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ORIGINAL PAPER

Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates

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Abstract The composition and ecological role of ciliates and dinoflagellates were investigated at one station in Kongsfjorden, Svalbard, during six consecutive field campaigns between March and December 2006. Total ciliate and dinoflagellate abundance mirrored the seasonal progression of phytoplankton, peaking with 5.8×10^4 cells l^{-1} in April at an average chlorophyll *a* concentration of 10 μg l^{-1}. Dinoflagellates were more abundant than ciliates, dominated by small athecates. Among ciliates, aloricate oligotrichs dominated the assemblage. A large fraction (>60%) of ciliates and dinoflagellates contained chloroplasts in spring and summer. The biomass of the purely heterotrophic fraction of the ciliate and dinoflagellate community (protozooplankton) was with 14 μg C l^{-1} highest in conjunction with the phytoplankton spring bloom in April. Growth experiments revealed similar specific growth rates for heterotrophic ciliates and dinoflagellates (<0–0.8 d^{-1}). Food availability may have controlled the protozooplankton assemblage in winter, while copepods may have exerted a strong control during the post-bloom period. Calculations of the potential grazing rates of the protozooplankton indicated its ability to control or heavily impact the phytoplankton stocks at most times. The results show that ciliates and dinoflagellates were an important component of the pelagic food web in Kongsfjorden and need to be taken into account when discussing the fate of phytoplankton and biogeochemical cycling in Arctic marine ecosystems.

Keywords Microzooplankton · Mesozooplankton · Phytoplankton · Food web · Carbon cycling · Arctic

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Introduction

Protozoans, such as heterotrophic ciliates and dinoflagellates, are major grazers on bacteria, flagellates, and diatoms in temperate marine environments (Sherr et al. 1989; Johansson et al. 2004; Aberle et al. 2007; Sherr and Sherr 2007). In cold waters, where large copepods were considered the principal grazers, the role of protozoans was traditionally thought to be of minor importance. A global comparison of the impact of protozoan grazers on phytoplankton did, however, not support such a dissimilarity between different geographic regions, but showed protozoan grazing to be the major source of phytoplankton consumption worldwide (Calbet and Landry 2004). In a cross-latitude comparison between the subpolar Disko Bay (Greenland) and temperate Kattegat (Denmark), Levinsen and Nielsen (2002) demonstrated that heterotrophic ciliates and dinoflagellates were important components of plankton in both systems, with similar seasonal patterns in abundance, taxonomic composition, and grazing impact. Yet the few studies on protozoan grazing in Arctic marine systems do indicate strong seasonal and spatial variability (Hansen et al. 1996; Sherr et al. 2009). Thus, the general role of

protozooplankton for carbon cycling throughout the pan-Arctic region is complex and not easily summarized.

The reported variability certainly reflects the extreme heterogeneity of Arctic marine systems, which are subjected to strong seasonality in light, temperature, and ice cover. At the same time, these studies also suggest strong biotic factors controlling the protozoan abundance. In the central Arctic, for example, Sherr et al. (2003) found the protozoan biomass to increase along with phytoplankton during spring and summer, indicating strong bottom-up control, while Rysgaard et al. (1999) reported strong top-down control by copepods in an ice-covered northeast Greenlandic fjord. In Disko Bay, West Greenland, the protozoan community was primarily controlled by the availability of food, but temporally also by copepod predation (Levinsen and Nielsen 2002). Ciliates and dinoflagellates build up a high biomass only when the dominating large copepods were absent from the euphotic zone in early spring and late summer (Levinsen and Nielsen 2002). Understanding the role and impact of protozoans in the food web thus demands particular consideration of key biotic factors, such as food availability and concentration of predators.

The Svalbard archipelago (74–81°N) is situated at the boundary of the European Arctic. Warm Atlantic water is carried along the west coast of Spitsbergen by the West Spitsbergen Current, the northernmost extension of the North Atlantic Current (Loeng 1991). The west coast harbours large glacial fjord systems, one of which is Kongsfjorden (79°N 12°E). The fjord has a wide opening and lacks a sill, which allows warm Atlantic water to advect into the fjord (Svendsen et al. 2002; Cottier et al. 2005). The copepod community of Kongsfjorden is known to heavily depend on these advective processes (Kwasniewski et al. 2003; Basedow et al. 2004; Willis et al. 2006; Walkusz et al. 2009). It is not clear to which extent the biomass-dominating large copepods, *Calanus finmarchicus* and *C. glacialis*, maintain local populations in the fjord (Walkusz et al. 2009). Their abundance, however, depends noticeably on the timing and magnitude of the shelf-fjord water mass exchanges (Kwasniewski et al. 2003; Walkusz et al. 2009), and the phytoplankton bloom in spring may often develop in the absence of significant stocks of copepods (Willis et al. 2006).

Despite extensive interest in the mesozooplankton fauna of Kongsfjorden (Hop et al. 2002, 2006 and references therein), no study has so far focused on the protozoan part (heterotrophic ciliates and dinoflagellates) of the zooplankton. Sparse accounts of dinoflagellates have been provided in the phytoplankton literature of the fjord (Hasle and Heimdal 1998; Keck et al. 1999; Wiktor 1999; Okolodkov et al. 2000; Wiktor and Wojciechowska 2005), while no reports exist on the ciliate assemblage in Kongsfjorden, to the best of our knowledge. Consequently, the description of the zooplankton community in Kongsfjorden lacks a key component. Further, seasonal cycles from Arctic marine ecosystems are rare and missing from Kongsfjorden.

The present work is first of all an attempt to fill some of these knowledge gaps by providing seasonal ciliate and dinoflagellate abundance and biomass data from Kongsfjorden. It also tries to investigate some of the regulatory mechanisms that control protozoan biomass. Finally, it attempts to estimate the potential grazing impact of heterotrophic ciliates and dinoflagellates.

Concomitantly with the present study, biomass measurements of bacteria, picoplankton, and nanoflagellates, as well as primary production, were conducted in Kongsfjorden (Rokkan Iversen and Seuthe *accepted*). These data show that the microbial food web in Kongsfjorden was seasonally pulsed, with a peak in biomass in spring and relatively low biomass thereafter. The vernal phytoplankton bloom advanced in April, dominated by the prymnesiophyte *Phaeocystis pouchetii* and diatoms. Apart from the vernal bloom, phytoplankton was dominated by cells <10 μm. Bacterial biomass peaked after the senescence of the phytoplankton bloom in May and remained high throughout the summer, sustaining a microbial food web of pico- and nano-sized heterotrophs.

Material and methods

Locality and sampling

The study was conducted at a station located in Kongsfjorden on the west coast of Spitsbergen (78°57′N, 11°56′E, approx. depth 300 m, Fig. 1). The station was sampled in 2006 on March 18, April 25, May 30, July 4, September 16, and December 2. Vertical profiles of temperature and salinity were recorded on each occasion (Seabird SBE19+). Water was sampled with Niskin bottles from six discrete depths (1, 5, 10, 15, 25, and 50 m) for the analyses of chlorophyll *a* (Chl *a*), protozooplankton, and phytoplankton. For analyses of Chl *a*, triplicate subsamples (25–1,000 ml) were filtered onto Whatman GF/F glass fibre filters. The filters were frozen (−20°C) immediately for 5–7 days, before being analysed fluorometrically (10-AU, Turner Designs) after extraction in 5 ml of methanol at room temperature in the dark for 12 h. All biological data processed from discrete water samples were integrated for the upper 50 m of the water column, using trapezoidal integration. Metazooplankton was sampled with WP2 net (mesh size of 63 μm, except for September and December when a mesh size of 90 μm was used), hauled vertically from 200 m to the surface.

