Structure and function of the pelagic ecosystem in Young Sound, NE Greenland

Torkel G. Nielsen[1], Lars D. Ottosen[2*] & Benni W. Hansen[3]

[1]Department of Marine Ecology, National Environmental Research Institute, PO Box 358, DK-4000 Roskilde, Denmark
[2]Unisense A/S, Brendstrupgaardsvej 21F, DK-8200 Aarhus N, Denmark
[3]Department of Life Sciences and Chemistry, Roskilde University, PO Box 260, DK-4000 Roskilde, Denmark
[*]Present address: Skejby Sygehus, Aarhus University Hospital, Fertility Clinic, Brendstrupgaardsvej 100, DK-8200 Aarhus N, Denmark

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Abstract

An annual carbon budget of the pelagic food web is constructed for a 36 m deep station in Young Sound. Data were collected during a 2-week mid-summer sea-ice covered period in 1999, during the open-water period of 1996, 2003, 2004, 2005 and during winters of 1997 and 2003. The measurements revealed that during sea-ice cover the water column of outer Young Sound was strongly heterotrophic and sustained by organic material advected into the fjord from the open sea. The pelagic community thus originated from the marginal ice zone at the entrance to the fjord. No succession was observed in the plankton community during this period, and the grazing pressure of the dominating zooplankton groups (ciliates, heterotrophic dinoflagellates, meroplankton and copepods) was 10 times higher than primary production, while the bacterial carbon demand was three times higher than primary production.

During the open-water period, the grazing community was completely dominated by copepods, which were capable of grazing down the entire primary production. This contrasts with several other investigated Arctic marine pelagic ecosystems further south, where the protozooplankton community is quantitatively more important than copepods. In Young Sound, both zooplankton groups are present simultaneously, and copepods thus act both as competitors for food and as predators in relation to the protozooplankton. On an annual basis, the carbon budget was unbalanced; the total carbon need of the grazers equaled primary production, leaving no room for the estimated bacterial carbon demand, which was of the same size as the carbon demand of the grazers. Thus, Young Sound is a net heterotrophic system relying on import of organic material from the open sea or possibly from land.

5.1 Introduction

Deep fjords are characteristic elements of the Greenland coastline (Chapter 3). They constitute a key element in the land-ocean interface and, consequently, in the nutrient and carbon dynamics of the coastal zone. In the Young Sound the freshwater input is very pulsed and the main impact is associated with the flushing of the Zackenberg River around midsummer (Chapter 2). This freshwater input creates a stratification of the upper part of the water column through establishment of a strong halocline, which is further strengthened by solar heating of the surface water. Consequently, the freshwater input has major implications for the stratification of the fjord and thus the vertical distribution and production of plankton in fjord systems (Rysgaard et al., 1999; Chapter 3).

In the past, most pelagic food-web investigations off Greenland have been associated with fisheries research and exploitation of the marine resources,

and the main focus has been on primary production (Smidt, 1979) and the distribution of mesozooplankton, i.e. the direct link to the fish stocks (Jespersen, 1934; Ussing, 1938; Smidt, 1979; Digby, 1953). These investigations have demonstrated the prominent role of the large copepod genus *Calanus* in the plankton around Greenland. But information about the pelagic ecology and the potential role of the other potential components of the food web is limited.

Knowledge about plankton dynamics in ice-covered Arctic fjords is scarce. Because of the thick ice cover the pelagic primary production is insignificant and the primary production is predominantly associated with the ice-water interface. This continues until sea-ice break-up, when ice algae, if any, are released to the water column and the pelagic primary producers start to flourish. Young Sound is normally ice-covered until mid-summer and is only open for a few months (Chapter 4).

During the last decades, methodological and technical advancements and process-oriented scientific approaches have demonstrated a more diverse picture of the Arctic pelagic ecosystem, in which the microbial food web has a key role (Levinsen & Nielsen, 2002). In an earlier study in Young Sound, the seasonal cycle of the pelagic food web (Rysgaard et al., 1999) suggested that the large *Calanus* copepods dominated pelagic grazing, and that all activity was restricted to the short open-water period. This contrasts with investigations in the Disko Bay, W. Greenland (Levinsen & Nielsen, 2002) where the protozooplankton community is highly important in the re-cycling of primary production. This difference is caused by strong predation on protozooplankton by copepods, as these co-occur in the short production window associated with the open-water period of Young Sound (Levinsen et al., 2000b).

The present investigation primarily presents a measuring campaign prior to sea-ice break with high radiation and unlimited nutrients, and the major purposes were to 1) describe the most important pelagic processes during this period, 2) resolve the pelagic dynamics under the ice cover, 3) evaluate the pelagic carbon flow pathways through establishment of a budget for the pelagic during June 1999 and compare this with previous investigations during the open-water period (Rysgaard et al., 1999), and, finally, 4) establish an annual pelagic carbon budget for Station A in Young Sound.

5.2 Methods

The present chapter combines the annual study conducted in 1996 (Rysgaard et al., 1999) with an ice-cover campaign carried out from 11 to 27 June 1999 in Young Sound prior to sea-ice break-up. Furthermore, data are included from the MarineBasic monitoring program during the ice-free period of 2002, 2004, 2005 as well as from research programs during the winters of 1997 and 2003. The applied methods and measured parameters were the same in all studies except that bacteria and nanoflagellates were considered only in 1999. All samples were taken around noon at a 36 m deep station (Station A; Fig. 5.1) through a hole in the ice, using a hand-driven winch and a tripod. Depth profiles of temperature, salinity and fluorescence were recorded throughout the water column using a CTD (DataSonde4 Hydrolab, Austin, USA) with a calibrated Dr. Hardt fluorometer. The salinity probe was calibrated against water samples collected at 5 to 7 depths per sampling day and measured in the laboratory using a Guildline Salinometer. Based on the water column structure and the depth distribution of fluorescence profiles, 7 depths (1, 2, 5, 10, 15, 25 and 35 m) were selected for further chemical and biological measurements. Water samples were collected using a 5-l Niskin bottle. Samples for the determination of nutrient concentrations (NO_2^-, NO_3^-, PO_4^{3-}, SiO_4^{3-}) were frozen immediately and measured at the National Environmental Research Institute (NERI) according to Nielsen & Hansen (1995).

Subsamples, some of them size fractionated, of 100–200 ml for chlorophyll a (Chl *a*) and phaeopigment (Phaeo.) were collected within 4 hours of sampling and processed according to Jespersen & Christoffersen (1987) and Strickland & Parsons (1972). To convert to carbon, 600 ml of seawater was filtered in duplicate onto pre-muffled GF/F filters and stored at -20°C until analysis. Filters were dried in a desiccator and analyzed for carbon on a CHN analyzer (EA 1110 CHNS, CE Instruments).

Primary production was measured *in situ* using the ^{14}C method (Steemann-Nielsen, 1952). Water samples from each of the selected depths were incubated for 2 h around noon (2 light and 1 dark Jena bottles; 100 ml) containing 4 µCi $H^{14}CO_3^-$ (International Agency for ^{14}C Determination) according to Nielsen & Hansen (1995). Daily primary production per m^2 was calculated by extrapolating to diurnal irradiance at the respective water depths by trapezoidal depth integration down to 36 m.

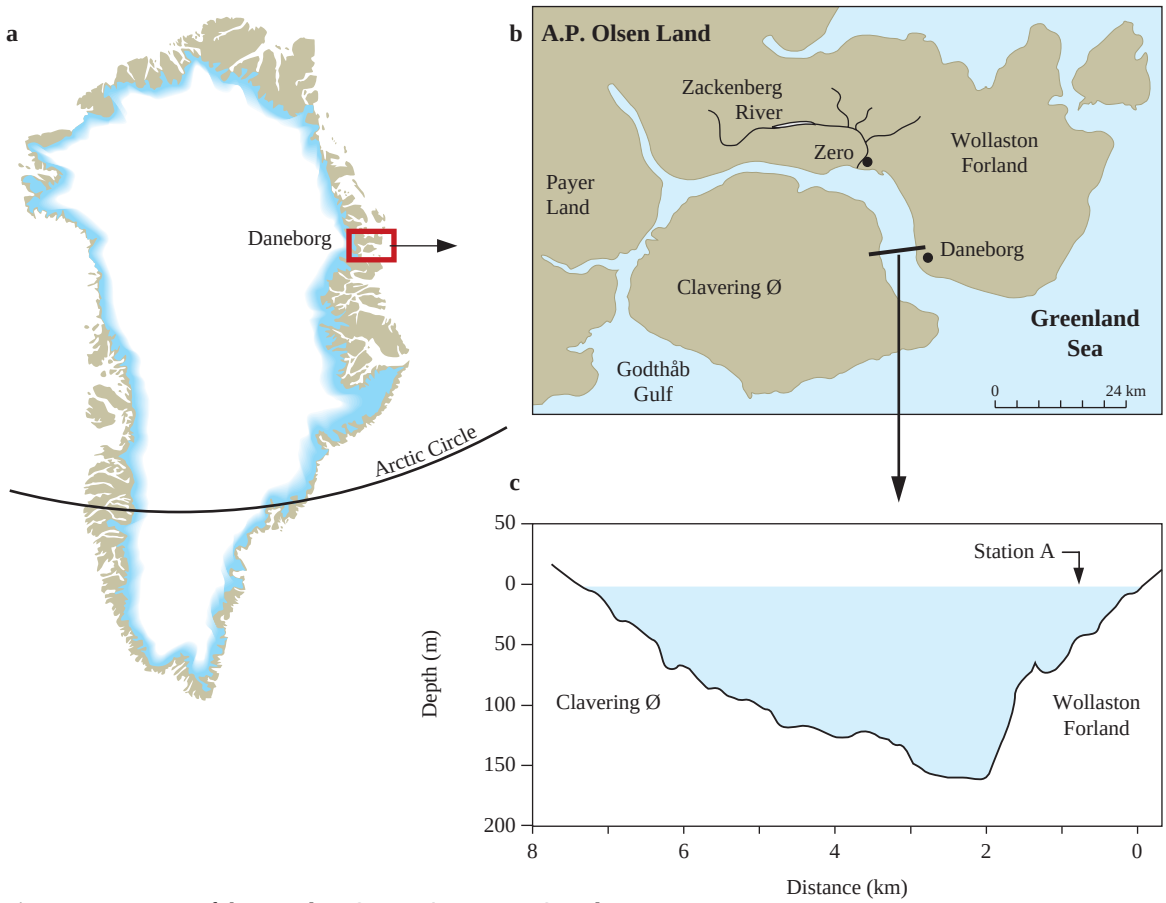

Figure 5.1 Position of the sampling Station A in Young Sound.

