RESEARCH ARTICLE

**Marte Lundberg · Haakon Hop · Ketil Eiane
Bjørn Gulliksen · Stig Falk-Petersen**

Population structure and accumulation of lipids in the ctenophore *Mertensia ovum*

Abstract We studied the abundance, length-frequency distribution and body composition (lipid accumulation) of the ctenophore *Mertensia ovum* in Kongsfjorden, Svalbard (79°N) between May 2001 and April 2002. The highest abundances were found during summer in the outer and middle areas of the fjord, possibly caused by the concentration of advected zooplankton. Polymodal length-frequencies indicated a life span of 2 years, with 0, 1 and 2-groups being present in summer. Total lipid for a standardized animal decreased from May to August, and increased to the highest level in September. Relative lipid content was always highest in the 0-group, probably reflecting reduction of lipid levels due to increased energy costs during reproduction for the older age groups. Lipids probably are used to fuel prolonged reproduction from May to August until spawning ends by September. The overwintering age groups (0 and 1) subsequently build up lipid reserves for the next years' spawning.

Introduction

Mertensia ovum (Tentaculata, Cydippida), a true Arctic ctenophore, is categorized as gelatinous zooplankton. It consists of about 95% water and the energy content is

M. Lundberg · H. Hop · S. Falk-Petersen
Norwegian Polar Institute, 9296 Tromsø, Norway

K. Eiane
University Centre in Svalbard, 9170 Longyearbyen, Norway

M. Lundberg (✉) · B. Gulliksen
Norwegian College of Fishery Science, University of Tromsø,
9037 Tromsø, Norway
E-mail: mlu000@nfh.uit.no
Tel.: +47-77-646212
Fax: +47-77-646020

therefore low (Percy and Fife 1981). Traditionally, ctenophores have been regarded as a dead end in the food web, since few predators have been shown to rely on them as a food source (Percy and Fife 1985). Unlike its boreal and tropical counterparts, *M. ovum* stores lipid in specialized storage structures called "oil sacs" (Larson and Harbison 1989), mostly in the form of wax esters and triacylglycerols (Falk-Petersen et al. 2002). This is probably an adaptation to a highly variable and seasonal food supply in the Arctic. Because of their transparent and fragile body with no hard parts, ctenophores are difficult to recognize in the gut of their predators, and traditional gut content analysis for studying predator–prey relationships is difficult. Species that have been suggested as predators on *M. ovum*, based on its occurrence in fresh stomach contents, include Polar cod (*Boreogadus saida*), Atlantic cod (*Gadus morhua*) (H. Hop, personal communication), Northern fulmar (*Fulmarus glacialis*) and black-legged kittiwake (*Rissa tridactyla*) (Harrison 1984), the medusa *Cyanea capillata* (Purcell 1991) as well as other ctenophores, especially *Beroë cucumis*. A recent study by Falk-Petersen et al. (2002), which used trophic markers, indicated that *B. cucumis* is the main predator on *M. ovum*.

Mertensia ovum has often been reported as the most abundant gelatinous zooplankton species in the Arctic (Percy and Fife 1985; Larson and Harbison 1989; Swanberg and Båmstedt 1991; Raskoff et al. 2005), constituting up to 70% of the total abundance of gelatinous zooplankton. At high abundances, ctenophore predation may significantly reduce copepod populations (Reeve et al. 1978; Deason and Smayda 1982; Swanberg and Båmstedt 1991). In the Barents Sea, it is estimated that *M. ovum* is able to consume up to 9% of the copepod biomass at times of high ctenophore abundance (Swanberg and Båmstedt 1991). The contribution by smaller copepods to the diet of *M. ovum* has not been investigated, but total zooplankton abundance is higher in Kongsfjorden than in many other areas around Svalbard (Walkusz et al. 2003) and could offer a variety of prey to opportunistic ctenophores. In Kongsfjorden, *Calanus*

spp., and especially *Calanus glacialis*, have been shown through lipid analyses to be a major food source for *M. ovum* (Falk-Petersen et al. 2002).

