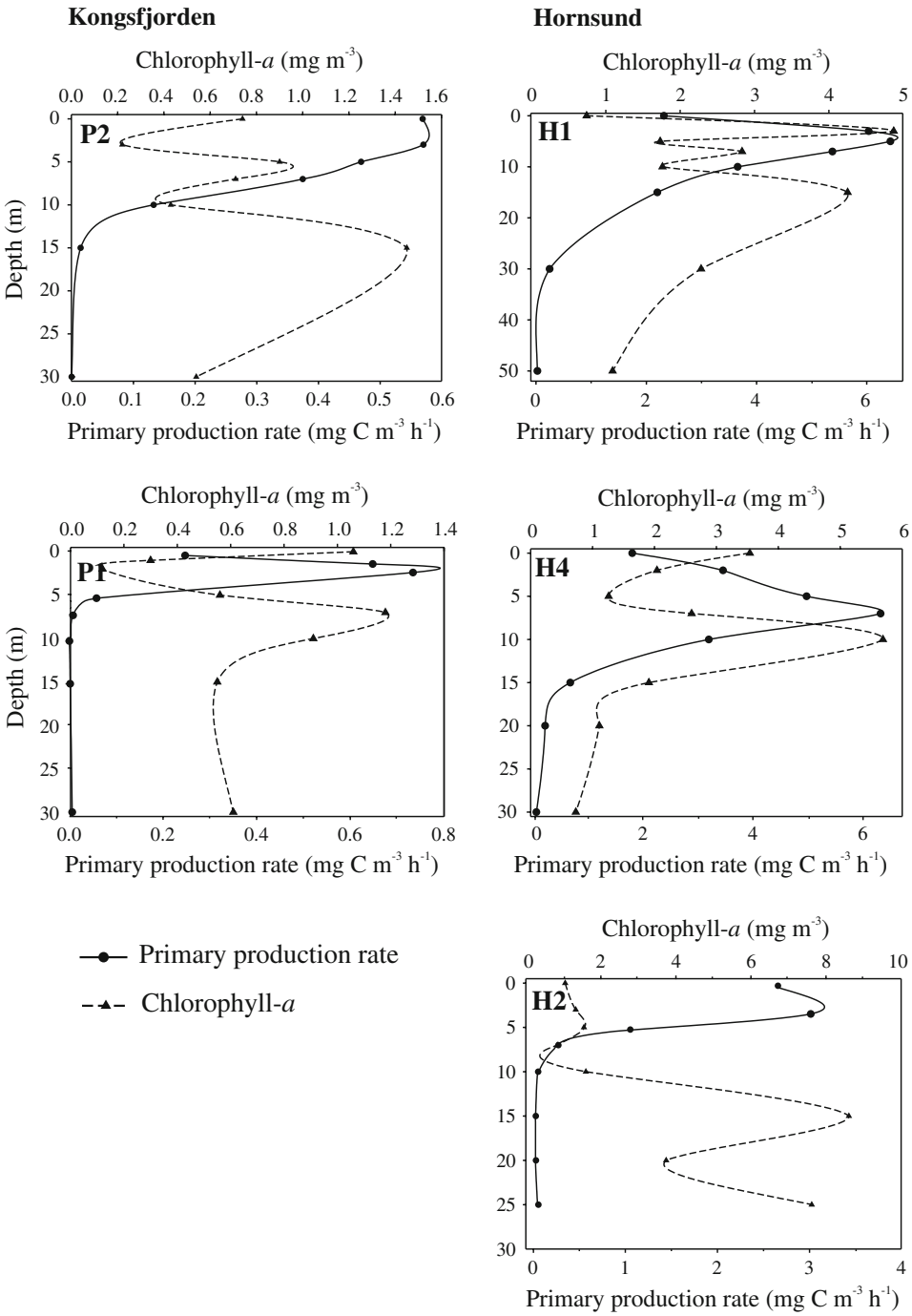

Fig. 6 Vertical profiles of primary production rates and chlorophyll-*a* concentrations in Kongsfjorden and Hornsund

concentrations were approximately an order of magnitude higher than in Kongsfjorden (Fig 6). In Kongsfjorden, at station P2, the chlorophyll-*a* maximum (1.4 mg Chl-*a* m^{-3}) was just below the productive zone at 15 m, representing a deep chlorophyll maximum (DCM). Turbidity was high in the surface layer (0 m), which made counting of the phytoplankton samples impossible, but chlorophyll-*a* concentrations were still relatively high compared to less turbid layers (0.74 mg Chl-*a* m^{-3} at 0 m vs. 0.22 mg Chl-*a* m^{-3} at 3 m). At the more inner station P1, a surface chlorophyll-*a* maximum (0 m: 1.18 mg Chl-*a* m^{-3}) as well as a DCM (1.06 mg Chl-*a* m^{-3}) at 7 m was observed.