Bacterial abundance was quantified on a FACS Calibur flow cytometer (Becton Dickinson) after staining of the fixed cells with the nucleic acid stain SYBR Green 1 (Molecular Probes) according to Marie et al. (1997). Bacterial volume was determined on slides stained with acridine orange (0.1%) and at least 50 cells per slide were analyzed using digital image analysis. Biovolumes were converted to biomass using a carbon-to-volume factor of 0.22 pg C μm^{-3} (Bratbak & Dundas, 1984).

Bacterial production was measured by incorporation of ^{3}H-thymidine (Fuhrman & Azam, 1980) using the assumptions of Riemann et al. (1987). The carbon requirement of the bacterioplankton was estimated assuming a growth efficiency of 33% as for the other heterotrophic components of the pelagic food web (Hansen et al., 1997).

The abundance of heterotrophic nanoflagellates and diatoms < 20 µm was determined by epifluorescense microscopy of filters stained with proflavine (Haas, 1982) and processed according to Nielsen & Hansen (1995). A 500-ml water sample for enumeration of heterotrophic/mixotrophic protozoa was fixed in 1% Lugol's solution (final concentration), and a subsample of 50 or 100 ml was counted after 24 hours of sedimentation using an inverted microscope. Biovolumes of cells were estimated from measurements of linear dimensions assuming simple geometrical shapes and converted to biomass according to Edler (1979). To investigate the population dynamics of the microprotozooplankton, a microcosm experiment was conducted. On 12 June, three 25-l Nalgene polycarbonate carboys were filled with 20 l of water from just below the ice. The growth potentials of ciliates and dinoflagellates were followed in a mesozooplankton-free incubation, i.e. surface water < 45 µm. A carboy spiked with 300 ml *Rhodomonas salina* culture (6×10^{5} cells ml^{-1}) and a carboy with sieved surface water served as controls. A diver placed the carboys under the ice about 10 m from the hole to

Table 5.1 Young Sound June 1999. Length vs. weight regressions used to provide biomass estimates for the individual mesozooplankton groups. Individual biomass (mg C) = $a \times L_{(\mu m)}^{b}$. Carbon = 0.45 × Dry weight.

Taxa	a	b	Reference
Calanus finmarchicus	$4.45x10^{-3}$	3.3838	Hirche and Mumm (1992)
Calanus glacialis	$4.45x10^{-3}$	3.3838	Hirche and Mumm (1992)
Calanus hyperboreus	$1.40x10^{-3}$	3.3899	Hirche and Mumm (1992)
Metridia longa	$6.05x10^{-3}$	3.0167	Hirche and Mumm (1992)
Acartia spp.	$1.11x10^{-11}$	2.92	Berggreen et al. (1988)
Pseudocalanus spp.	$0.45x(1.22x10^{-10})$	2.7302	Klein Breteler et al. (1982)
Microcalanus spp.	$9.47x10^{-10}$	2.16	Sabatini and Kiørboe (1995) as *Oithona* sp.
Oithona spp.	$9.47x10^{-10}$	2.16	Sabatini and Kiørboe (1995)
Oncaea spp.	$9.47x10^{-10}$	2.16	Sabatini and Kiørboe (1995) as *Oithona* sp.
Microsetella spp.	$8.5x10^{-5}$	1.0275	Satapoomin (2000)
Nauplii spp.	$4.17x10^{-9}$	2.03	Hygum et al. (2000)
Bivalvia	$3.06x10^{-11}$	2.88	Fotel et al. (1999)
Thecosomata			$2.27x10^{-2}$ ind^{-1} Beers (1996)
Gastropoda	$2.31x10^{-8}$	2.05	Hansen and Ockelmann (1991)
Polychaeta	$1.58x10^{-7}$	1.38	Hansen (1999) as *Polydora* spp.
Hyperiidae	$1.40x10^{-3}$	3.3899	Hirche and Mumm (1992) as *Calanus hyperboreus*
Decapoda			$2.50x10^{-1}$ ind^{-1} Uye (1982)
Echinodermata	$3.06x10^{-11}$	2.88	Fotel et al. (1998) as Bivalvia
Appendicularia	$7.33x10^{-11}$	2.627	King et al. (1980)
Others	$3.06x10^{-11}$	2.88	Fotel et al. (1999) as Bivalvia

avoid the altered light regime in the vicinity of the hole (Chapter 4).

Mesozooplankton were sampled from the bottom to the surface by triplicate vertical hauls using a modified WP-2 net (45-µm mesh) equipped with a flowmeter (Digital Model 438 110, Hydro Bios) and a large flow-meter non-filtering cod-end. The samples were preserved in buffered formalin (2% final concentration) and at least 300 individuals were analyzed. To distinguish between copepodites of *Calanus* spp., the cephalothorax length criteria of Madsen et al. (2001) were used. Copepod nauplii were not distinguished to species, but according to size the majority was *Calanus* spp. Biomass of meroplanktonic organisms and planktotrophic holoplankton other than copepods was calculated from length measurements. Individual biomass of all mesozooplankton was calculated according to length regressions taken from the literature (Table 5.1).

To determine egg production by free-spawning species of copepods, a sample of gently collected zooplankton was diluted with surface water and brought to the laboratory. Production of eggs by *Calanus glacialis* and *C. finmarchicus* and the fraction of reproductively active females were measured by incubating individual females in 600-ml polycarbonate bottles filled with 50-µm sieved *in situ* water (at least 12 replicates) for approximately 24 h. The bottles were incubated in the dark in a thermo box covered with snow to mimic *in situ* temperature. At the end of the experiments, the spawned eggs were counted and egg size was measured on a batch of eggs. Weight-specific egg production (SEP) was calculated from individual female carbon content according to Hirche & Mumm (1992) assuming a body carbon:dry weight ratio of 0.6 (Eilertsen et al., 1989), and an egg carbon content of 0.14 pg C μm^{-3} (Kiørboe et al., 1985). The egg production and SEP of egg-carrying *Oithona* spp. was calculated according to the equations in Nielsen et al. (2002). Egg numbers in sacs from at least 25 individuals per net

haul were counted. Secondary production by all the copepods was calculated from the weight-specific egg production of *C. glacialis* for the calanoids and *Oithona* for the non-calanoid copepods, assuming juvenile somatic growth rates resembling SEP (Berggreen et al., 1988). Copepod community grazing was assumed to be 3 times SEP as in Hansen et al. (1997). Meroplankton (all considered as planktotrophic) and planktotrophic holoplankton other that copepods were assumed to have a specific growth rate of 0.05 d^{-1} (Hansen et al., 1999) and be grazed by the same efficiency as for the copepods (Hansen et al., 1997).

To establish a pelagic carbon budget for the sea-ice campaign in 1999, mean ± SE of depth-integrated values of biomass, carbon demand and production of all components in the pelagic are presented in a flow chart as mg C m^{-2} d^{-1}. In the case of heterotrophic nanoflagellates, ciliates and heterotrophic dinoflagellates, of which rates were not measured, daily clearance (F) was calculated according to Hansen et al. (1997) and grazing (I) as I = F × C, where C is the integrated prey biomass. Production was calculated by assuming a growth efficiency of 33% (Hansen et al., 1997). Secondary production of all copepods was calculated by multiplying the specific egg production (SEP) by total copepod biomass. Ingestion was calculated by assuming a growth efficiency of 33% (Hansen et al., 1997).

The annual carbon budget for the pelagic community in Young Sound was approximated by combining the present data set from June with the data from 1996 (Rysgaard et al., 1999). In the case of bacteria, which were not included in the 1996 study, the annual production was calculated assuming that the midwinter value obtained in 2005 by Rysgaard et al. (*in press*) of 3.1 mg C m^{-2} d^{-1} represents 271 d, the present investigation covering 14 days during the ice cover, and the bacterial production during the open-water period (80 d) is calculated as 20% of the primary production according to Rysgaard et al. (1999).

5.3 Results

5.3.1 Hydrography, nutrients and chlorophyll

The locality sampled was covered with 1.8 m of sea ice and was strongly influenced by advection, so no clear succession pattern of the water column characteristics could be identified during the 1999 campaign. Consequently, the depth distributions of physical and chemical parameters are presented as averages (Fig. 5.2 and Table 5.2). In particular, the water-column salinity was highly variable. Just below the ice the salinity was 30.6, decreasing to a minimum of 28.3 1 m below the ice, from where it increased to 32.0 at 10 m and gradually to 32.6

Figure 5.2 Young Sound June 1999. Vertical distribution of **(a)** Salinity, **(b)** Temperature (°C), **(c)** Nutrients (dark blue) phosphorus, (light blue) nitrate , (red) silicate and **(d)** Chlorophyll *a* concentration (µg Chl *a* l^{-1}).