Most ctenophores are hermaphrodites and have direct development, through cydippid larvae resembling the adult cydippids (Pianka 1974). Prolonged spawning from early open-water season through the summer has been reported for *M. ovum* (Percy 1989; Siferd and Conover 1992).

The aims of this study were to (1) estimate the abundance and distribution of *M. ovum* in Kongsfjorden, (2) determine the population structure including age groups, growth and time of reproduction, and (3) determine the body composition of *M. ovum*, including wet weight, dry weight and total lipid weight.

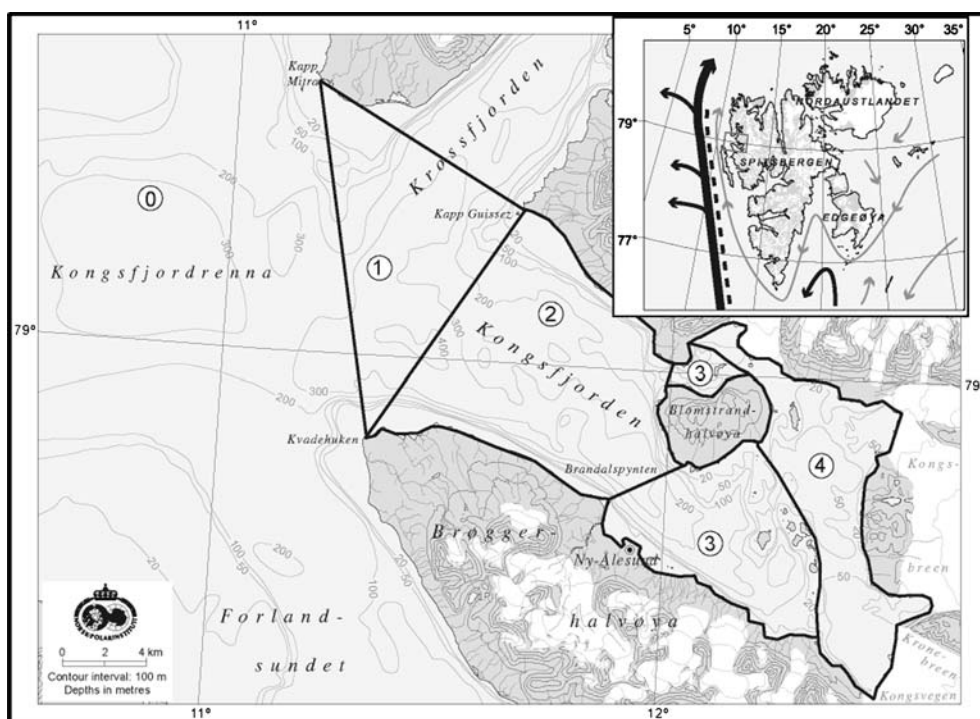## Materials and methods

Study area

Kongsfjorden is located between 78°40′–79°05′N and 11°30′–13°E in Spitsbergen, Svalbard (Fig. 1). The fjord is approximately 20 km long, varies in width from 4 to 10 km and consists of several basins that vary in bottom depth from <50 m in the inner basin to >300 m in the outer basin. The shelf outside the fjord varies in depth from 250 to 1,150 m along the shelf break. The fjord has been divided into different areas (Hop et al. 2002; Fig. 1), and we sampled the shelf (Area 0), the outer- (Area 1), middle- (Area 2) and transitional (Area 3) areas. Since the fjord has no sill at its entrance, the outer areas are strongly influenced by oceanic processes in the surrounding shelf areas (Ingvaldsen et al. 2001; Svendsen et al. 2002; Cottier et al. 2005). On the shelf, relatively warm and saline Atlantic water masses ($T > 3$°C, $S > 34.9$ psu) mix with colder and fresher Arctic water ($T < 0$°C, $34.3 < S < 34.8$ psu) as well as with local fjord water. The resulting water enters the fjord as Transformed Atlantic water ($T > 1$°C, $S > 34.7$ psu), which becomes the dominant water mass in the fjord during summer. Arctic water is mostly found in the surface layer, whereas local fjord water ($T < 1$°C, $S > 34.4$ psu) may be present in the basins (Svendsen et al. 2002). During summer, the water masses are strongly stratified restricting wind-driven currents to the surface layer. A combination of prevailing down-fjord winds during summer and physical forcing from the shelf drive an inflow of water on the southern side of the fjord and an outflow on the northern side (Svendsen et al. 2002). Eddies, with sizes up to the width of the fjord (2–4 km), have been detected in the middle area (Ingvaldsen et al. 2001; Basedow et al. 2004).