Protist biomass and taxonomic composition

Samples for diatom, ciliate, and dinoflagellate identification and enumeration (500–1,000 ml) were fixed with acid Lugol (2% vol. final concentration). The samples were stored dark and cool, before being gently concentrated down to 50 ml by inverse gravitational filtration (10-µm mesh size) after settling in a glass cylinder for 48 h. From the concentrate, a subsample (10 ml) was settled in an Utermöhl sedimentation chamber. The whole chamber was examined under an inverted microscope (Nikon TE200) at a magnification of ×200 and ×400. Cell sizes were measured on 30 specimens of each species using a camera (5 Mega pixel) attached to the microscope. Standard geometric forms were used to determine the cellular volume from length and width measurements. The biovolume was converted to biomass using a volume to carbon conversion factor of 0.19 pg C μm^{-3} (Putt and Stoecker 1989) and 0.053 pg C μm^{-3} (Verity and Langdon 1984) for aloricate and loricate ciliates, respectively. For dinoflagellates, a carbon conversion factor of pg C $cell^{-1} = 0.760 \times volume^{0.819}$ (Menden-Deuer and Lessard 2000) was used.

For ciliates, loricate (tintinnids) and aloricate forms were distinguished, with aloricates being divided into oligotrichs (*Laboea strobila*, *Strombidium conicum*, and *Strombidium* spp.), aloricate choreotrichs (*Leegaardiella* sp., *Lohmanniella* sp., and *Strobilidium* sp.), *Myrionecta rubra*, and holotrichs (here used for all ciliates with even cilia coverage of the cell). Dinoflagellates were identified to the lowest taxonomic level possible and divided into thecates and athecates. Athecate dinoflagellates were divided into two size groups of equivalent spherical diameter (ESD) of smaller and larger than 20 µm.

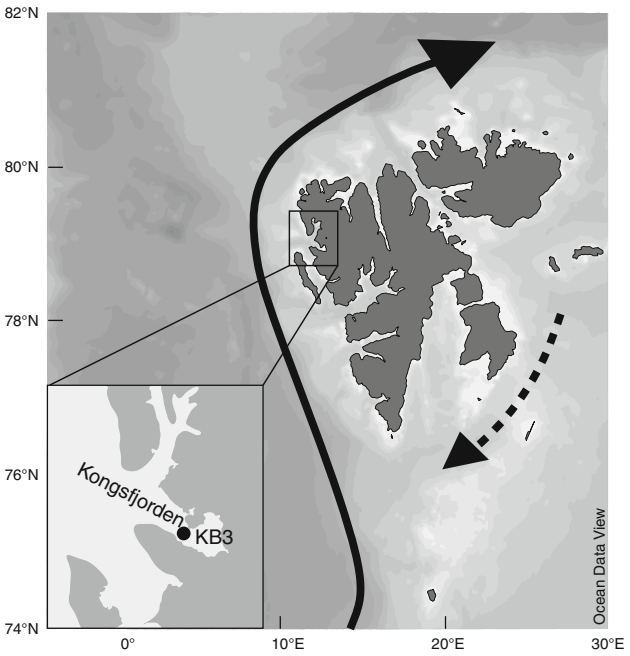

Fig. 1 Schematic overview over the main current system around the Svalbard Archipelago, with the West Spitsbergen Current (*black arrow*) transporting warm Atlantic water along the west coast of Spitsbergen. The present study was conducted in Kongsfjorden (station KB3, 78°57′N, 11°56′E, ca. 300 m) at the west coast of Spitsbergen

Protozooplankton was divided into two groups depending on the presence or absence of chloroplasts, respectively, called phototrophs and heterotrophs hereafter. Since fixation with acid Lugol largely prohibits the visual examination of the presence of chloroplast, the division was undertaken according to literature. In ciliates, chloroplast-bearing species were *Myrionecta rubra* (Hansen and Fenchel 2006), *Laboea strobila* (Stoecker et al. 1988; Stoecker and Michaels 1991), *Tontonia* sp. (Laval-Peuto and Rassoulzadegan 1988), and *Strombidium conicum* (Stoecker and Michaels 1991), with the three latter ones being mixotrophs. In dinoflagellates, chloroplast-bearing species were identified according to Thomas (1997). All species classified as plastidic are indicated in Table 1.

Protozoan growth experiments

Protozooplankton growth rates were calculated from changes in cell abundance in the natural plankton community over the course of 2 days. Incubation water was sampled from the respective depths (1, 5, 10, 15, 25, 50 m) at the same station and time as the profile using an acid-washed Go Flo bottle. The water from the different depths was pooled in equal parts in a 20-l acid-washed Nalgene polycarbonate bottle. The pooled incubation water was gently pre-screened on 63 µm by reverse filtration to exclude larger predators, which might have led to the loss of larger protozoans (e.g., tintinnids). In March, incubation water was taken from the surface by a 20-l acid-washed Nalgene polycarbonate bottle only, because very low air temperatures and strong wind made it impossible to handle the Go Flo bottle without freezing. On all occasions, the pre-screened incubation water was carefully siphoned over into three acid-washed polycarbonate bottles (Nalgene, 2.5 l), which were incubated in the dark at 2 ± 1°C (March, April, May) and 4 ± 1°C (July, September). The incubation temperatures did not mirror in situ temperatures precisely, due to technical restrictions. The change in incubation temperature between spring and summer attempted to mirror the increase in in situ temperatures. The incubation bottles were gently rotated each day before sampling to homogenize the sample. Aliquots of 500 ml were taken in the beginning (t_1) and in the end (t_2) of the experiment and fixed with acid Lugol (2% vol. final concentration) for later quantification.

Growth rates (μ) were calculated for different protozooplankton morphotypes (athecate dinoflagellates ESD

Table 1 Species-specific integrated (0–50 m) abundance (cells × 10^6 cells m^{-2}) and biomass (mg C m^{-2}; in brackets) of dinoflagellates and ciliates