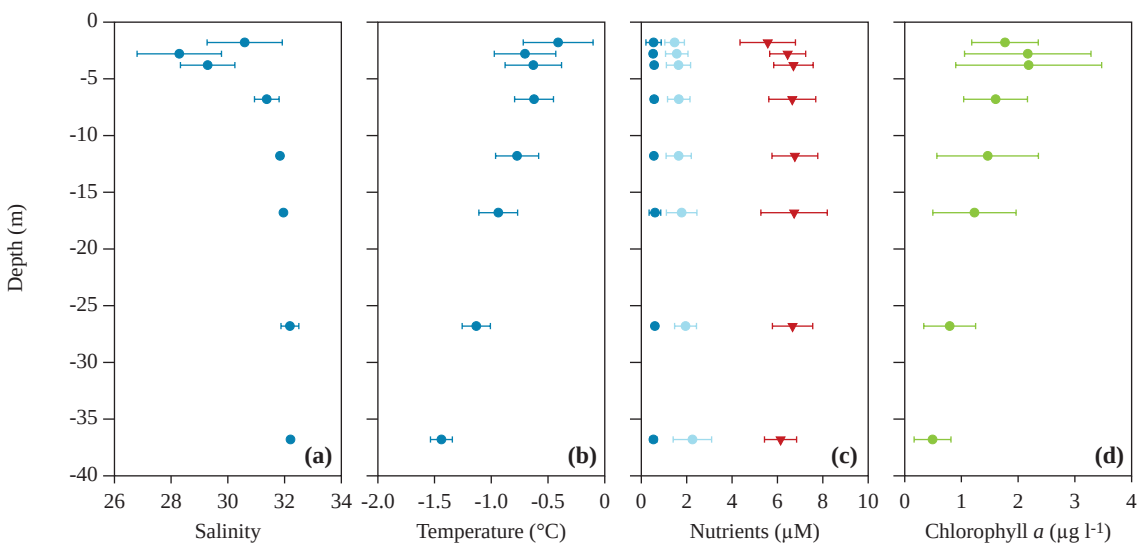

Table 5.2 Young Sound June 1999. Water column characteristics at the sampling depths, mean ±SD, range (min-max) and %CV (= SD/mean × 100) of parameters considered.

Depth (m)	Salinity	Temp. (°C)	PO_4 (µM)	NO_3 (µM)	SiO (µM)	Chl a (µg l^{-1})
0	30.59±1.32 27.09-31.74 4.33	-0,41±0,31 -1.03-0.03 75	0.54±0.34 0.29-1.35 62	1.47±0.43 0.95-2.13 29	5.58±1.22 3.34-7.40 22	1,77±0.59 0.50-2.27 33
1	28.29± 0.49 26.13-30.27 5.26	-0,70±0,27 -1.00-0.15 39	0.52±0.14 0.26-0.69 27	1.57±0.50 0.85-2.33 32	6.45±0.79 5.11-7.24 12	2,17±1.11 1.19-4.81 51
2	29.29±0.96 27.91-30.76 3.27	-0,63±0,25 1.01-0.15 40	0.57±0.13 0.36-1.73 23	1.64±0.53 1.08-2.45 33	6.71±0.87 5.15-7.58 13	2,19±1.29 1.10-5.26 59
5	31.37±0.43 30.54-31.84 1.38	-0,62±0,17 -0.93-0.42 27	0.57±0.15 0.34-0.75 26	1.65±0.50 0.89-2.42 30	6.66±1.03 4.86-7.63 16	1,60±0.56 0.74-2.22 35
10	31.84±0.11 31.63-32.01 0.34	-0,77±0,19 -1.03-0.47 25	0.56±0.11 0.40-0.78 20	1.65±0.55 0.68-2.34 34	6.77±1.01 5.06-8.04 15	1,46±0.90 0.52-2.80 61
15	31.96±0.08 31.84-32.10 0.25	-0,94±0,17 -1.15-0.66 18	0.60±0.26 0.19-0.95 43	1.78±0.67 0.80-2.58 38	6.74±1.46 4.27-8.07 22	1,23±0.73 0.38-2.25 60
25	32.19±0.31 31.98-32.99 0.97	-1,13±0,12 -1.32-0.83 11	0.60±0.13 0.37-0.79 22	1.95±0.48 1.26-2.87 25	6.67±0.89 5.17-8.13 13	0,79±0.46 0.23-1.47 58
35	32.21±0.09 32.06-32.32 0.27	-1,44±0,10 -1.53-1.27 7	0.54±0.15 0.37-0.85 28	2.25±0.85 1.44-4.05 38	6.14±0.71 5.16-7.30 12	0,49±0.33 0.18-1.01 66

close to the sea floor. The same overall pattern was observed for temperature, i.e. a quite high variability at the surface, decreasing toward more stable conditions above the bottom (Table 5.2). Because of the thick sea ice cover and the unstable water column, the pelagic primary production was low. Consequently, all nutrients were present in the surface water at quite high concentrations throughout the investigation. The major nutrients, phosphorus, nitrate, and silicate, were all present in excess, and no vertical difference was observed in concentrations. In general, the highest Chl *a* concentration was observed in connection with the low salinity few meters below the sea ice (Fig. 5.2). A carbon:Chl *a* ratio of 58 was calculated by linear regression between POC and Chl *a*.

Following the break-up of sea ice, the immediate increase in light penetration to the water column triggered a steep increase in pelagic primary production and Chl *a* values (Fig. 5.3). Diatoms dominate the phytoplankton community and constitute 62–74% of the total phytoplankton assemblage during the ice-free period (Rysgaard et al., 2004; Rysgaard et al., 2005). When the sea ice breaks up, the spring bloom quickly depletes the nutrients in the surface layer, causing the highest concentration of Chl *a* to be located at a water

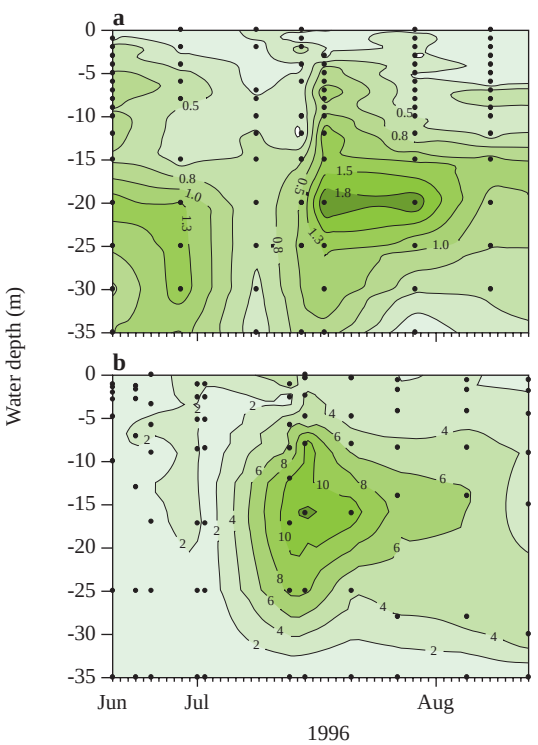

Figure 5.3 Young Sound June-August 1996. Vertical distribution of **(a)** Chl *a* (µg l^{-1}), and **(b)** primary production (µg C l^{-1} d^{-1}). Dots indicate the resolution of measurements. Data from Rysgaard et al. (1999).

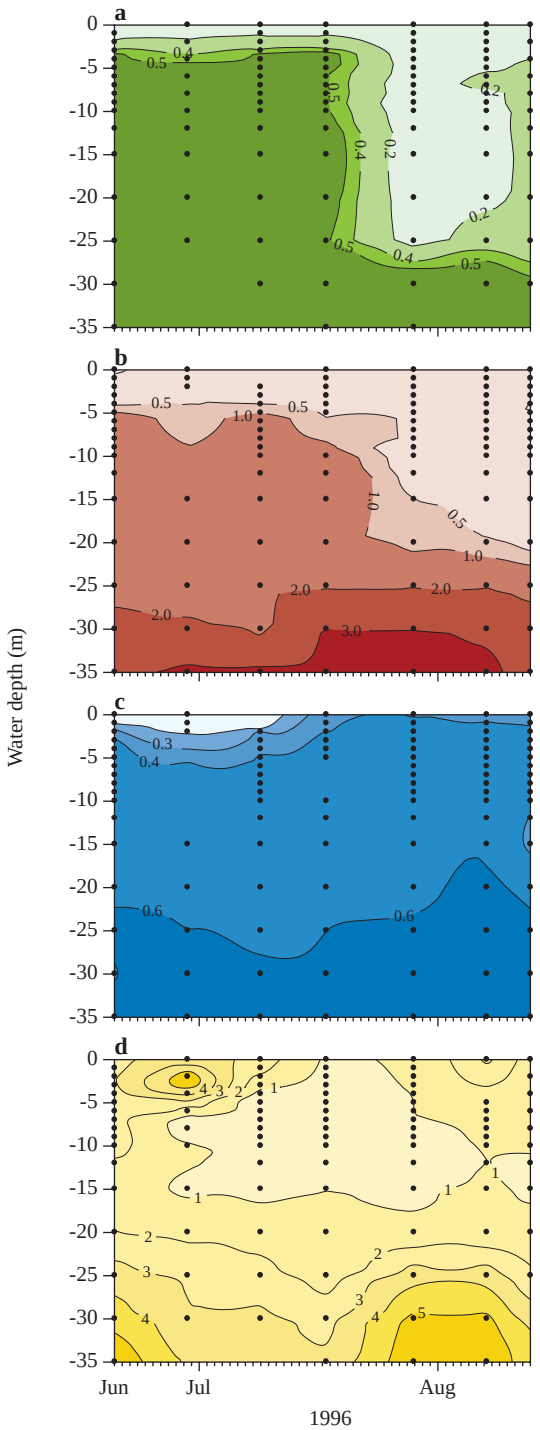

Figure 5.4 Young Sound June-August 1996. Vertical distribution of **(a)** ammonium, **(b)** nitrate, **(c)** phosphorus and **(d)** silicate. All measurements are in µM values, and dots indicate the resolution of measurements. Data from Rysgaard et al. (1999).

depth of 15–20 m. The stability of the water column during the summer season effectively seals the nutrients in the deeper water layers. Thus, the subsurface bloom usually lasts until August when primary production starts to descend to greater water depths (Fig. 5.4) due to initial limitation by SiO_4, followed by NO_3^- and NH_4^+, whereas PO_4^{3-} does not seem to limit production (Fig. 5.4; Rysgaard et al., 1999).