In Hornsund, at stations H1, the maximum chlorophyll-*a* concentration (4.88 mg Chl-*a* m^{-3}) occurred at the depth where primary production was highest (5 m) (Fig. 6). In addition, a DCM (4.26 mg Chl-*a* m^{-3}) was observed at 16 m. In deeper layers, chlorophyll-*a* concentrations gradually decreased to 1.10 mg Chl-*a* m^{-3} at 50 m. The lowest chlorophyll-*a* concentration was at 0 m (0.75 mg Chl-*a* m^{-3}; Fig. 6). In the central basin (H4), the DCM was at

11 m and reached 5.69 mg Chl-*a* m^{-3}. The chlorophyll-*a* concentration was also relatively high in the surface layer (0 m) (3.54 mg Chl-*a* m^{-3}). At the innermost station (H2) DCM was well below the productive layer, with 8.61 mg Chl-*a* m^{-3} at 15 m, and a secondary peak (7.62 mg Chl-*a* m^{-3}) at 25 m. In the productive zone, chlorophyll-*a* concentrations were relatively constant, ranging from 0.84 to 1.55 mg Chl-*a* m^{-3}.

Zooplankton

Zooplankton abundances in Kongsfjorden increased threefold towards the inner part of the fjord, reaching 30,340 ind. m^{-3} at station K3 (Table 1). Among herbivorous taxa, Calanoida nauplii, *Fritillaria borealis*, *Calanus finmarchicus* and *Pseudocalanus* spp. were the most abundant. The most abundant omnivorous taxa included *Oithona similis* and Echinodermata larvae. In general, omnivorous taxa were numerically dominant over herbivorous taxa and the percentage of omnivorous taxa slightly increased towards the inner fjord reaching 86 and 75% at K1 and K3, respectively (Fig. 7a).

In Hornsund, total zooplankton abundance in the surface layers showed a different trend than in Kongsfjorden. Zooplankton abundances in surface layers were similar at all stations and abundances increased towards the inner fjord (Table 2). At station H4, *C. glacialis* was numerically dominant, whereas *Pseudocalanus* spp. was most abundant at H1 and H2, towards the inner fjord. An opposite trend was observed for Cirripedia nauplii, as their abundances were highest at station H2. Omnivorous taxa outnumbered herbivores at station H1, although deeper in the fjord (H4 and H2) herbivores were numerically dominant (Fig. 7b).

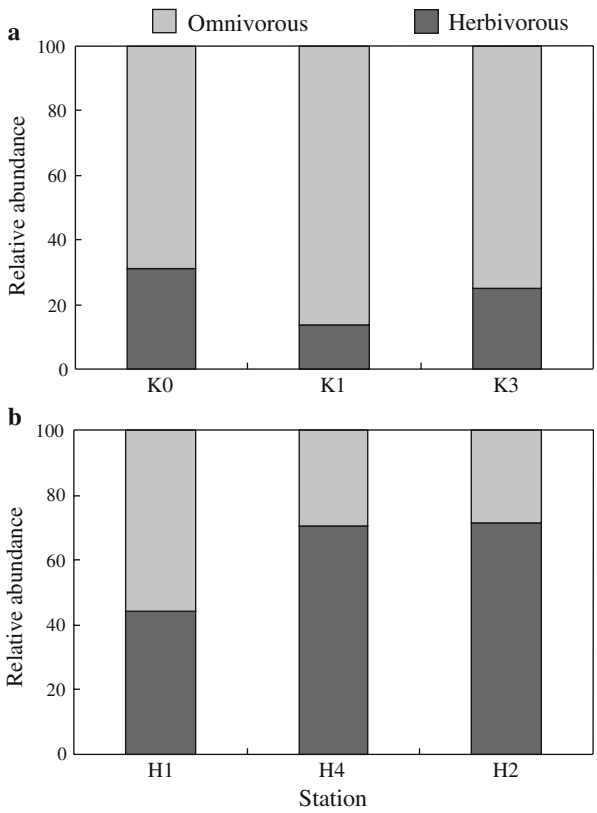

Fig. 7 Relative abundance (%) of trophic groups in Kongsfjorden (**a**) and Hornsund (**b**)