	Mar	Apr	May	Jul	Sep	Dec
Thecate dinoflagellates						
*Alexandrium minutum**		20 (5)		14 (4)	13 (3)	
Alexandrium sp.*		46 (12)	12 (3)	36 (10)	0.8 (0.2)	0.2 (0.04)
*Ceratium arcticum**				0.1 (1)		
*C. macroceros**					0.4 (3)	
*Dinophysis acuminata**			1 (2)			0.1 (0.2)
Dinophysis sp.				0.3 (0.7)	0.3 (0.7)	
Diplopelta parva	4 (3)					
*Gonyaulax grindleyi**	0.6 (4)					
*G. scrippsiella**	0.03 (0.03)					
*Heterocapsa rotundata**	3 (0.1)					
*H. triquetra**		266 (231)				
Lessardia elongata	16 (1)					
*Scrippsiella trochoidea**		8 (3)			0.3 (0.1)	
*Oxytoxum criophilum**	3 (0.5)					
Peridinium subinerme	0.03 (0.1)					
Protoperidinium bipes		45 (14)		19 (6)	31 (10)	
P. brevipes					26 (27)	
P. divergens				0.3 (1)		
P. granii		0.6 (2)		0.1 (0.4)		
*P. pallidum**		0.2 (2)			0.05 (0.2)	
P. pellucidum		11 (36)	0.2 (0.7)	1 (5)	0.7 (2)	
P. steinii						0.4 (1)
Protoperidinium sp. 1				0.2 (3)		
Protoperidinium sp. 2		54 (174)	1 (4)	1 (4)	1 (4)	
Total thecates	27 (9)	451 (480)	15 (11)	73 (33)	74 (51)	0.7 (2)
Athecate dinoflagellates						
Amphidinium crassum	5 (1)					
*A. fusiforme**	8 (1)					
*A. larvale**	2 (0.1)					
A. longum	4 (0.7)					
A. sphaenoides	1 (0.1)	0.1 (0.01)				
Gymnodinium albulum	7 (0.2)					
*G. arcticum**	0.1 (0.03)	1902 (991)	197 (103)	29 (15)	76 (39)	42 (22)
*G. japonicum**	4 (0.2)					
*G. pulchellum**		13 (0.5)			501 (18)	199 (7)
*G. simplex**					15 (0.5)	
G. wulfii	2 (0.2)	266 (28)	57 (6)			
Gymnodinium sp. 1	7 (11)	11 (17)		0.4 (0.5)		19 (28)
Gymnodinium sp. 2	0.03 (0.1)		5 (8)			
Gymnodinium sp. 3					4 (6)	
Gymnodinium sp. 4		6 (9)	0.3 (0.4)		1 (2)	
Gyrodinium aureolum	0.3 (0.7)					
G. calyptroglyphe	9 (2)					
G. fusiforme		21 (24)	7 (8)	1 (1)	9 (10)	0.1 (0.1)
G. lachryma		8 (55)	2 (11)	0.1 (0.8)	1 (9)	
G. pingue	3 (4)					
Gyrodinium sp. 1		4 (0.9)			25 (5)	50 (10)

Table 1 continued

	Mar	Apr	May	Jul	Sep	Dec
Gyrodinium sp. 2			32 (7)		191 (39)	
Gyrodinium sp. 3		10 (87)		0.2 (2)	0.3 (2)	
*Karlodinium veneficum**	6 (0.7)					
Katodinium glaucum	4 (0.6)	21 (3)	0.5 (0.1)		9 (1)	30 (4)
Nematodinium sp.					0.3 (2)	0.1 (0.4)
Pronoctiluca pelagica					4 (2)	0.2 (0.1)
*Torodinium robustum**	4 (3)					
*T. teredo**					0.5 (0.4)	1 (0.4)
Total athecates	67 (26)	2,263 (1214)	301 (143)	31 (20)	835 (135)	342 (73)
Loricate ciliates						
Acanthostomella cf. *norvegica*				0.3 (0.2)		
Parafavella sp.				0.1 (0.2)	2 (3)	
Ptychocylis sp.					0.5 (20)	0.1 (3)
Salpingella sp.					0.4 (0.9)	0.2 (0.5)
Tintinnida indet.		6 (168)	2 (63)	1 (47)	2 (101)	1 (40)
Total loricates		6 (168)	2 (63)	2 (47)	5 (125)	1 (43)
Aloricate ciliates						
Didinium cf. *gargantua*						0.03 (0.1)
*Laboea strobila**		16 (291)	0.5 (9)	7 (130)	0.5 (10)	
Leegaardiella cf. *ovalis*		0.1 (2)		0.2 (5)	0.4 (8)	2 (37)
Lohmanniella cf. *oviformis*		3 (3)	2 (2)		1 (1)	
*Myrionecta rubra**	8 (48)	6 (39)	0.7 (4)		0.1 (0.6)	0.3 (2)
Strombidium cf. *acuminata*		0.2 (0.5)				
*S. conicum**	2 (6)	34 (91)	8 (21)	2 (5)	0.5 (1)	0.5 (1)
S. wulffi		87 (59)	10 (7)	1 (0.7)	2 (1)	2 (1)
Strombidium sp. 1		7 (1)	8 (1)			0.2 (0.03)
Strombidium sp. 2		2 (5)				
Strombidium sp. 3		9 (6)	3 (2)	0.4 (0.3)	0.4 (0.3)	0.3 (0.2)
Strombidium sp. 4		0.2 (0.4)			0.4 (0.8)	
Strobilidium cf. *spiralis*						0.3 (7)
Tontonia sp.*		0.1 (0.1)				0.1 (0.05)
Holotrich ciliates	8 (56)	3 (24)			0.05 (0.3)	0.4 (3)
Total aloricates	18 (110)	168 (522)	32 (46)	11 (142)	5 (24)	6 (51)

Species reported to contain chloroplasts or cleptochloroplasts are marked (*)

10–20, 20–30 μm, *Protoperidinium* sp., aloricate ciliates ESD 10–20, 20–30, >40 μm, and holotrich ciliates) assuming exponential growth: $\mu = (\ln N_{t2} - \ln N_{t1})t^{-1}$, where N_{t2} and N_{t1} are the number of protozooplankton at time t_2 and t_1, respectively, given in days. Growth rates were calculated only for morphotypes of which >20 specimens were counted. Unfortunately, no growth was measured for tintinnids, which contributed significantly to the biomass of heterotrophic ciliates. Therefore, the growth rate of tintinnids was assumed to have been 0.38 d^{-1} at 5°C (Hansen and Jensen 2000) and corrected to in situ temperatures with a Q_{10} of 2.8 (Hansen et al. 1997), for further calculations of the production and grazing rate of heterotrophic ciliates.

Protozoan production and grazing calculations

Daily production and grazing rates were calculated for heterotrophic ciliates and dinoflagellates only, excluding mixotrophic species. Protozoan production was calculated from the experimentally determined growth rates multiplied by the respective heterotrophic ciliate and dinoflagellate biomass. Protozoan growth rates were corrected to in situ temperature using a Q_{10} of 2.8 (Hansen et al. 1997). Grazing

of the heterotrophs was calculated from the production rates, assuming a growth efficiency of 33% (Hansen et al. 1997).

Metazooplankton composition and biomass

Metazooplankton samples were stored in buffered formalin (4% vol. final concentration). Aliquots were subsampled using a Motoda splitter and counted in a Bogorov tray using a Nikon SMZ 1000 stereomicroscope. At magnification ×8 to ×80, copepods and meroplankton larvae were identified to genus or species level and enumerated. Calanoid and cyclopoid nauplii were discriminated according to their size and morphology (Gibbons and Ogilvie 1933; Ogilvie 1953). Prosome length or developmental stages of copepodids and total length of nauplii and meroplankton larvae were determined and abundances converted into carbon biomass following equations chosen from relevant references. For copepodids, *Calanus* spp. carbon was converted according to Hirche and Mumm (1992), Cyclopoids and other minor orders from Sabatini and Kiørboe (1994, eq. for *Oithona similis*), *Metridia longa* from Hanssen (1997), *Pseudocalanus* spp. from Conover and Huntley (1991), and *Microcalanus* spp. from Klein Breteler et al. (1982, eq. for *P. minutus*). Cyclopoid nauplii were converted from Sabatini and Kiørboe (1994), calanoid and cirripeda nauplii from Klein Breteler et al. (1982), and for pluteus and veliger larvae, we used Fotel et al. (1999, eq. for *Mytilus edulis*). When necessary, ash-free dry weight to dry weight conversion factor was taken from Mauchline (1998) and a carbon weight to dry weight ratio of 0.473 was used (Conover and Huntley 1991).

Statistical analyses

A multiple linear regression analysis (Systat 12©) was conducted to evaluate whether in situ water temperature or bulk food concentration (total Chl *a*, Chl *a* >10 µm, POC) explained best the observed variance in heterotrophic ciliate and dinoflagellate biomass. All biomass values were log-transformed to account for non-normal distribution. With help of stepwise backward elimination, all potential explanatory variables that fell below the 5% significance level were excluded.