5.3.2 Primary producers

There was a pronounced decrease in depth-integrated phytoplankton biomass from about 4 g C m^{-2} to 2 g C m^{-2} at the end of the sea ice covered campaign (Fig. 5.5a). The reduction in the standing stock of phytoplankton was related to a shift in composition of the phytoplankton community. This change is illustrated by a shift in size fractions of the phytoplankton, from dominance of the Chl *a* fraction >11 µm at the beginning of the study to dominance of the smaller size fractions by the end of June (Fig. 5.5b). The change in size fractions is corroborated by the microscopic phytoplankton counts, according to which the diatoms (dominated by *Chaetoceros* spp.) present during the first days were succeeded by a community of autotrophic flagellates, primarily *Pyramimonas amylifers*, *P. grossi*/*orientalis*, *Dinobryon* spp. and *Apedinella*/*Pseudopedinella* (Fig. 5.5c). The overall mean biomass of primary producers during the sea-ice-covered period studied here was 2634 ± 405 mg C m^{-2}.

Because of the thick sea ice cover and poor light conditions, pelagic primary production was very low. The integrated primary production followed the development in the phytoplankton standing stock and showed a pronounced decrease from 122.5 to 28 mg C m^{-2} d^{-1} during the investigation (Fig. 5.5a, right axis) with a mean ± SE of 44.3 ± 11.8 mg C m^{-2} d^{-1}. After the ice breaks up, the spring bloom quickly develops and the pelagic primary production increases (Fig. 5.3b). The annual pelagic primary production, based on 11 direct measurements during the productive summer season and 1 during the unproductive winter is 10.5 g C m^{-2} yr^{-1} (Rysgaard et al., 1999)

5.3.3 Bacterioplankton and HNF

The depth-integrated bacterial biomass was quite stable throughout the ice-covered campaign 691 ± 45 mg C m^{-2} (Fig. 5.6a). In contrast, the bacterial production was more variable, but reached an average value of 52 ± 9 mg C m^{-2} d^{-1}, which corresponds to an average

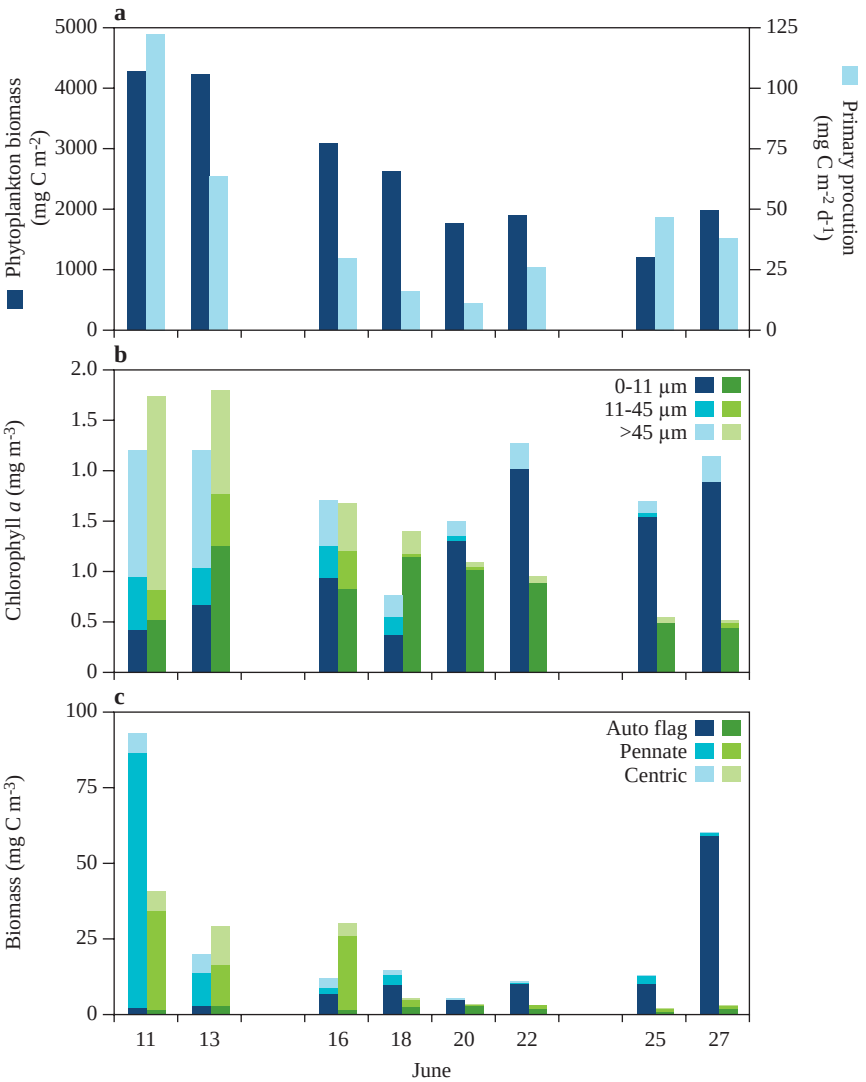

Figure 5.5 Young Sound June 1999. **(a)** Integrated phytoplankton biomass (0-36 m) calculated from the vertical profiles of chlorophyll *a* fluorescence (light blue bars; left axis) and integrated primary production (dark blue bars; right axis), **(b)** Size fractions of the phytoplankton community just below the ice (blue bars) and in 10 m (green bars), and **(c)** Main taxonomic phytoplankton groups just below the ice (blue bars) and in 10 m (green bars).

turnover of the bacterial standing stock of 8 ± 3% d^{-1} (Fig. 5.6b). Small heterotrophic nanoflagellates with an average cell volume of 60 ± 25 μm^3, n = 21 dominated the community of protist bacterial grazers, but the depth-integrated biomass remained low at 48 ± 7 mg C m^{-2} (Fig. 5.5c). The estimated clearance potential of the heterotrophic nanoflagellates was 0.5% of the water column per day giving rise to a grazing potential of 3.7 ± 0.4 mg C m^{-2}, which corresponds to < 10% of the daily bacterial production.

5.3.4 Microprotozooplankton

Naked oligotrich ciliates dominated the microprotozooplankton. In association with the change in phytoplankton community composition the ciliate biomass increased (Fig. 5.7a). At the two first sampling dates, where larger phytoplankton species dominated, the heterotrophic dinoflagellates constituted 40% of the microprotozooplankton biomass (Fig 5.7b) and the biomass of the heterotrophic dinoflagellates was quite constant throughout the investigation (40 ± 3 mg C m^{-2}), giving a grazing potential of 6 ± 1 mg C m^{-2} d^{-1}. However, because of the increase in the ciliate biomass the relative contribution of heterotrophic dinoflagellates decreased to 25% at the end of the investigation. The ciliate biomass was 98 ± 14 mg C m^{-2} with an estimated grazing of 73 ± 10 mg C m^{-2} d^{-1}. The average cell volume of ciliates and heterotrophic dinoflagellates was 5614 and 7060 μm^3, respectively, and the estimated mean grazing of ciliates was a factor of 10 higher than that of heterotrophic dinoflagellates. The initial biomass levels

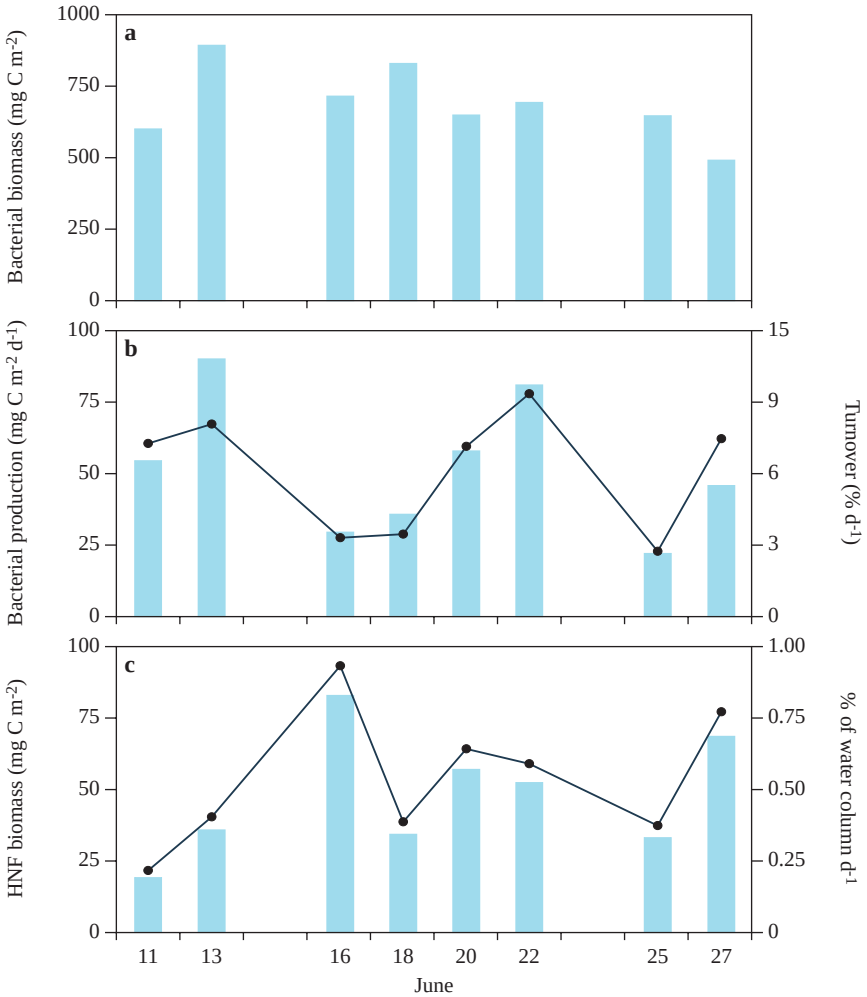

Figure 5.6 Young Sound June 1999. **(a)** Integrated bacterial biomass, **(b)** bacterial production (bars) and turnover rate, and **(c)** integrated biomass of heterotrophic nanoflagellates (bars) and their clearance capacity in % of the water column d^{-1}.