Sampling of ctenophores

Sampling of ctenophores encounters different challenges, such as very patchy distribution, damage when sampled with plankton nets and net avoidance (Hamner et al. 1975; Omori and Hamner 1982). To partly overcome these problems we used different sampling methods: plankton vertical net sampling (quantitative), surface sampling from small boat (qualitative) and sampling by SCUBA diving (qualitative). Qualitative samples were collected during three time periods in 2001 (25–29 May, 20 July–23 August, 6–20 September). Operating from

Fig. 1 Map of Kongsfjorden with areas; *0* shelf, *1* outer area, *2* middle area, *3* transitional area, *4* inner area (from Hop et al. 2002). The small map shows the Svalbard area with main currents. *Thick arrows* indicate warm Atlantic water in the West Spitsbergen Current, whereas *thin arrows* indicate cold Arctic water in the South Cape Current. The *dashed line* indicates the front between the two currents (from Svendsen et al. 2002, printed with permission)

small boats, individuals were collected from the surface with a jar mounted on a rod or with hand-held jars by SCUBA divers. Sampling was concentrated around the southern shore of Kongsfjorden, mainly from Kvadehuken to Brandalspynten (Fig. 1). The animals were transported live in buckets, back to the laboratory in Ny-Ålesund, where the body lengths (BL) of all individuals sampled were measured to the nearest millimetre (Fig. 2) while submerged in seawater. Individuals were put in polystyrene weighing boats and frozen at $-20°C$ immediately afterwards. The qualitative samples were used for analyses of body composition and population structure. Quantitative samples were collected during four cruises in the Kongsfjorden area (14–17 April 2002 and 20–22 May, 23 July and 3–5 September 2001) with WP-3 plankton nets in vertical hauls (net opening 0.78 m^2, mesh size 1,000 μm). Generally, three hauls to 100 m and one haul to 300 m (or to the bottom at shallow localities) were obtained at each station. All *M. ovum* were counted, and individuals without damage were length-measured and frozen. Quantitative samples were used for estimation of abundance and population structure. Some quantitative samples were also included in the body composition analyses to supplement low number of qualitative samples (e.g. for May 2001). Only individuals without visible prey in their guts were analysed for body composition. The quantitative and qualitative sampling schemes collected different sized individuals. Individuals >40 mm were not caught in the quantitative samples, whereas individuals up to 50 mm were caught qualitatively. In addition, the smallest individuals were more abundant in the quantitative samples than in the qualitative samples. The combined length-frequency distribution gives a more representative picture of the entire population structure, which is the reason for including qualitative samples in the length-frequency analysis.