Results

Hydrography

In late January to early March 2006, an oceanographic mooring in the outer basin of Kongsfjorden recorded a strong inflow of Atlantic water (Cottier et al. 2007). In concert with a period of intense atmospheric cooling in the fjord, a homogenous water column of 0.6 ± 0.1°C and salinity of 34.7 ± 0.2 were formed in March 2006 (Fig. 2). In April, the water temperature remained low (0.6 ± 0.1°C), but showed a weak pycnocline at approximately 30 m. Surface water temperature increased to 2°C in May and reached temperatures of 3–6°C in July and September. A minor inflow of Atlantic water was recorded by the oceanographic mooring at depth in mid-May, while a major inflow took place in mid-July (pers. comm. F. Cottier). From the time of the snow-melt (May/June) and onwards, the fjord was influenced by freshwater run-off from glaciers and land, resulting in a shallow stratified water column (approximately 10 m in July and 30 m in September) with surface water salinity of 33.8 ± 0.9 (July/September, Fig. 2). In December, the water had been cooled down to 1.5°C and formed a homogenous body with a salinity of 34.6 ± 0.02. The depth of the euphotic zone ranged between 0 m (December) to 40 m (March), and intermediate depths of 12

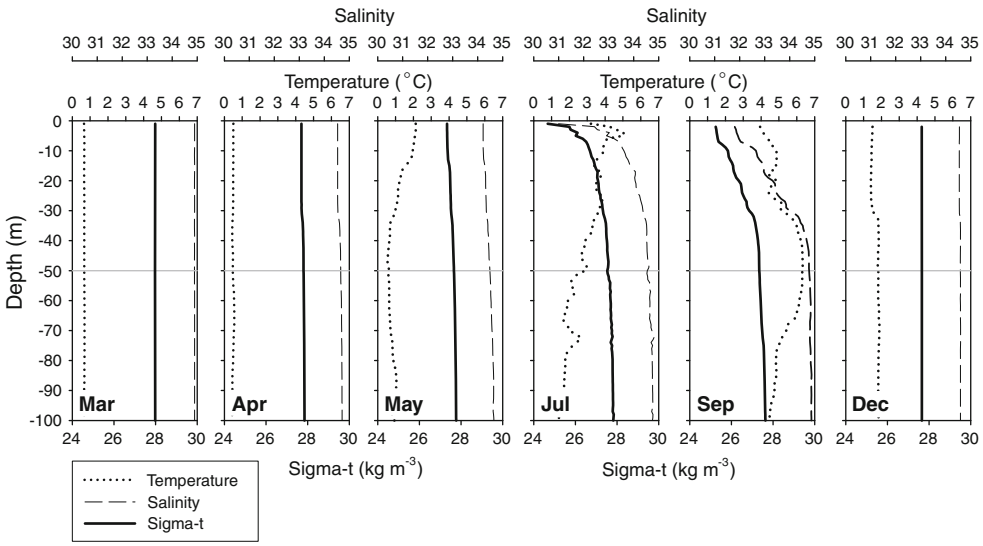

Fig. 2 Hydrographical profiles of temperature (°C; *stippled line*), salinity (*broken line*), and density (kg m^{-3}; *solid line*) of the upper 100 m of the water column at station KB3 for the different months of sampling. The *horizontal line* indicates the depth of the biological sampling programme (0–50 m)

and 18 m in April and May, respectively (pers. comm. E. Nøst Hegseth).

Seasonal abundance and composition of protists

The spring phytoplankton bloom developed in April (Fig. 3a, b). Chl *a* concentration increased from 0.02 to 10 µg Chl *a* l^{-1} from March to April, respectively (Fig. 3a). In April, 70% of the Chl *a* was in the >10 µm size class (Rokkan Iversen and Seuthe *accepted*), reflecting the high abundance of larger diatoms (Fig. 3b). The importance of large (>10 µm) phytoplankton decreased to only 5% of the total Chl *a* during summer, when pico- and nano-sized phototrophs dominated the phytoplankton (Rokkan Iversen and Seuthe *accepted*). Centric diatoms showed a small second increase in abundance in September (Fig. 3b). Pico- and nano-sized heterotrophs were most abundant in July and September (Rokkan Iversen and Seuthe *accepted*; our Table 4).

The seasonal abundance of ciliates and dinoflagellates mimicked the distribution of phytoplankton, with highest abundance in April (Fig. 3c–e). Ciliates reached peak abundance with up to 3.5 × 10^3 cells l^{-1} in April, while their abundance was lower by a factor of ten during the other seasons (Fig. 3c). Dinoflagellates were more abundant than ciliates, with a highest total abundance of 54 × 10^3 cells l^{-1} in April. In general, small dinoflagellates (ESD < 20 µm) constituted the largest bulk of total dinoflagellate abundance (60–99%, Fig. 3d, e).

Numerically, aloricate forms dominated the ciliate assemblage with >80%, except in September when aloricate and loricate forms were equally abundant (Table 1). In March, aloricate ciliates were dominated by *M. rubra* and holotrich ciliates with 44 and 42%, respectively. Strombidiids became with >90%, the most important aloricate ciliate group in April, May, and July. Their contribution to total aloricate numbers decreased in September to <70%, when strobilidiids became more abundant. Dinoflagellates were numerically dominated by athecate forms at all times (Table 1). Predominant athecate genera were *Gymnodinium* and *Gyrodinium*, except in March when also species of *Amphidinium* were present.

Biomass of heterotrophic ciliates and dinoflagellates

A large fraction of the ciliates' and dinoflagellates' biomass was constituted of chloroplast-bearing species, especially in April, May, and July (Fig. 4; Table 1). Plastidic ciliates, such as *Myrionecta rubra*, *Laboea strobila*, and *Strombidium conicum*, contributed with 60 and 70% to the total ciliate biomass in April and July, respectively (Fig. 4; Table 1). Among dinoflagellates, chloroplast-containing species, such as *Heterocapsa triquetra*, *Scripsiella trochoidea*, and