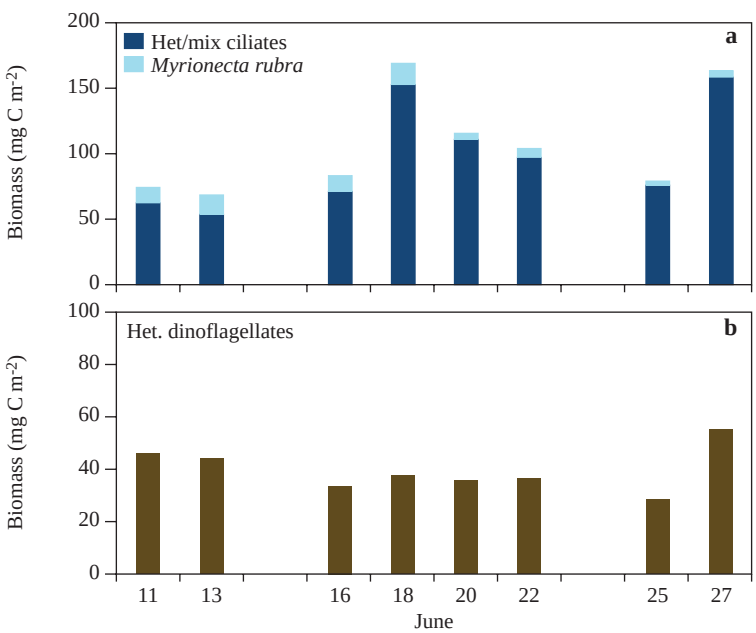

Figure 5.7 Young Sound June 1999. **(a)** Integrated biomass of ciliates, and **(b)** integrated biomass of heterotrophic dinoflagellates.

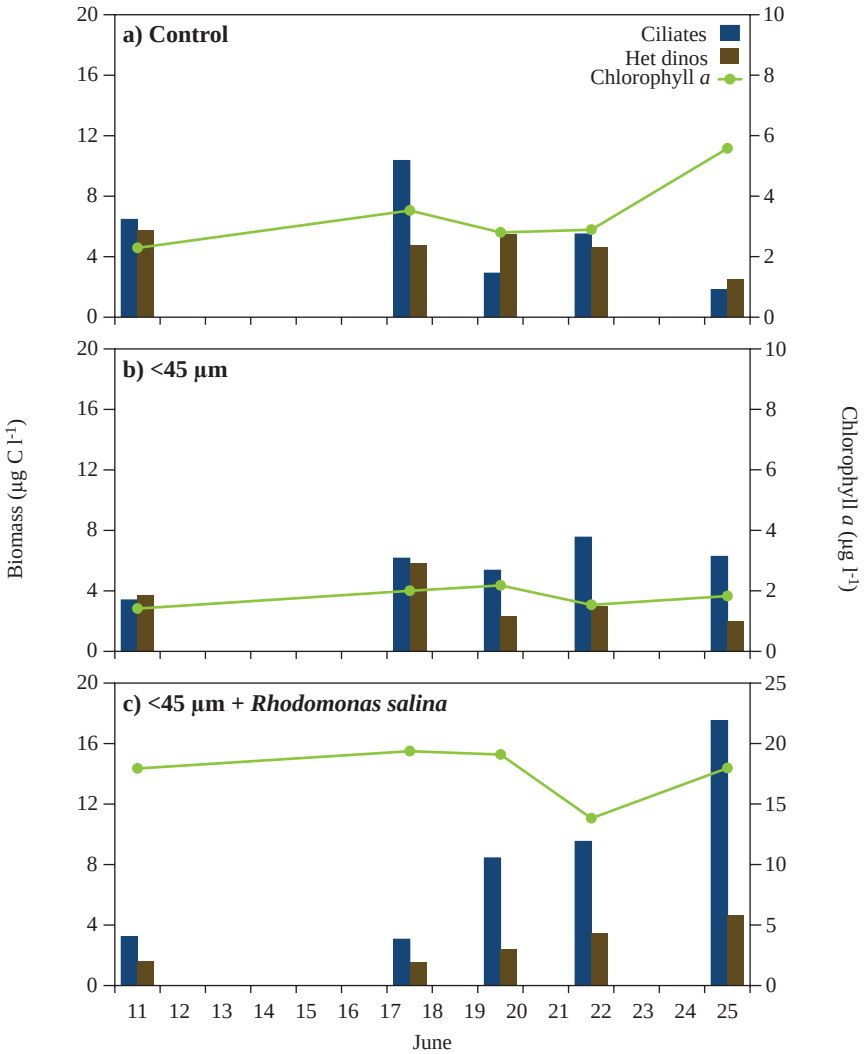

Figure 5.8 Young Sound June 1999. Microcosm experiments **(a)** control, **(b)** 45-µm fractionated surface water, and **(c)** 45-µm fractionated surface water spiked with the flagellate *Rhodomonas salina*.

of ciliates and heterotrophic dinoflagellates in the microcosm experiment were significantly higher in the control compared with the biomass in the phytoplankton size-fractionated carboys (Fig 5.8). This was primarily due to the removal of the largest ciliates (*Strombidium*, *Legardiella*) and the heterotrophic dinoflagellates (*Gyrodinium spirale*). In the control, the biomass of the ciliates increased initially followed by a gradual decrease, and the biomass of dinoflagellates was quite stable until the final days (Fig. 5.8a). In the 45-µm fractionated carboy the ciliate community increased-slightly, while the heterotrophic dinoflagellates decreased after the second sampling (Fig. 5.8b). In the *Rhodomonas*-spiked carboy, however, both protozooplankton groups increased during the incubation, indicating that the microprotozooplankton community in the fjord was food limited during this period (Fig. 5.8c).

The two main components of the microzooplankton, the ciliates and the heterotrophic dinoflagellates, contribute equally to the protozooplankton biomass in Young Sound, and the vertical and seasonal distributions of protozooplankton generally follow those of the phytoplankton (Rysgaard et al., 1999). The species composition and relative contribution of the two groups of protozoa are comparable with observations from the Disko Bay on the west coast of Greenland (Nielsen & Hansen, 1995; Levinsen et al., 1999). However, the absolute biomasses of ciliates and heterotrophic dinoflagellates in Young Sound are lower compared with the more productive Disko Bay (Levinsen & Nielsen, 2002).

5.3.5 Mesozooplankton

Young Sound mesozooplankton was numerically dominated by holoplankton, mainly copepods (Fig. 5.9 and Fig. 5.10). The copepods were present at mean abundances of 500–1200 ind m^{-3} and dominated by the cyclopoid species *Oithona* spp. and *Oncaea* spp. However, *Calanus* spp. and in particular *C. glacialis* and *C. hyperboreus* were nearly as abundant. The development of either total or species-specific abundance did not show any trend during the study. *Calanus finmarchicus* was represented by all copepodite stages except males, but the main components were CIV and V copepodites. The same stage composition was observed for *C. glacialis*, except that a few males were recorded. In contrast, *C. hyperboreus* was represented predominantly by CI-II copepodites, with fewer later copepodites, although some females were present. All the small calanoid and cyclopoid copepod species were present in all six copepodite stages, with only a few males. The harpacticoid *Microsetella* spp. was represented by CIV adults (Table 5.3). In terms of copepod biomass, the community was totally dominated by *Calanus* spp., particularly *C. glacialis* (Fig. 5.9b). No temporal trend was observed, and the total mean biomass was 40.7 ± 4.4 mg C m^{-3}, equal to 1465 ± 158 mg C m^{-2} (Fig. 5.9b).

The meroplankton was assumed to be planktotrophic, and holoplankton other than copepods were represented by 10 taxa. The gastropods, the polychaetes and the bivalves were the most important meroplankton groups, and the hyperiidae and the thecosomata dominated the holoplankton (Fig. 5.10). The development of both total abundance and relative species abundance showed a clear pattern during the study. The total abundance decreased from >600 ind. m^{-3} on the first three sampling dates to <100 ind. m^{-3} during the rest of the period. The thecosomata accounted for the main part of the biomass, followed by the hyperiidae and the gastropods. The total biomass was 2.7–3.8 mg C m^{-3} in the first three samplings, decreasing to 1 mg C m^{-3} in the rest of the period (Fig. 5.10b & Table 5.5), and the mean area biomass was 65 ± 49 mg C m^{-2}.

Seasonal studies covering the open-water period in Young Sound (Rysgaard et al., 1999; Rysgaard et al., 2004; Rysgaard et al., 2005) have shown that the mesozooplankton community is composed of *Calanus* spp., *Pseudocalanus* spp., *Microcalanus* spp., *Oithona* sp., *Oncaea* spp. and harpacticoid copepods. In addition, a few pelagic larvae of bivalvia, gastropoda and polychaeta have been identified, and the appendicularians are represented by *Fritillaria* sp.

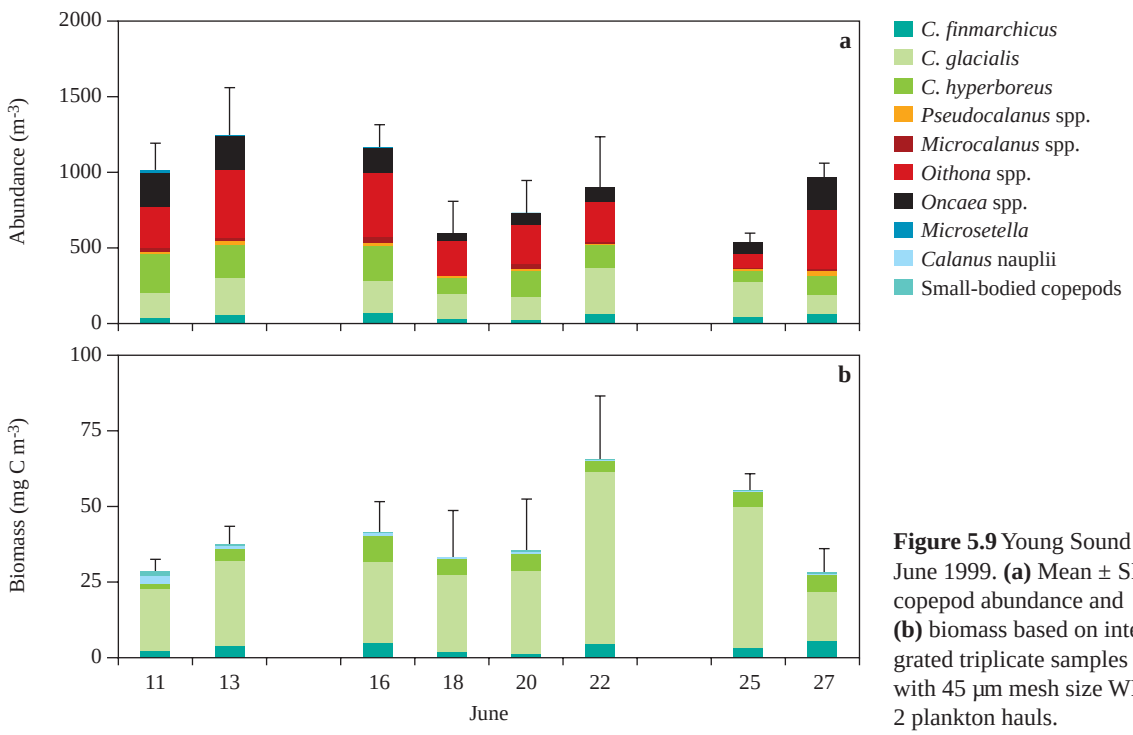

Figure 5.9 Young Sound June 1999. **(a)** Mean ± SE copepod abundance and **(b)** biomass based on integrated triplicate samples with 45 µm mesh size WP-2 plankton hauls.

and *Oikopleura* sp. In general, the mesozooplankton community is dominated numerically by copepods. In terms of biomass, the three *Calanus* species *C. glacialis*, *C. hyperboreus* and *C. finmarchicus* dominate the standing stock, constituting 70–90% of the total copepod biomass (Rysgaard et al., 1999).