Laboratory analyses

Samples were analysed for wet weight (WW) as frozen, dry weight (DW) and total lipid (TL) according to Folch et al. (1957). Frozen samples were put in pre-weighed crucibles and WW measured by weighing the frozen individuals (to nearest 0.1 g). Samples were then dried to constant weight in crucibles overnight in a drying oven at 55°C and subsequently weighed (DW). To extract the lipid content, the dry samples were dissolved in 3 ml chloroform:methanol (C:M 2:1, v:v) and spun for 10 min at 4,000 rpm. The supernatants were transferred to graded centrifuge tubes. This extraction was done three times to end up with 9 ml of supernatant (C:M and lipids in solution). Two millilitres of NaCl (0.09%, giving a 20% salt solution) was added to the centrifuge tubes, which were spun for 10 min at 3,000 rpm. The upper water phase was removed by pipette, before the samples were put into a 55°C water bath and left under ventilation for approximately 2 days. Samples were weighed to the nearest 10 μg when all the fluid had evaporated and only the lipids remained (TL).
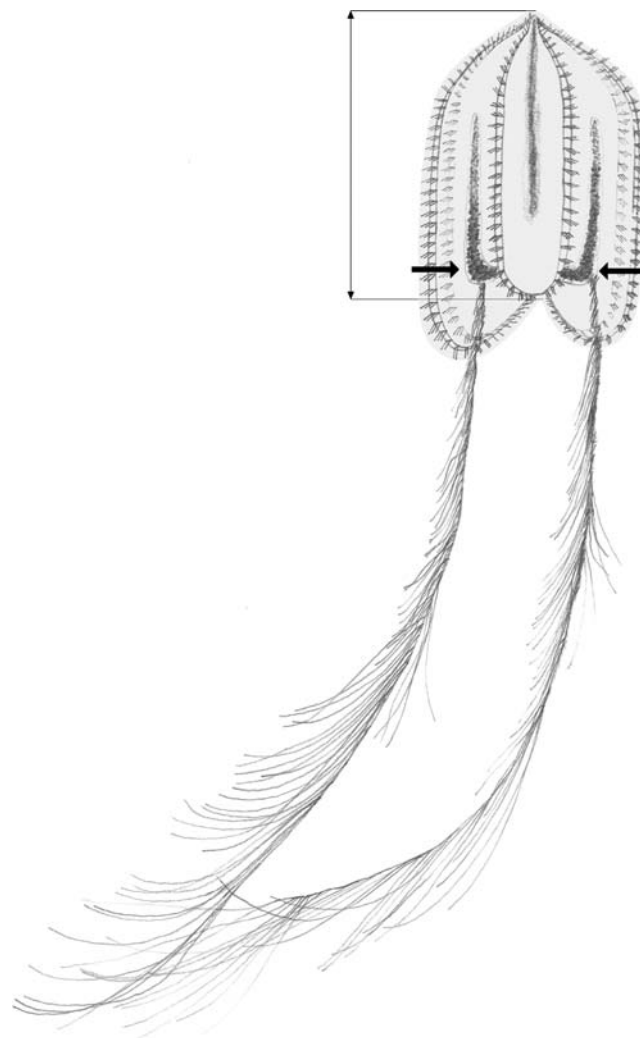

Fig. 2 *Mertensia ovum*. Length measured from oral- to anal opening indicated by *vertical bar*. *Thick arrows* point to the lipid sacs, with special emphasis on the lipid droplets perceptible to the eye

Statistical analyses

All data were analysed either in the statistical package "R" (The Development Core Team © 2003; Venables et al. 2002) or "S PLUS" (Insightful Corporation © 1987–2001; Venables and Ripley 2002).

Mean abundance (ind. m^{-2}) was calculated for each area separately, and for each month, based on all WP-3 samples. An ANOVA model (on square root transformed data) was used to test how the abundances of *M. ovum* varied with time and area. Comparing the means and their corresponding 95% confidence intervals between months for each area identified significant differences in abundance. Differences were termed significant when the confidence intervals did not overlap. Abundance data in this study are based on the assumption that net avoidance is persistently constant between samples. Between-sample variation (within the same area and time period, maximum interval of a few days), indicated by the confidence

intervals, is assumed to reflect their patchy distribution. Differences in abundance between months are assumed to indicate seasonal patterns.

To assess the change in population structure over the season, age groups were separated in polymodal length-frequencies using the "mix.dist" package in "R". The package applies a "distribution mixture analysis technique" (Macdonald and Pitcher 1979) to frequency data to find maximum likelihood estimates from grouped data. The Chi-square test optimizes relative abundance, mean and variance for each age group. We are not using cohorts in our study, due to the constant recruitment observed. We are using age groups with pooling of individuals spawned over the entire open-water season into one group. Lengths from combined quantitative and qualitative samples were separated into 3 mm groups for population structure analysis (Table 1). Growth was calculated as the increase in mean length within an age group over time (Falk-Petersen 1985). Days between the initial day of two consecutive sampling periods were used as time factor (April–May 36 days, May–July 64 days, July–September 42 days, September–April 223 days).