Discussion

Both fjords were influenced by Atlantic-derived water masses covered by thin layer of freshwater runoff from the glaciers. This type of stratification has been observed every year in the Svalbard fjords; however, the amount of Atlantic-derived water in the fjords depends on the general oceanographic situation in the North Atlantic (Cottier et al. 2005). Closer to the glaciers, where the great discharge of freshwater occurs, strong stratification in temperature and salinity is observed, but this gradient diminishes towards the fjord opening (Swerpel 1985; Svendsen et al. 2002). Together with the melting waters, vast amounts of inorganic sediments are released (Zajaczkowski 2008). The resulting turbidity controls the depth of the euphotic zone as well as the spectral composition of penetrating radiation (Urbański et al. 1980; Svendsen et al. 2002), which directly influences phytoplankton composition and primary production. In Hornsund, the thickness of the euphotic layer decreased rapidly from the mouth towards the inner basin. In Kongsfjorden, we observed a front between relatively clean, blue waters of the outer basins and turbid, reddish-brown waters in the inner basins.

Observed changes in the physical environment influenced phytoplankton assemblages. In Kongsfjorden, diatoms and autotrophic dinoflagellates were more important in the outer basins. Several oceanic species, e.g. *Protoperidinium pallidum* (Ostenfeld, 1902) Balech, *P. steinii* (Jörgensen) Balech, *C. arcticum*, *Phalacroma rotundatum* (Claparede and Lachmann) Kofoid and Michener 1911, *Rhizosolenia hebetata* Bailey 1856, and *Chaetoceros concavicornis* Mangin 1917 were found in the outer basin. These species did not occur in the inner basin and were most likely transported to Kongsfjorden with Atlantic-derived waters (Hasle and Heimdal 1998; Okolodkov et al. 2000; Hop et al. 2002). The details of species composition in both fjords and basins have been published elsewhere (Wiktor and Wojciechowska 2005). In the inner basin of Kongsfjorden, cryptophytes and other nanoflagellates were important contributors to phytoplankton biomass. This resulted in a decrease in total phytoplankton biomass in the inner basin, because individuals from these groups are smaller than diatoms. However, the decrease in biomass

integrated over the entire sampling depth was more influenced by reduction of the euphotic zone than changes in the phytoplankton composition. High biomass at the mouth of Kongsfjorden was mainly caused by presence of diatoms in deeper layers. However, the poor conditions of the diatoms suggest that DCMs consisted mainly of sinking, unproductive cells. Observed phytoplankton assemblages, except for the absence of *Dinobryon balticum* (Schutt) Lemmermann 1900, have been described (Hasle and Heimdal 1998; Okolodkov et al. 2000; Hop et al. 2002), and their transition towards the inner reaches has been explained as the result of gradients of physical factors (Keck et al. 1999).

Similar gradients of physical factors were observed also in Hornsund (Urbański et al. 1980; Swerpel 1985). However, the phytoplankton assemblages were different from the ones found in Kongsfjorden. The most remarkable difference was the presence of species that are considered to be cryo-pelagic, e.g. *Bacterosira bathyomphala* (Gran) Syversten and Hasle 1993, *Gonioceros septentrionalis* (Ostrup) Crawford 1994, *Fragilariopsis cylindrus* (Grunow) Krieger 1954, *Navicula pelagica* Cleve 1896 (for details refer to Wiktor and Wojciechowska 2005). Diatoms contributed more to phytoplankton biomass in productive layers, and their occurrence in deeper layers most likely resulted from sinking cells. At depths below 30 m, we also observed spores of *Chaetoceros* sp. and *Thalassiosira* sp. Other phytoplankton groups were generally of minor importance in Hornsund. The only exception was nanoflagellates, which even dominated biomass at some depths, despite their relatively small sizes. Unfortunately, the lack of published studies from Hornsund makes it impossible to say whether the observed phytoplankton species formed typical summer assemblages in this fjord.

The differences in phytoplankton composition could have resulted from inflow of different waters to the fjords. Although it is not clear from the temperature and salinity plots (Fig. 2), the presence of cryo-pelagic species in Hornsund indicates recent inflow of Arctic waters from the Sørkapp Current. Inflow of Atlantic-derived waters in Kongsfjorden was indicated both on TS plot and by presence of oceanic species. On the other hand, freshwater runoff carrying vast load of mineral particles drastically changes hydrological and light regimes in the fjords, creating unfavourable conditions for both autochthonous and allochthonous phytoplankton. Deep biomass maxima in the inner basins of the fjords may have resulted from submerging surface oceanic waters.