Only few ripe *Calanus finmarchicus* females were present during the 1999 campaign and those incubated did not produce any eggs (data not shown). The initial egg production by *C. glacialis* was, however, high, 68.3 eggs female^{-1} d^{-1}, corresponding to a SEP of 0.10 d^{-1} (Fig. 5.11a & Table 5.4). However, the production consequently decreased with time, reaching zero at the end of June. This development was supported by the observation that the fraction of reproductively active females decreased (Fig. 5.11a), as did the abundance of free-floating copepod eggs and copepod nauplii (Fig. 5.11b & Fig. 5.11c). In contrast, the egg production of the egg-carrying cyclopoid *Oithona* spp. was less variable throughout the investigation. When the egg production by *C. glacialis* approached zero, the *Oithona* egg production remained high (Fig 5.11c & Table 5.4). The SEP of *Oithona* spp. was, however, several orders of magnitude lower than that of *C. glacialis* (Fig. 5.11a & Table 5.4).

The secondary production by the copepod community was calculated by multiplying SEP by the total biomass. This yielded a secondary production within the range 2.9–0.1 mg C m^{-3} d^{-1}, with a mean of 1.3 ± 0.4 mg C m^{-3} d^{-1} (Table 5.4). Calculating the copepod community grazing from the secondary production gave a mean of 3.9 ± 1.1 mg C m^{-3} d^{-1}, which is considered an underestimation, since a copepod biomass was present despite no SEP on the last two dates. Assuming that the entire copepod biomass was actively grazing throughout the study period at a specific rate corresponding to cover the SEP as recorded initially, 0.10 d^{-1} for *C. glacialis* (Nielsen & Hansen, 1995), the community grazing ends up at 441 ± 42 mg C m^{-2} d^{-1}, which is assumed to be more valid, and is therefore the one incorporated into the pelagic carbon budgets (see below). The mean secondary production by the meroplankton and holoplankters other than copepods was calculated at 0.09 ± 0.02 mg C m^{-3} d^{-1}, equal to 3.2 mg C m^{-2} d^{-1}, giving rise to a community grazing an order of magnitude lower than that of the copepod community (Table 5.5).

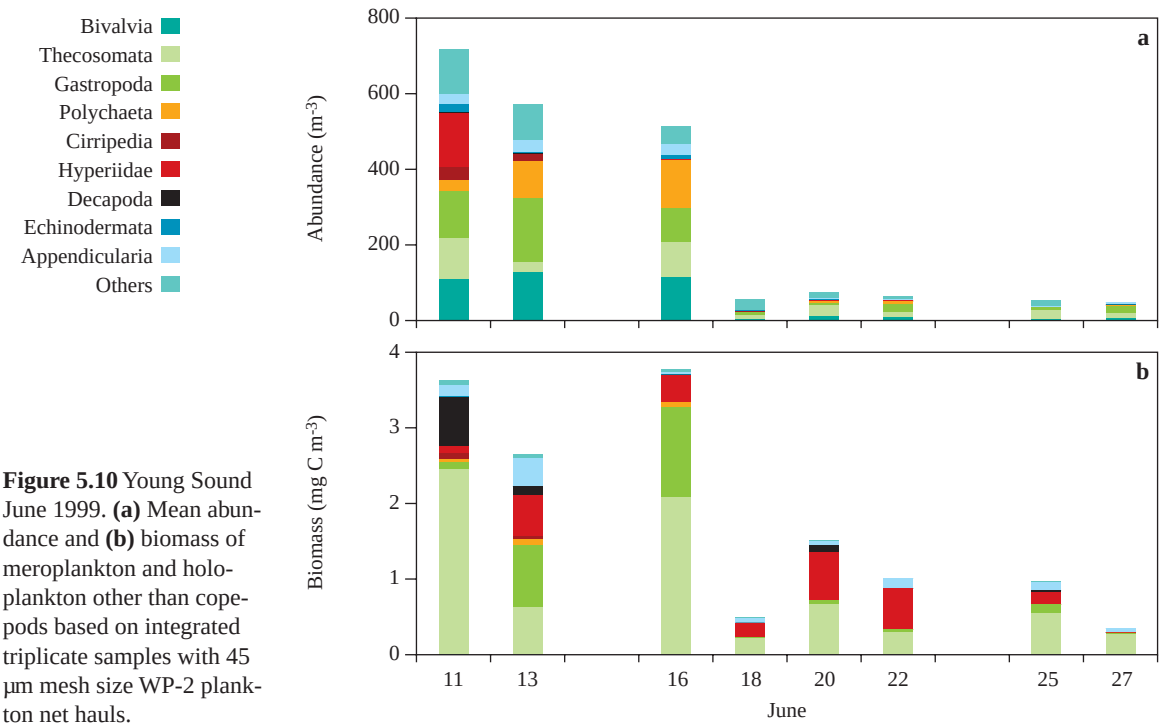

Figure 5.10 Young Sound June 1999. **(a)** Mean abundance and **(b)** biomass of meroplankton and holoplankton other than copepods based on integrated triplicate samples with 45 µm mesh size WP-2 plankton net hauls.

Table 5.3 Young Sound June 1999. Copepod species and mean ± SD. stagewise abundance (numbers m^{-3}) based on 8 sampling dates with 3 replicates per date = 24 samples.

Taxa	CI	CII	CIII	CIV	CV	Male	Female
Calanus finmarchicus	3.1±4.7	1.5±2.2	2.6±2.5	21.1±25.5	15.5±13.1	0	3.8±3.5
Calanus glacialis	15.5±22.8	6.8±8.0	11.7±12.1	98.7±53.2	56.2±43.9	0.1±0.2	11.2±8.5
Calanus hyperboreus	94.6±61.9	45.8±24.2	4.9±4.1	11.7±10.0	9.2±9.2	0	0.9±1.2
Metridia longa	0.2±0.6	0	0	0	0	0	0.5±1.8
Pseudocalanus spp.	4.7±5.6	3.5±3.9	2.0±2.5	1.4±2.3	1.2±1.9	0.3±0.7	2.8±1.9
Microcalanus spp.	6.2±5.8	4.0±4.6	3.4±4.3	4.1±4.6	1.2±2.4	0.1±0.3	0.6±1.1
Oithona spp.	68.9±54.7	56.0±66.3	14.4±12.5	18.8±17.1	58.0±40.8	5.1±3.7	43.7±30.1
Oncaea spp.	2.6±9.7	13.5±26.6	31.9±32.0	65.6±62.5	22.7±24.2	3.1±3.1	0.9±1.5
Microsetella spp.	0	0	0	0.3±1.1	1.6±5.2	0.2±0.6	1.8±5.3

Table 5.4 Young Sound June 1999. Egg production and specific egg production (SEP) of *Calanus glacialis* (mean ± SE. max. min. number of observations) and egg production and specific egg production of *Oithona* spp.

	June 11	June 13	June 16	June 18	June 20	June 22	June 25	June 27
C. glacialis Eggs fem.$^{-1}$d^{-1}	68.3±10.3 122.6; 4.1 15	52.2±10.2 142.6; 4.9 12	22.2±11.1 121.0; 0.0 13	26.5±10.9 109.6; 0.0 16	21.3±5.3 55.7;0.0 13	2.4±1.5 21.6; 0.0 15	No females	No females
SEP d^{-1}	0.10±0.017 0.20; 0.05	0.08±0.01 0.18; 0.01	0.04±0.023 0.29; 0.0	0.04±0.02 0.14; 0.0	0.03±0.01 0.08; 0.0	0.004±0.003 0.04; 0.0		
Oithona Eggs fem.$^{-1}$ d^{-1}	0.16	0.09	0.11	0.10	0.10	0.12	0.12	0.15
SEP d^{-1}	0.0024	0.0014	0.0018	0.0016	0.0015	0.0018	0.0018	0.0023

Table 5.5 Young Sound June 1999. Planktotrophic meroplankton and holoplankton other than copepods. Mean biomass ±SE (mg C m^{-3} and m^{-2} of triplicate plankton hauls); community secondary production (G = mean biomass × 0.05 d^{-1}; Hansen et al., 1999); and community grazing (I = G × 3; Hansen et al., 1997).

	June 11	June 13	June 16	June 18	June 20	June 22	June 25	June 27	Mean±SE m^{-3}	Mean±SE m^{-2}
Biomass mg C m^{-3}	3.61±3.73	2.65±1.00	3.79±1.28	0.52±0.48	1.52±0.98	1.02±1.39	0.96±0.11	0.37±0.40	1.81±4.46	65±49
Secondary production mg C m^{-3} d^{-1}	0.18	0.13	0.19	0.026	0.076	0.051	0.048	0.019	0.090±0.022	3.2±0.8
Community grazing mg C m^{-3} d^{-1}	0.54	0.39	0.57	0.078	0.23	0.153	0.144	0.138	0.280±0.01	10.1±2.3

Table 5.6 Young Sound. Annual pelagic carbon budget on the 36 m deep Station A based on the investigations in 1996 and 1999 (Rysgaard et al., 1999 and the present chapter).