An ANCOVA model was used to analyse variation over time for wet- (WW), dry- (DW) and total lipid (TL) weight. By using a standardized length (22.62 mm, the mean length of all individuals), size was eliminated as a variable in the ANCOVA model, and the mean weight could then be compared between months (Percy 1989). When month was found to contribute significantly to the variation in weight, Tukey's test for Honest Significant Differences (Tukey HSD) was used to determine significant differences in weight parameters between months. Percentage DW of WW and percentage TL weight of DW were compared between age groups and between months. Differences were termed significant when the 95% confidence intervals did not overlap.

Results

Abundance

Abundances ($\pm$ SE) were highest in July and September in the outer and middle parts of the fjord. The highest mean abundance was found in the outer area in July (94.9$\pm$17.8 ind. m^{-2}), but the distribution was patchy, which is reflected in the high variation (Fig. 3). The effect of month varied with area (two-way ANOVA, interaction month × area: $F_{8,75} = 13.64$, $P < 0.001$). Overall, month explained more of the variation in abundance ($F_{3,86} = 22.01$, $P < 0.001$, $r^2 = 0.43$) than did area ($F_{3,86} = 12.59$, $P < 0.001$, $r^2 = 0.31$) and, consequently, a one-way ANOVA was applied to each of the areas separately to test for the effect of month on the variation in abundance within areas. Abundance in the transitional area was generally low, although significantly higher in May (3.5$\pm$1.4 ind. m^{-2}) and July (3.0$\pm$0.4 ind. m^{-2}) than in April (0.6$\pm$0.4 ind. m^{-2}) and September (0.4$\pm$0.3 ind. m^{-2}). Month explained 34% of the variance ($F_{3,18} = 3.10$, $P = 0.05$, $r^2 = 0.34$). In the middle area, significantly higher mean abundance was found in September (25.5$\pm$5.1 ind. m^{-2}) and July (21.3$\pm$7.7 ind. m^{-2}) than in May (2.9$\pm$1.3 ind. m^{-2}) and April (1.0$\pm$1.0 ind. m^{-2}). Month explained 62% of the variation in abundance ($F_{3,11} = 5.91$, $P = 0.01$, $r^2 = 0.62$). In the outer area, mean abundance in July (94.9$\pm$17.8 ind. m^{-2}) was significantly higher than in all other months. Additionally, abundance in September (17.8$\pm$3.9 ind. m^{-2}) was significantly higher than in May (2.8$\pm$1.0 ind. m^{-2}) and April (1.3$\pm$0.9 ind. m^{-2}). Month explained 91% of the variation in abundance ($F_{3,12} = 38.91$, $P < 0.001$, $r^2 = 0.91$). On the shelf, mean abundance was low, ranging from 0 individuals in April to 0.8 ($\pm$0.3) ind. m^{-2} in May and 2.0 ($\pm$1.1) ind. m^{-2} in September. May and September were not significantly different, and month explained only 18% of the variance in abundance ($F_{2,34} = 3.66$, $P = 0.04$, $r^2 = 0.18$). No samples were taken in July on the shelf due to limited cruise time.

Population structure

Individuals <5 mm were found during all months, but only one individual was caught in September. Individuals >40 mm were only found in July and September. In April, two size groups were recognized by the MIX analysis ($\chi^2_5 = 2.26$, $P = 0.81$), and we interpret these to correspond to age groups 0 and 1 (Table 1). Three size groups were found in May ($\chi^2_9 = 6.83$, $P = 0.65$) and in July ($\chi^2_{10} = 17.13$, $P = 0.07$), which we interpret as three age groups (0, 1 and 2-groups). In September, only two size groups were recognized ($\chi^2_{13} = 11.80$, $P = 0.54$), which probably corresponds to age groups 0 and 1.