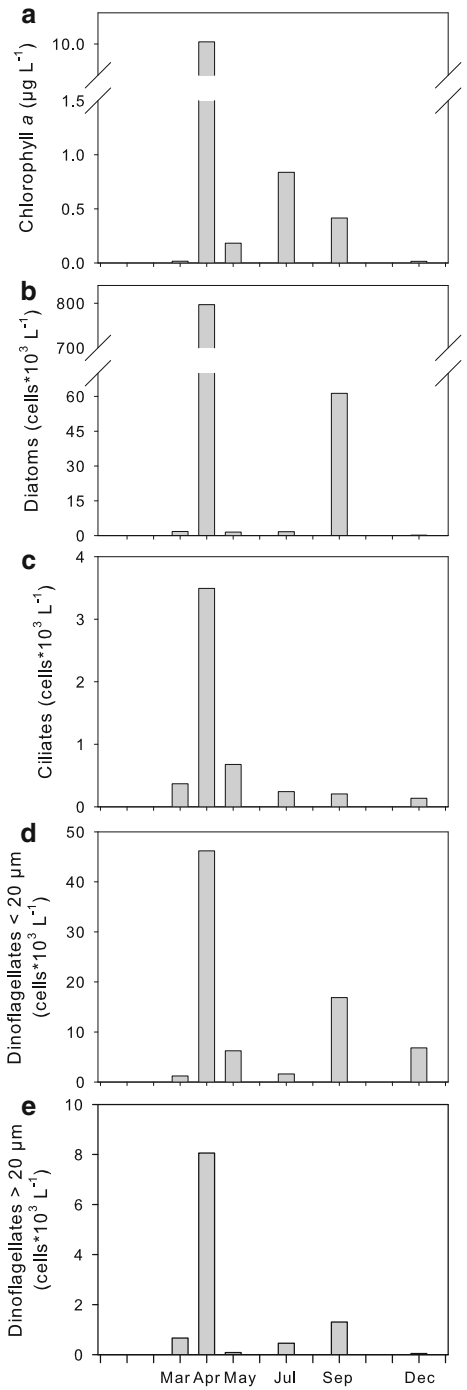

Fig. 3 Average integrated (**a**) concentration of chlorophyll *a* (µg Chl *a* l^{-1}), and abundance of (**b**) diatoms (cells × 10^3 l^{-1}), (**c**) ciliates (cells × 10^3 l^{-1}), (**d**) dinoflagellates <20 µm (cells × 10^3 l^{-1}), and (**e**) dinoflagellates >20 µm (cells × 10^3 l^{-1}) for the upper 50 m of the water column. Ciliates and dinoflagellate abundance is given as total number, including both plastidic and heterotrophic species. Note the difference in scales

Gymnodinium arcticum, were most dominant in April and May with about 70% (Fig. 4). The contribution of plastidic ciliates and dinoflagellates decreased considerably in

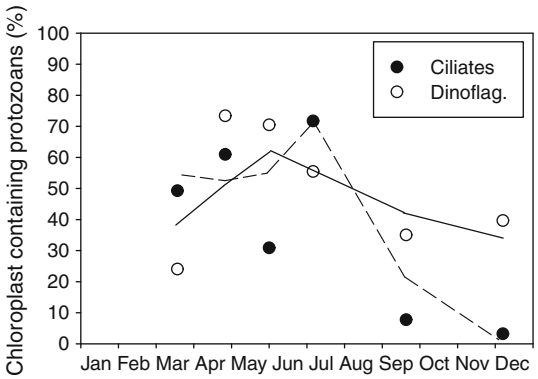

Fig. 4 Percentage (%) of chloroplast-containing ciliates and dinoflagellates over the year, based on biomass estimates. The trend in the data is visualized by a trend line (LOWLESS smoother, tension = 0.85, SYSTAT 12), with a *stippled line* for ciliates and a *solid line* for dinoflagellates

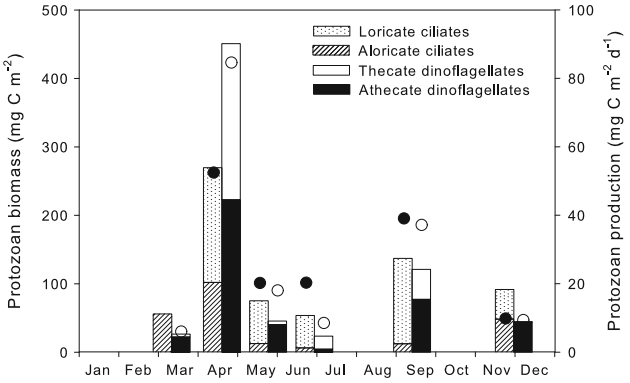

Fig. 5 Biomass (*left axis*: mg C m^{-2}; *bars*) of heterotrophic dinoflagellates and ciliates integrated for the upper 50 m of the water column. Calculated integrated community growth (*right axis*: mg C m^{-2} d^{-1}) for heterotrophic dinoflagellates (athecate and thecate; *open circles*) and heterotrophic ciliates (aloricate and loricate; *filled circles*) is given

September and December, with <10% in ciliates and about 40% in dinoflagellates.

The biomass of heterotrophic ciliates exceeded that of heterotrophic dinoflagellates except in April (Fig. 5), when heterotrophic dinoflagellates peaked with 451 mg C m^{-2} (compared to a biomass of heterotrophic ciliates of 269 mg C m^{-2}). Loricate ciliates, such as *Acanthostomella cf. norvegica, Parafavella* sp., and *Ptychocylis* sp., dominated the heterotrophic ciliate biomass except for March and December (Fig. 5; Table 1). Athecate forms dominated the biomass of heterotrophic dinoflagellates except in July, when thecate forms of the genus *Protoperidinium* dominated the heterotrophic dinoflagellate biomass with 81% (Fig. 5; Table 1).

Protozooplankton growth rates

Experimentally determined growth rates of oligotrich ciliates and athecate dinoflagellates ranged from -0.3 ± 0.2 d^{-1} to 0.8 ± 0.4 d^{-1} (Table 2). The seasonal pattern in the daily protozoan production was similar for heterotrophic ciliates and dinoflagellates (Fig. 5). It peaked for both protozoan groups in April (52 and 85 mg C m^{-2} d^{-1} for heterotrophic ciliates and dinoflagellates, respectively) and was lowest in March and December. Ciliate production was negative in March.

Metazooplankton

Metazooplankton composition, abundance, and biomass were highly variable across seasons (Fig. 6). Variations in total abundance were essentially due to larval forms (i.e., copepod nauplii and meroplankton larvae) and showed a considerable maximum in May (5.6×10^3 ind. m^{-3}). Total biomass changed by an order of magnitude over time, from about 2.5 g C m^{-2} in March and May to 0.24 g C m^{-2} in December. In April, the metazooplankton biomass was 0.9 g C m^{-2} and consequently much lower than in March and May. Large copepodids dominated overall the community biomass, exceeding 90% in March, July, and September, but their contribution was as low as 40% in April and May. Large copepodids (stages IV–VI) of *Metridia* spp. were responsible for the very high biomass in March. Apart from March, large copepodids consisted almost exclusively of *Calanus glacialis* and *C. finmarchicus*.

The small copepod fraction (≤1 mm) consisted of cyclopoid and calanoid nauplii, as well as copepodids from small species. They represented 70–99% of total copepod abundance and 23–41% in terms of biomass in April, May, and December, but only 4–6% of biomass in March, July, and September. Copepod nauplii had a peak in abundance and biomass in May (2.4×10^3 ind. m^{-3} and 0.22 g C m^{-2}, respectively), and cyclopoid nauplii were observed at all seasons. Small copepodid abundance was fairly stable over the year ($0.22–0.54 \times 10^3$ ind. m^{-3}), and the biomass was maximal in April (0.21 g C m^{-2}), earlier than for copepodids of larger species. Among small copepodids, *Oithona similis* was a major component from May to December (54–85% in abundance; 13–63% in biomass). *Pseudocalanus* spp. showed an increased importance in April and July, whereas during March and December, *Microcalanus* spp., Oncaeidae, and three other orders (Harpactoida, Monstrilloida, and Mormonilloida) were significant contributors.