	Carbon need (g C m^{-2} yr^{-1})	Production (g C m^{-2} yr^{-1})	Origin
Phytoplankton		10.4	Rysgaard et al. 1999
Bacteria	10.8	3.6	Present paper*
Ciliates	0. 8	0.3	Rysgaard et al. 1999
Dinoflagellates	0.6	0.2	Rysgaard et al. 1999
Copepods	9.7	3.2	Rysgaard et al. 1999
Total	**21.9**		

* Assuming that the mid winter data from Rysgaard et al. (*in press*) of 3.1 mg C m^{-2} d^{-1} represents 271 d, the present investigation covering 14 d during the ice cover, and bacterial production during the open-water period (80 d) is considered as 20% of the primary production according to Rysgaard et al. (1999).

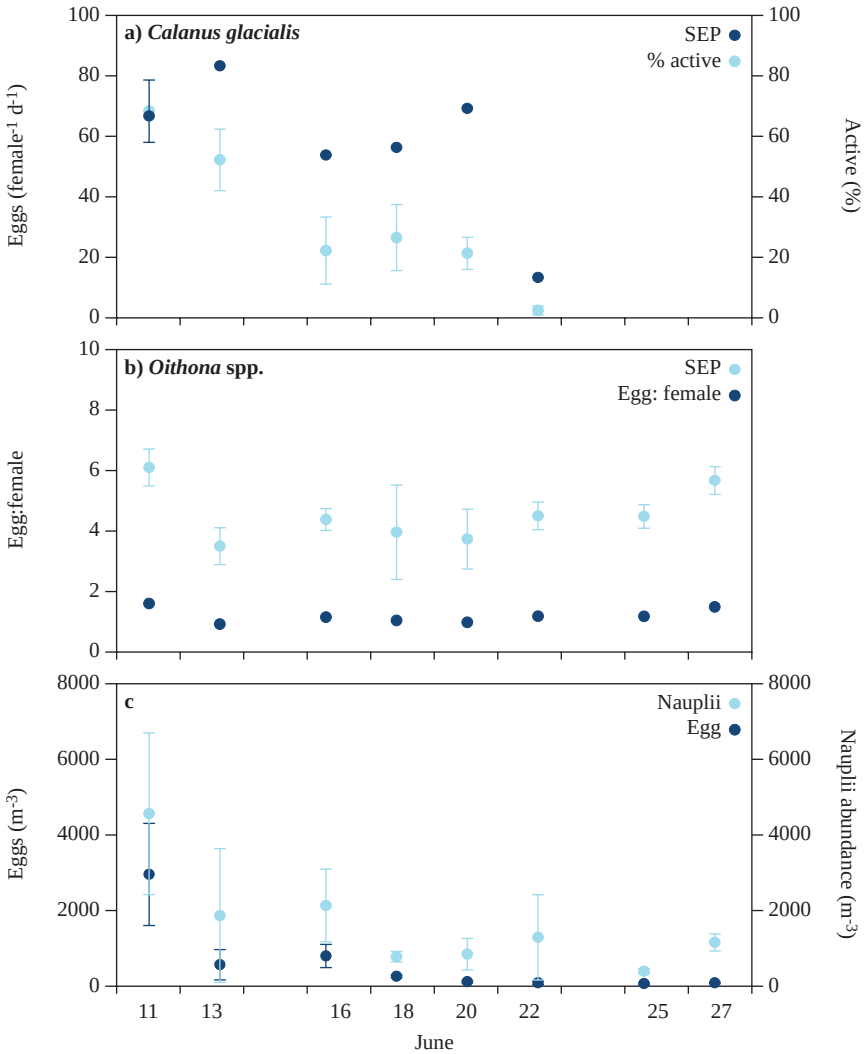

Figure 5.11 Young Sound June 1999. **(a)** *Calanus glacialis* egg production mean ± SE (left axis) and fraction of incubated females reproductively active (right axis), **(b)** *Oithona* spp. egg production (left axis) and egg: female ratio (right axis) and **(c)** mean ± SE abundance of free-floating copepod eggs (left axis) and copepod nauplii abundance (right axis).

5.3.6 Pelagic carbon budget for the ice-covered period

The total loss due to pelagic grazing was higher than the primary production during the 1999 field campaign, the carbon need of the grazers (copepods, meroplankters, ciliates and heterotrophic dinoflagellates) being 20% of the standing stock of phytoplankton (Fig. 5.12). This was presumably the reason for the observed decrease in phytoplankton biomass during the study period (Fig. 5.5a). In general, the copepod grazing was much more important that the rest of the pelagic grazing.

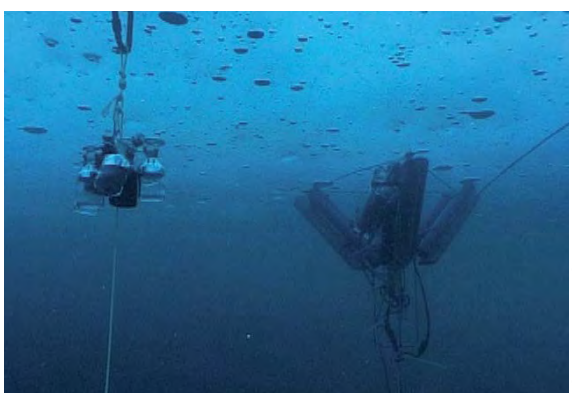

Photo: Peter B. Christensen

Incubation flasks for primary production incubated *in situ* below sea ice. Flasks are mounted in the sea ice with an ice-auger (front). Microprofiling instrument is seen in back (see Chapter 4).

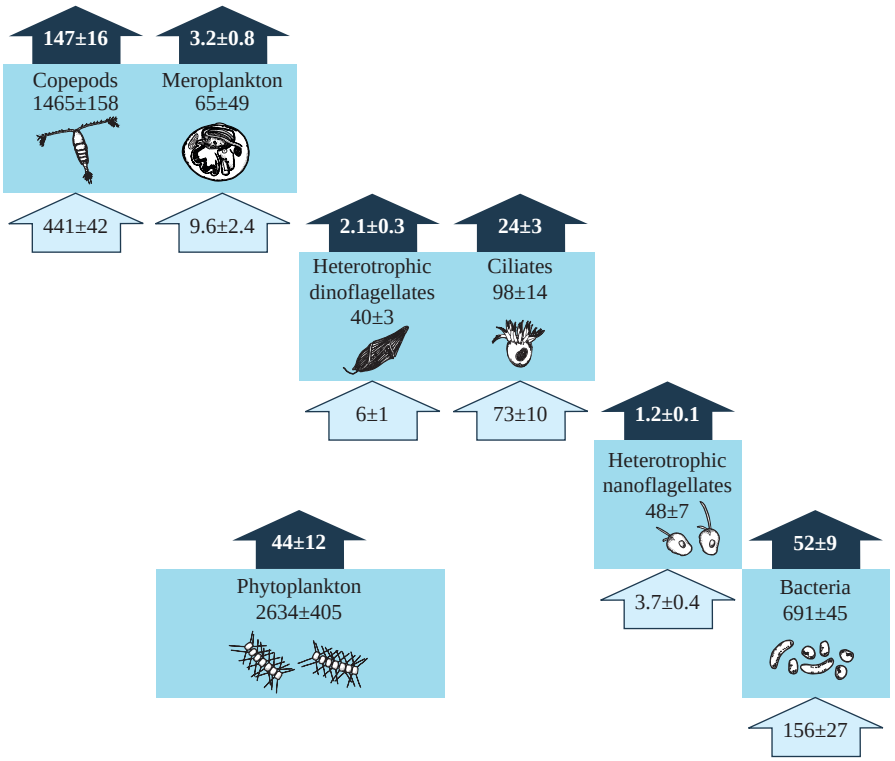

Figure 5.12 Young Sound June 1999. Carbon budget constructed as integrated mean ±SE (0-36 m) values of 8 sampling dates. Biomass in boxes (mg C m^{-2}), grazing in arrows going into the boxes, and production in arrows leaving the boxes (mg C m^{-2} d^{-1}).

5.3.7 The annual pelagic carbon budget

The annual pelagic carbon budget for Young Sound (Table 5.6) illustrates that the primary production at Station A (10.4 g C m^{-2} y^{-1}) cannot, on its own, cover the carbon need of the heterotrophic components of the pelagic food web (21.9 g C m^{-2} y^{-1}).

Calanus hyperboreus from Young Sound.

Photo: Torkel G. Nielsen.

5.4 Discussion

Combining the study performed at Station A during sea-ice cover with the open-water study conducted in 1996 at the same station (Rysgaard et al., 1999), documented that most of the annual pelagic productivity took place during the short open-water period (Fig. 5.13). The integrated annual carbon budget (Table 5.6) revealed that the estimated carbon need of the heterotrophs was more than twice the annual pelagic primary production at Station A, underlining the fact that Young Sound is a net heterotrophic system relying on import of organic material from the open sea or possibly from land.

Although a high phytoplankton biomass was present under the sea-ice cover during mid-summer, the low irradiance prevented nutrients from limiting primary production. However, nutrient limitation does occur when the sea ice breaks up and the pelagic community is exposed to full mid-summer irradiance in the middle of July, causing primary production to accelerate (Fig. 5.3; Rysgaard et al., 1999). During sea-ice cover, the relatively high phytoplankton biomass, 2634 mg C m^{-2}, expresses only a low productivity of, on average, 44 mg C m^{-2} d^{-1}. Bacterial production was higher than primary pro-

duction, 52 mg C m^{-2} d^{-1}, illustrating the importance of the microbial food web in this light-limited Arctic environment. Phytoplankton was grazed by copepods at a rate of 441 mg C m^{-2} d^{-1} and by ciliates, heterotrophic dinoflagellates and meroplankton at rates of 73, 6 and 10 mg C m^{-2} d^{-1}, respectively. Thus, total zooplankton ingestion corresponds to c. 20% of the total phytoplankton biomass and grazing therefore exceeds daily primary production by a factor of ten. Despite the high carbon demand of the heterotrophic compartments of the pelagic food web, the phytoplankton biomass did not change accordingly during June 1999, illustrating that the pelagic community must be renewed from elsewhere. The most plausible source is the open areas at the entrance to the fjord. As soon as the sea ice broke up, and meltwater from sea ice and from terrestrial runoff stabilized the water column, the developing spring bloom changed the entire pelagic system from heterotrophic to autotrophic dominance until the sea ice reformed and once again reduced pelagic photosynthesis.