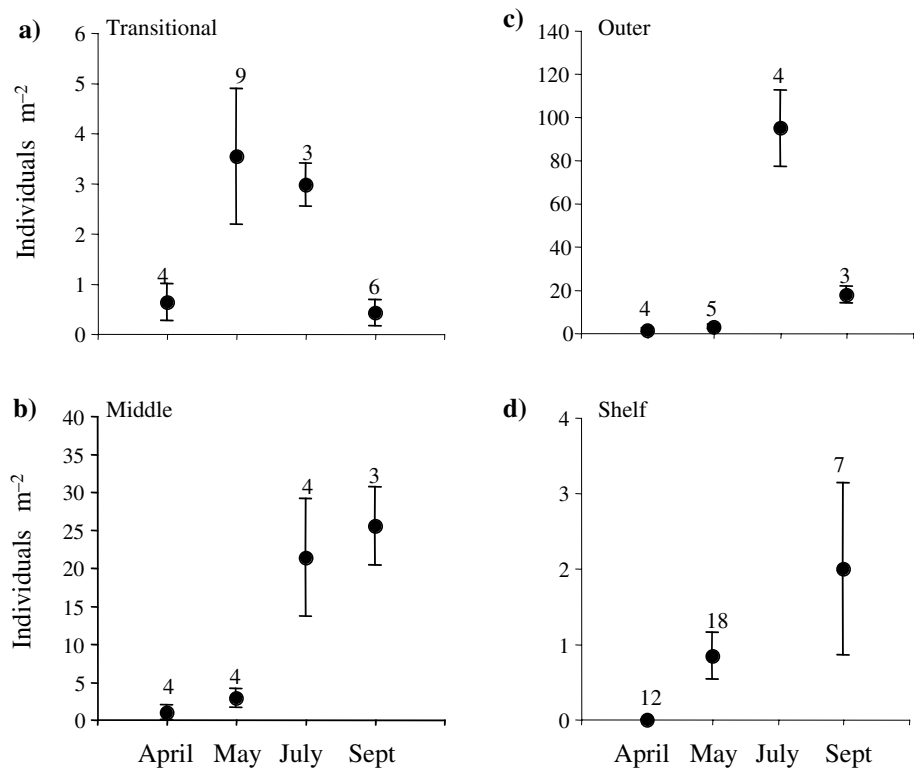**Table 1** Mean length (mm) of age groups ($\pm$ SE) of *Mertensia ovum* in different months, analysed in "Rmix", with the corresponding Chi-square statistic (χ^2)

Month	Number (n)	Age-0	Age-1	Age-2	df	χ^2	P
April 2002	9	5.51$\pm$1.15	21.52$\pm$0.81		5	2.26	0.81
May 2001	108	9.00$\pm$1.49	22.27$\pm$1.39	33.17$\pm$3.86	9	6.83	0.65
July 2001	492	11.94$\pm$0.26	34.39$\pm$0.58	43.50$\pm$0.57	10	17.13	0.07
September 2001	307	18.06$\pm$0.30	39.42$\pm$1.73		13	11.80	0.54