Meroplankton larvae were present in spring and summer only and consisted of cirripede nauplii in late spring (tripling from late April to late May, up to 1.2×10^3 ind. m^{-3}). Towards summer, veliger and pluteus larvae (about. 1.2×10^3 ind. m^{-3} and $0.1–0.2 \times 10^3$ ind. m^{-3} from late May to July) appeared. The meroplankton biomass

Table 2 Experimentally determined growth rates μ (average ± standard deviation; d^{-1}) of heterotrophic ciliates and dinoflagellates at 2 ± 1°C (March, April, May) and 4 ± 1°C (July, September)

Group	ESD (μm)	Vol. (μm^3)	Growth rate μ (d^{-1})				
			March	April	May	July	September
Ciliates							
Holotrichs		416	−0.270 ± 0.182				
Oligotrichs[a]	10–20	2,671	−0.072 ± 0.141	0.219 ± 0.094	0.318 ± 0.152	0.754 ± 0.514	−0.051 ± 0.095
	20–30	9,000		0.537 ± 0.110			
	>40	56,250		0.096 ± 0.039			
Dinoflagellates							
Protoperidinium spp.		2,000		0.275 ± 0.127			0.367 ± 0.292
Athecates[b]	10–20	2,220	0.259 ± 0.260	−0.026 ± 0.376	0.244 ± 0.209	0.796 ± 0.399	0.211 ± 0.134
	20–30	8,860		0.278 ± 0.164	0.716 ± 0.500		

[a] Dominated by *Strombidium* spp.

[b] Dominated by *Gymnodinium* spp. and *Gyrodinium* spp.

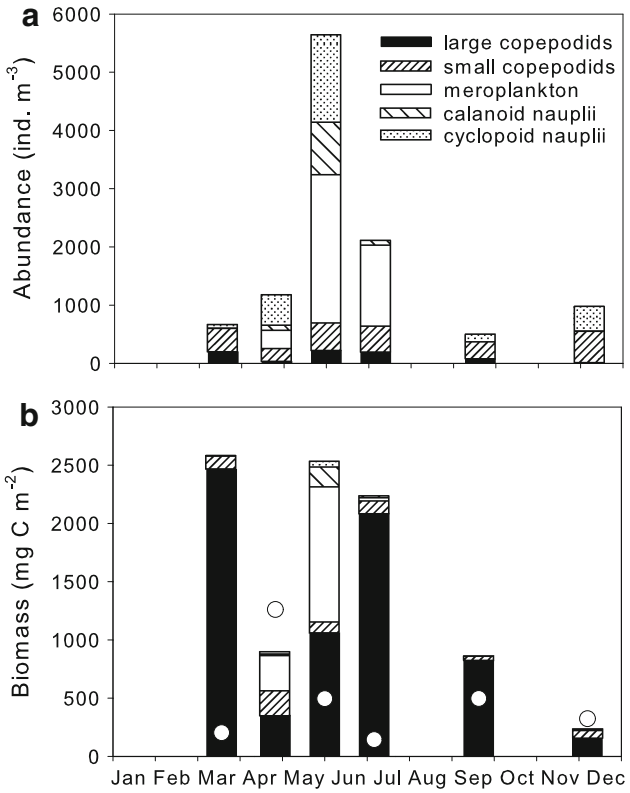

Fig. 6 Contribution of different developmental stages and size groups to the total metazooplankton (**a**) abundance (10^3 ind. m^{-2}) and (**b**) biomass (mg C m^{-2}; *bars*), integrated for 200–0 m. For comparison, protozoan biomass is given (mg C m^{-2}; *open circles*), integrated for the upper 200 m of the water column by using trapezoidal integration of the measured biomass at 50 m to an assumed biomass of zero at 200 m

contribution relied essentially on cirripede nauplii and was maximal in May (1.2 g C m^{-2}).

Protozooplankton (heterotrophic ciliate and dinoflagellate) biomass exceeded that of metazooplankton in April and December with a factor of 1.4 and 1.3, respectively (Fig. 6b), but was otherwise lower by a factor of <0.6.

Discussion

Biomass and taxonomic composition of proto- and metazooplankton

The total ciliate and dinoflagellate assemblage in Kongsfjorden was numerically dominated by aloricate ciliates, such as *Strombidium* spp., and athecate dinoflagellates of the genera *Gymnodinium* and *Gyrodinium* (Table 1), as reported from other marine ecosystems (Tillmann and Hesse 1998; Levinsen and Nielsen 2002; Sherr et al. 2009). In the purely heterotrophic fraction of the assemblage in Kongsfjorden, loricate ciliates were dominating. However, the contribution of loricate ciliates would have been significantly smaller if mixotrophic species, such as *Laboea strobila* and *Strombidium conicum*, would have been taken into account as part of the phagotrophic plankton, as done in other studies (e.g., Levinsen and Nielsen 2002). The biomass of heterotrophic ciliates and dinoflagellates observed in Kongsfjorden showed largely the same range as reported from other subarctic and arctic areas (Table 3).

In contrast to other Arctic systems, where heterotrophic dinoflagellates generally account for over half of the total protozooplankton biomass (Levinsen and Nielsen 2002; Sherr et al. 2009), ciliates dominated the protozooplankton in Kongsfjorden at most times (Fig. 5). These results are, however, heavily dependent on the classification of dinoflagellates (heterotrophic or phototrophic). In the present study, dinoflagellates were classified according to the description of chloroplasts of a given species in the literature. Thus, e.g., *Heterocapsa triquetra* was classified

Table 3 Mean standing stocks (μg C l^{-1}) of heterotrophic ciliates, dino-, and nanoflagellates (Dino. and Flag.) reported from different subarctic and arctic areas

Region	Months	Depth	Biomass (μg C l^{-1})			References
			Ciliates	Dino.	Flag.	
Kongsfjorden	Mar–Dec	0–50	1–5	0.5–9		This study
	Mar–Dec				0.1–11	Rokkan Iversen and Seuthe (accepted)
Norwegian fjord	April	0–120	18	17	23	Archer et al. (2000)
Barents Sea	Jun–Jul	1	3–9	4–10	3–10	Verity et al. (2002)
	May	0–100	≤8[a]	≤34[a]		Jensen and Hansen (2000)
	May	0–60	≤24[b]	≤35[b]	≤14[b]	Hansen et al. (1996)
	Mar–Jul	0–90	≤18[c]	0.1–9	3–120[d]	Ratkova and Wassmann (2002)
Greenland Sea	Aug–Sep	0–100	0.1–20			Antia (1991)
Fram Strait	Jun	0–100	0.2–17			Auf dem Venne (1994)
NE Greenland fjord	Jun–Aug	0–35	0.6–4	0.6–2		Rysgaard et al. (1999)
W Greenland	Jul–Sep	0–30	5–24	2–32		Levinsen et al. (1999)
	14 months	0–200	<0.1–4	<0.1–6		Levinsen et al. (2000)
	Mar–May	1+15	<1–6	<1–20		Madsen et al. (2008)
	Jun–Jul	0–30	7–20	10–16	2–5	Nielsen and Hansen (1995)
Franklin Bay	Dec–Mar	0	0.3		2	Vaqué et al. (2008)
	Mar–May		0.4		4	
Canada Basin/Chuckchi Sea	May–Aug	Chl max	0.5–25	0.8–53		Sherr et al. (2009)
Gulf of Alaska	May–Sep	0–80	2–6	0.6–3	2–10	Booth et al. (1993)
SE Bering Sea	Apr	0–70	0.1–5	0.2–5		Howell-Kübler et al. (1996)
Arctic Ocean (Makarov Basin)	Aug	0–25	≤5	≤9	≤38[e]	Olli et al. (2007)

The biomasses are the integrated mean over the given depth ranges or concentrations of single depths (m)

[a] Maximum biomass values estimated from Fig. 4

[b] Maximum biomass values estimated from Fig. 3

[c] Value estimated from Fig. 6

[d] Calculated from Table 4 taking cryptophytes, chrysophytes, and choanoflagellates into account

[e] Calculated from Table 3 taking cryptophytes, chrysophytes, prymnesiophytes, and zoomastigophores into account