In recent monitoring reports on the Young Sound pelagic seasonal cycle, Rysgaard et al. (2004; 2005) observed that *Pseudocalanus* spp., *Oithona* spp. and *C. hyperboreus* dominate during August. Furthermore, Rysgaard et al. (1999) showed that *Calanus* spp. dominated the pelagic grazing during the short open-water period. Hence, the food web structure of the pelagic community was comparable with observations reported during spring in other Arctic ecosystems with longer open-water periods, i.e. with significant contributions from *Calanus* (Nielsen and Hansen, 1995; Hansen et al. 1996; Hirche & Kwasniewski, 1997; Levinsen & Nielsen 2002; Ringuette et al., 2002; Møller et al., 2006). However, the total dominance of the *Calanus* genus contrasted with reports from the Disko Bay, W. Greenland (69°N), where the protozooplankton succeeded as the main grazers after mid-summer when *Calanus* left the euphotic zone to descend to hibernation depths (Levinsen & Nielsen, 2002). Thus, the protozooplankton community in the Young Sound is of less importance in the re-cycling of primary production. This pronounced difference is probably caused by significant predation on the protozooplankton by the copepods (Levinsen et al., 2000b) due to the temporal co-occurrence of protozooplankton and copepods in the short production window associated with the open-water period.

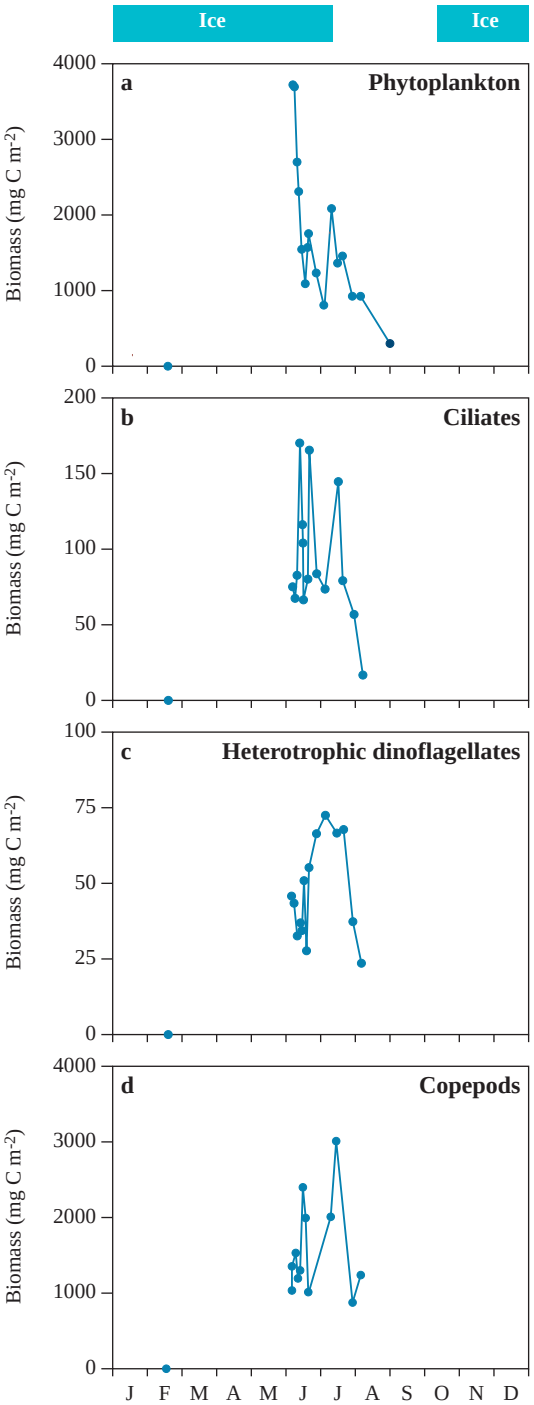

Figure 5.13 Young Sound. Annual cycle of integrated biomasses (mg C m^{-2}) of **(a)** phytoplankton, **(b)** ciliates, **(c)** dinoflagellates, and **(d)** copepods based on a combination of the investigations performed by Rysgaard et al. (1999) during 1996 and the present study in 1999.

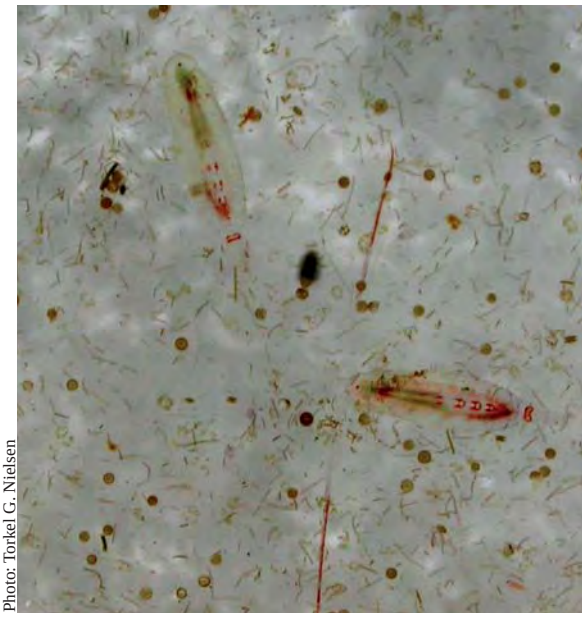

Photo: Torkel G. Nielsen

Copepods swimming in algal soup. Sample from Young Sound.

The main contributor to the copepod biomass was *Calanus* spp. Rysgaard et al. (2004; 2005) and Sejr et al. (2006) likewise reported dominance by this genus. During the ice-covered campaign the vast majority of copepods consisted of *C. glacialis* copepodite stages IV and V and females. This indicates that the population had reached maturity and that juvenile copepodites had grown up. *Calanus glacialis* was, however, not present in August 2003 and was assumed to have migrated to deeper waters, i.e. outside Young Sound or in the deeper parts of the fjord. The decrease in egg production rate, in the fraction of spawning females in the population, and in abundance of free-floating eggs and nauplii suggests that *C. glacialis* had its peak spawning in late May to early June. In Disko Bay, a high egg production rate was observed throughout June and July until descent of *C. glacialis* (Madsen et al., 2001). The *C. finmarchicus* population probably initiated spawning after *C. glacialis* as observed in the Disko Bay population (Madsen et al., 2001), and was indeed increasingly present during August 2003, 2004, and 2005 (Rysgaard et al., 2004; Rysgaard et al., 2005; Sejr et al., 2006). The *C. hyperboreus* was not present as advanced copepodites but primarily as CI copepodites, indicating pre-bloom reproduction as described elsewhere (e.g. Hirche & Niehoff, 1996; Madsen et al., 2001; Niehoff et al., 2002). In contrast, *C. hyperboreus* was numerous during August 2004 (Sejr et al., 2006).

In general, the relatively low water depth in the outer parts of Young Sound, far below reported diapause depth requirements for all three *Calanus* spp. (e.g. Hirche, 1998), indicates that no self-sustaining populations of any of the *Calanus* species exist here. Hence, all reproduction must be based on advected adult specimens originating from the Greenland Sea or from further inside the fjords where deeper waters are found (Chapter 3). Based on several years of monitoring during the program MarineBasic (Chapter 12) a decreased ratio between *C. hyperboreus* and *C. finmarchicus* is proposed to be indicative of an increased influence of Atlantic Water, as *C. finmarchicus* is considered an Atlantic Water species and *C. hyperboreus* a typical Arctic species. In contrast to the large copepods, all small-bodied calanoids were present in all copepodite stages, confirming the presence of several generations per year in Young Sound. The dominant cyclopoid *Oithona* spp., also reported by Rysgaard et al. (2004) and Rysgaard et al. (2005), apparently continued its reproduction after the large free-spawning species had terminated theirs. This pattern resembles those reported from West Greenland and the Greenland Sea (Møller et al., 2006).

The relative importance of the microbial food web qualitatively confirms the observations from the Greenland Sea (Møller et al., 2006), the Barents Sea (Hansen et al., 1996) and the Disko Bay, West Greenland, (Nielsen & Hansen, 1995; Møller & Nielsen, 2000; Levinsen & Nielsen, 2002). However, in contrast to the Barents Sea and Disko Bay the classical food chain seems to dominate the grazing pattern in Young Sound. Grazing, biomass as well as secondary production by copepods appears to be the major pathways for converting phytoplankton to higher trophic levels. Hence, the major structural difference between Young Sound and Disko Bay plankton communities is apparently that the observed succession, i.e. large *Calanus* spp. followed by protozoans and eventually by small copepods (Levinsen et al., 2000a; Madsen et al., 2001), does not take place in Young Sound. This difference is most likely due to the much deeper Disko Bay offering hibernation habitats for *Calanus* spp. and also the limited open-water period in Young Sound forcing all the major trophic groups to be temporarily present in concert.

To fully resolve the pelagic dynamics and model the succession of the pelagic food web in the Young Sound, more knowledge about the exchange processes between Young Sound and the Greenland Sea is essential. Additionally, better knowledge of the horizontal resolution of all the interacting compartments would enable us to obtain a comprehensive overview of the biological oceanography of Young Sound. Knowledge of the structure, succession and productivity of the pelagic community at the entrance to the Sound is especially crucial, since we hypothesize that this is what periodically fuels the ice-covered Young Sound with organic material.

5.5 Acknowledgements

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