Zooplankton composition observed in both fjords was typical for the summer season (Hop et al. 2002; Walkusz et al. 2004; Hop et al. 2006; Walkusz et al. 2008) with the co-occurrence of taxa originating from different ecological domains—Arctic (e.g. *C. glacialis*, *L. helicina*) and boreal (e.g. *C. finmarchicus*, *O. atlantica*). However, high abundances of Echinodermata larvae and *O. similis* as compared to previous years suggest stronger than normal impacts of warm Atlantic-derived water on the ecosystem (Walkusz 2006). Decreasing phytoplankton biomass towards the fjord's inner reach seems to correspond well, not only with the decreasing light penetration, but also with increasing zooplankton abundance. It is particularly noticeable when herbivore abundance is compared with diatoms' biomass. Since zooplankton gut content was not examined at the time of sampling, it is difficult to make a strong statement regarding zooplankton diet composition. Thus, further investigation, preferably in seasonal approach, would be of great help to better understand light–phytoplankton–zooplankton relationship in the Svalbard fjords.

The most conspicuous difference between the two investigated fjords, however, was in primary production rates and chlorophyll-*a* concentration (Fig. 6). Unfortunately, we do not have these data from the outer parts of Kongsfjorden, but even when we compared the innermost stations of the two fjords, the rates were an order of magnitude higher in Hornsund. The most obvious explanation seems to be the difference in light regime. Unfortunately, because of equipment failure, we lack light data from Kongsfjorden, but we can still compare the thickness of productive layers at the innermost sampling stations, since it strongly depends on the thickness of euphotic layer. The productive layer thickness was ~15 m at station H2 (PAR <1% of surface intensity) and only ~5 m at station P1. Moreover, in Kongsfjorden high water turbidity could be observed when sampled from the ship. The differences in primary production rates and chlorophyll-*a* concentration could also have resulted from different phytoplankton assemblages in both fjords. At the stations in Kongsfjorden where primary production was measured (P2 and P1), autotrophic flagellates (dinoflagellates and cryptophytes) contributed most to phytoplankton biomass in productive layers. These algae have been reported to have relatively low primary production rates (Throndsen 1970). High values of primary production in outer Hornsund coincided with high biomass of diatoms, whereas heterotrophic dinoflagellates and undetermined flagellates contributed most to the biomass in the inner basins. Previous studies have shown that the majority of the unidentified nanoflagellates is heterotrophic (Wiktor 1999, 2000; Wiktor et al., unpublished data). But still, the primary production rates and chlorophyll-*a* concentration were much higher than at the stations in Kongsfjorden.

Finally, the timing of the phytoplankton bloom may have caused some of the observed differences. Even if sampling was conducted at about the same time in July in both fjords, the phytoplankton bloom, and thus plankton communities, may have been more advanced in Kongsfjorden than in Hornsund. Typically, the spring bloom starts with

diatoms and progresses into flagellates and smaller algae during summer, and the original surface blooms will sink down to become DCM. The fact that the diatoms at DCM were in rather poor condition, with bleached chloroplasts and plasmolysed cytoplasm, is consistent with a senescent and sinking bloom. Because of the Atlantic influence in Kongsfjorden, which induces earlier melting of the ice cover, the bloom may have started earlier and progressed further in this fjord than in Hornsund. Thus, some of the differences may be due to different blooming stages, although this cannot be properly assessed in this study since the development of the phytoplankton blooms were not followed in two fjords.

Based on our temporally limited data set, we suggest that Kongsfjorden is much less productive than Hornsund. Diatoms are clearly the most important producers in both systems, and if they are replaced by flagellates and smaller algae during the progression of the bloom, the system becomes less productive. There are also some indications that this will happen when the system warms up due to climate warming with increased influx of Atlantic water. For instance, sampling in Kongsfjorden in May 2007 revealed low abundances of diatoms (E. N. Hegseth, University of Tromsø, personal communication) Values of summer primary production in water column for Kongsfjorden ranged from 0.3 to 92 mg C m^{-2} h^{-1} (Eilertsen et al. 1989; Hop et al. 2002), which also implies that primary production in Spitsbergen fjords is very variable. Similar data for Hornsund from summer are unavailable, but Eilertsen et al. (1989) state that the differences in primary production rates in March were approximately ten times lower than in April. Their values in April (up to 15 mg C m^{-3} h^{-1}, based on Fig. 5 therein) were twice as high as observed in this study, which mainly reflects the spring bloom versus summer bloom situation. Undoubtedly, more studies concerning phytoplankton and primary production, as well as their dependence on physico-chemical factors, are necessary in Spitsbergen fjords in order to reveal whether the differences between the fjords are permanent or periodical. Such studies should follow the progression of phytoplankton blooms from spring to summer with regard to timing of blooms and changes in phytoplankton communities.

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