Table 4 Integrated biomass (0–50 m) of heterotrophic protozooplankton (pico-, nano-, and microprotozooplankton), and the contribution of the different size groups (in percentage, %) in Kongsfjorden in 2006

Month	Protozoooplankton	Proportion of total protozooplankton biomass (%)			
	(mg C m^{-2})	Picoplankton	Nanoflagellates	Dinoflagellates	Ciliates
Mar	89	0.1	7	30	63
Apr	796	<0.1	9	57	34
May	132	0.1	8	35	57
Jul	635	0.4	87	4	8
Sep	323	0.1	20	38	42
Dec	161	0.1	15	28	57

Biomass values on heterotrophic pico- and nanoplankton are taken from Rokkan Iversen and Seuthe (accepted)

as phototroph (Thomas 1997). This species has, however, been observed to ingest fluorescently labelled algae (Legrand et al. 1998). Similarly, food vacuoles have been noticed in *Scripsiella* sp. (Jacobsen and Anderson 1996), another species here excluded from the biomass of heterotrophic dinoflagellates. Consequently, the contribution of heterotrophic dinoflagellates to the total protozooplankton biomass may have been underestimated in the present study. Interestingly, heterotrophic dinoflagellates contributed more to the total protozooplankton biomass in April and September (Fig. 5; Table 4) when diatoms were abundant (Fig. 3b), mirroring the ability of dinoflagellates

to efficiently feed on large-celled phytoplankton (Hansen 1991; Sherr and Sherr 2007).

Combined reports on heterotrophic ciliate, dinoflagellate, and nanoflagellate biomasses from Arctic areas are scarce (Table 3), but where all three groups were investigated simultaneously, their biomasses were either of the same magnitude (Booth et al. 1993; Verity et al. 2002) or the biomass of ciliates and dinoflagellates dominated over that of nanoflagellates (Nielsen and Hansen 1995). Where nanoflagellates were reported to dominate the protozooplankton biomass, the system appeared to be in a low productive state, e.g., under the land-fast ice in winter–spring (Vaqué et al. 2008), or the central Arctic Ocean (Olli et al. 2007). In Kongsfjorden, heterotrophic ciliates and dinoflagellates greatly dominated the total protozooplankton biomass at all times, except in July when heterotrophic nanoflagellates constituted 87% of the total protozooplankton biomass (Table 4), coinciding with high abundances of phototrophic picoplankton (Rokkan Iversen and Seuthe *accepted*).

The metazooplankton biomass was in the range reported previously from Kongsfjorden during summer (Hop et al. 2002). As characteristic for arctic and subarctic copepod communities, the metazooplankton was dominated by small copepods, such as *Oithona similis*, in terms of numbers, while large calanoid copepods, such as *Calanus* spp., dominated the zooplankton biomass (Arashkevich et al. 2002; Ashjian et al. 2003; Hopcroft et al. 2005). As typical for shallow coastal Arctic waters (Turner et al. 2001) and shelf seas (Pasternak et al. 2008), high abundance and biomass of meroplankton added a strong seasonal signal to the metazooplankton assemblage. In addition, copepod nauplii exhibited high abundance in May, which is in accordance with earlier reports from Kongsfjorden (Lischka and Hagen 2005).

Proto- and metazooplankton composition and biomass in Kongsfjorden thus did not differ profoundly from those of other Arctic ecosystems and heterotrophic ciliates and dinoflagellates dominated over heterotrophic flagellates at most times.

Growth and potential bottom-up control of protozooplankton

The experimentally determined growth rates of heterotrophic ciliates and dinoflagellates in Kongsfjorden (Table 2) were within the range reported previously from cold waters (Levinsen et al. 1999; Hansen and Jensen 2000; Møller et al. 2006). In March, positive growth was only observed for heterotrophic athecate dinoflagellates in the size class 10–20 µm, while heterotrophic ciliates decreased in abundance in the incubation bottles over time. Negative growth rates were reported previously in similar experiments and have been argued to reflect trophic interactions between protozooplankton, with dinoflagellates most likely preying on ciliates (Hansen et al. 1999; Møller et al. 2006). Predation by dinoflagellates on ciliates may have constituted a possible source of nutrition in the relatively food-poor environment in March.

Concentrations of food thresholds have been discussed for heterotrophic ciliates and dinoflagellates in the literature, but divert greatly between species (e.g., Jakobsen and Hansen 1997; Gismervik 2005). In a recent review of culture-based growth studies, Sherr and Sherr (2009) found maximal growth rates of heterotrophic ciliates and dinoflagellates reduced by 50% at food concentrations of 0.25–5 µg Chl *a* l^{-1} and to be zero at 0.1–2 µg Chl *a* l^{-1}. According to these thresholds, no growth of heterotrophic ciliates and dinoflagellates should have occurred in Kongsfjorden in March and December, when Chl *a* concentrations were <0.1 µg l^{-1} (Fig. 3a). The persistence and even low growth of protozooplankton in similar food-poor conditions have been related to possible patches of higher food concentration, which are successfully detected and exploited by protozoans (Jakobsen and Hansen 1997; Paffenhofer et al. 2007). Interestingly in March, the encountered ciliate assemblage consisted almost exclusively of holotrichs and *Myrionecta rubra* (Table 1). Holotrich ciliates have been observed to be bactivorous in low-productive environments (Sime-Ngando et al. 1999), and *M. rubra* depends on very low prey abundance to retrieve chloroplasts for its phototrophic mode (Smith and Hansen 2007). It thus appears that the scarcity of potential food in March selected for certain groups of ciliates.

Growth rates by heterotrophic ciliates and dinoflagellates were largely enhanced in spring and summer (Table 2), when Chl *a* concentrations had increased by a factor of 11–615 (Fig. 3a). Both ciliates and dinoflagellates prey on a large variety of food, depending on own cell size and feeding strategy (Pierce and Turner 1992; Jeong 1999). In general, ciliates are thought to have a narrower predator-size to prey-size ratio than dinoflagellates (Hansen et al. 1994). Tintinnids, which dominated the heterotrophic ciliate biomass in Kongsfjorden, have been described to consume primarily nano-sized (2–20 µm) prey, while the aloricate-dominating oligotrichous ciliates mainly graze on cells <10 µm (Pierce and Turner 1992, and references therein). Nevertheless, ciliates have also been observed to feed on diatoms (Aberle et al. 2007). Consequently, ciliates should have encountered a rich grazing ground in Kongsfjorden from April onwards, when pico- and nanoplankton were highly abundant (Rokkan Iversen and Seuthe *accepted*). The ability of many dinoflagellates to efficiently graze on diatoms was reflected in their co-occurrence with elevated diatom abundances in Kongsfjorden in April and September. Especially the pallium-feeding thecate

Protoperidinium spp. showed increased abundance in conjunction with diatoms (Table 1), as seen previously in other marine systems (e.g., Hansen 1991; Sherr and Sherr 2007). Athecate dinoflagellates, such as the dominating *Gymnodinium* spp. and *Gryrodinium* spp., also responded to the increased abundance of large phytoplankton in April and September. However, due to their feeding strategy by direct engulfment of prey, these protozoans are able to feed on a larger prey-size spectrum (Jeong 1999), which was mirrored in their more even abundance throughout the year (Table 1).

Heterotrophic ciliates and dinoflagellates in Kongsfjorden thus appeared to have been controlled by food concentration in March and December, while adequate food should have been available from the spring bloom onwards. Consistently, the variance in protozooplankton biomass observed in Kongsfjorden over the year was best explained by food concentration, such as total Chl *a* for ciliates (multiple linear regression: $F_{1,34} = 27.568$, $P < 0.001$, $r^2 = 0.448$) and Chl $a > 10$ μm for dinoflagellates (multiple linear regression: $F_{1,34} = 57.655$, $P < 0.001$, $r^2 = 0.629$), rather than in situ temperature. Consequently, other controlling mechanisms must have acted during the other times, when prey availability was high but heterotrophic ciliate and dinoflagellate abundance was low.

Potential top-down control of the protozoan stock by copepods

The large calanoid copepods, *Calanus* spp., are known to prey on protozooplankton (Levinsen et al. 2000; Campbell et al. 2009), making them apparent candidates for controlling ciliate and dinoflagellate stocks due to their high biomass and ingestion rates. *Calanus hyperboreus*, for instance, accounted for a daily loss of the protozoan stock of 5–6% in the Greenland Sea (Antia 1991). A suite of studies also reported *C. finmarchicus* (Ohman and Runge 1994; Nejstgaard et al. 1997; Irigoien et al. 1998) and *C. glacialis* (Campbell et al. 2009) to select positively for ciliates. However, large seasonal and individual variations in the contribution of protozoan to the copepods diet prevail (Koski and Wexels Riser 2006; Castellani et al. 2008; Campbell et al. 2009). For example, most of the daily ingestion of *C. finmarchicus* consisted of protozooplankton during a post-bloom scenario in Disko Bay (Greenland), while this diet component was negligible during the early phase of a phytoplankton bloom (Levinsen et al. 2000).

Levinsen et al. (2000) reported clearance rates of *Calanus* spp. of 1 and 4 ml (μg C)$^{-1}$ d^{-1} on ciliates of ESD 15 and 50 μm, respectively, and 0.5 and 2 ml (μg C)$^{-1}$ d^{-1} on dinoflagellates ESD 15 and 50 μm, respectively. Calculations of the potential grazing impact of *C. finmarchicus* and *C. glacialis* on heterotrophic ciliates and dinoflagellates in Kongsfjorden, applying these literature values and correcting for temperature with a Q_{10} of 2.8 (Hansen et al. 1997), revealed a different scenarios during the spring bloom and the post-bloom summer situation. In April, the calculated daily *Calanus* ingestion was 3 and 19 times lower than that of daily heterotrophic ciliate and dinoflagellate production, respectively. Since the clearance rates of *Calanus* on protozoans seem to decrease during rich phytoplankton blooms (Levinsen et al. 2000), these calculations most likely even overestimate the grazing impact during spring. Therefore, the two *Calanus* species exerted little or no control on the protozoan stock in Kongsfjorden in April. At the same time, small omnivorous calanoid copepods, such as *Pseudocalanus* sp., constituted equally in biomass and may have contributed to the grazing on protozoans by their higher specific grazing rates (Levinsen et al. 2000; Campbell et al. 2009). In the period after the spring bloom (May, July, and September), *Calanus* spp. daily ingestion of dinoflagellates never accounted for >10% of the daily dinoflagellate production, but the ingestion of ciliates exceeded their heterotrophic production in July. Moreover, also the ubiquitous small copepods *Oithona similis* and *Pseudocalanus* spp. (Møller et al. 2006; Castellani et al. 2008), as well as the periodically highly abundant copepod and cirripede nauplii (Turner et al. 2001), are known to prey on ciliates and dinoflagellates. Consequently, metazooplankton may well have had a controlling impact on the protozoan stock during the post-bloom period in Kongsfjorden.

Due to the great plasticity in behaviour and prey selectivity of copepods, calculations of the possible grazing impact by copepods from literature values have to be interpreted with caution. It is, however, striking that the maximum protozoan biomass in our data set occurred in concert with a low abundance of large copepods and a two times lower metazooplankton biomass compared to May and July. In April, heterotrophic ciliates and dinoflagellates dominated the total zooplankton (protozoan and metazoan) biomass (58%, Fig. 6b). During the post-bloom period, also the structure of the food web indicated that top-down control was an important controlling factor for the protozoan assemblage. This was suggested by (a) low abundances of large protozoan despite high abundances of their flagellate prey and (b) high concentrations of metazooplankton and large calanoid copepods at times when >70% of the Chl *a* was in the size fraction <10 μm (Rokkan Iversen and Seuthe *accepted*) and therefore unavailable to a large fraction of the metazooplankton. Thus, especially during the post-bloom period, the structure of the protozoan assemblage must have partly been dependent on dynamics of the metazooplankton.

Protozooplankton regulation and potential grazing impact

In Disko Bay, western Greenland, Levinsen and Nielsen (2002) attributed high biomasses of protozooplankton to periods with low predation by copepods, either because copepods were satiate by phytoplankton (i.e., during the spring bloom) or because copepods were absent from the euphotic zone (as in late summer after the descend of *Calanus* spp. to overwintering depths). The authors suggested that heterotrophic ciliates and dinoflagellates should be important grazers in all arctic ecosystems, where protozoan can escape the grazing pressure in periods. In Kongsfjorden, the time of the phytoplankton spring bloom must have been a period of reduced top-down control for ciliates and dinoflagellates, due to moderate abundance of large copepods in conjunction with high concentration of phytoplanktonic food. The protozooplankton could thus build up a significant biomass in concurrence with the spring phytoplankton bloom in April.

Calculations of the potential grazing rate of heterotrophic ciliates and dinoflagellates from their likely daily production (Fig. 5), assuming a gross growth efficiency of 33% (Hansen et al. 1997), indicated that protozooplankton could have grazed equivalent to 100% of the daily primary production in April. This calculation assumed complete algaevory, which most probably does not reflect the true composition of the diet of ciliates and dinoflagellates. Nevertheless, it illustrates the great potential of protozooplankton to cycle a significant fraction of primary production even under phytoplankton bloom conditions. The higher biomass of protozooplankton compared to metazooplankton in April, in combination with an order of magnitude greater specific ingestion rates of protozoans than copepods (Hansen et al. 1997 and references therein), suggests further that heterotrophic ciliates and dinoflagellates were the principal grazers in Kongsfjorden under these conditions. In the post-bloom period, the potential grazing impact of protozooplankton was reduced to 26% (May) and 56% (July) of the daily primary production. At this time, picoplankton and nanoflagellates dominated the phytoplankton (Rokkan Iversen and Seuthe *accepted*), and thus a large fraction of primary producers may have been too small for copepods to utilize directly. Under these conditions, heterotrophic ciliates and dinoflagellates may have constituted an important trophic link between microbial primary producers and the larger copepods.

Conclusion

The present study demonstrates that ciliates and dinoflagellates were an important component of the pelagic food web in Kongsfjorden and did not differ in their biomass from other Arctic and subpolar regions. Food availability may have limited heterotrophic ciliates and dinoflagellates in March and December, while predation by copepods was most probably the controlling factor on the protozoan community in May, July, and September. High biomass of heterotrophic ciliates and dinoflagellates was observed in April during the phytoplankton spring bloom, coinciding with moderate abundance of large copepods. The observed regulatory mechanisms of the protozooplankton community in Kongsfjorden thus did not differ from those in other regions. The importance of the protozooplankton in the pelagic food web of Kongsfjorden was reflected in the calculated potential grazing impact of the protozoan community, which suggested a strong control of the phytoplankton by heterotrophic ciliates and dinoflagellates. Consequently, ciliates and dinoflagellates need to be taken into account when discussing the fate of phytoplankton and biogeochemical cycling in Arctic marine ecosystems.

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