Length data was pooled to 3 mm groups prior to analysis

Fig. 3 Mean abundance (ind. m^{-2} ± SE) of *Mertensia ovum* in four areas of Kongsfjorden: **a** transitional, **b** middle, **c** outer and **d** shelf, in May, July and September 2001 and April 2002. *Numbers above error bars* indicate total net hauls included in the mean
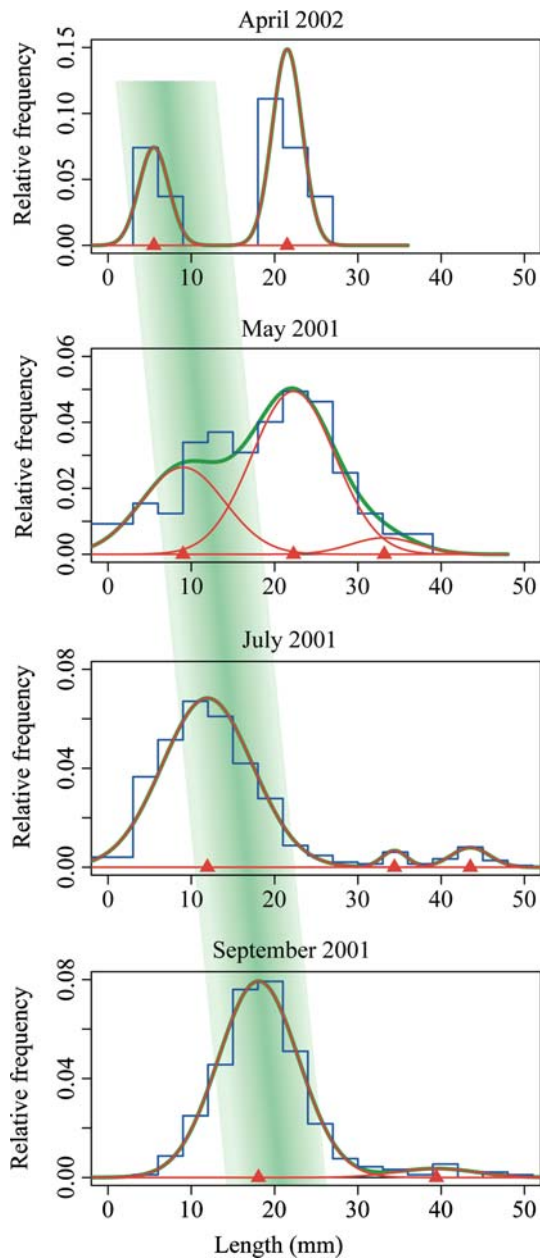

Mean length for the 0-group increased from 5.51 mm in April to 9.00 mm in May, with an estimated growth rate of 0.10 mm day^{-1}, assuming the populations to be constant and treating the samples as if they were from the same year. From May to July the 0-group increased its mean length to 11.94 mm, giving a growth rate of only 0.05 mm day^{-1}. Higher growth rate was estimated from July to September (0.15 mm day^{-1}), when mean length became 18.06 mm. In April the following year this group was recognized as age group 1, with a mean length of 21.52 mm, giving an estimated low growth rate of 0.02 mm day^{-1} over winter. Only a slightly longer mean length was found in May (22.27 mm). The 1-group increased its mean length to 34.39 mm in July, with an estimated growth rate of 0.19 mm day^{-1}. Mean length in September was 39.42 mm, with an estimated growth rate of 0.12 mm day^{-1}. The 1-group from September was assumed to give rise to the 2-group found in May with a mean length of 33.17 mm, giving an estimated, slightly negative growth rate (−0.02 mm day^{-1}). The 2-group was last recognized in July with a mean length of 43.50 mm, and estimated growth rate from May to July was 0.16 mm day^{-1} (Fig. 4).

Body composition

Mean standardized WW (for an individual of 22.62 mm) increased from May (1,281.94 mg) to September (2,158.90 mg), with highest increase between May and July (1,790.48 mg) (Table 2; Fig. 5a). Mean WW for August (2,144.65 mg) was similar to September. Month explained most of the variation in WW ($F_{3,183}$ = 72.6,

$P < 0.001$), after removing the variation related to body length (Table 3). The relationship between WW and month changed with BL, evident from the significant interaction term between month and BL ($F_{3,183}$ = 13.5, $P < 0.001$). Differences in WW between months could therefore not be tested statistically. Mean standardized DW increased the most from May to July (Table 2; Fig. 5a) and was significantly different between months ($F_{3,186}$ = 35.01, $P < 0.001$). DW for a standardized animal in July (93.07 mg), August (100.81 mg) and September (94.68 mg) were all significantly higher than in May (64.95 mg). Mean standardized TL weight was significantly higher in May (8.11 mg) and September (9.07 mg) than in August (6.41 mg) ($F_{3,186}$ = 9.33, $P < 0.001$) (Table 2; Fig. 5b). Mean TL weight for July (7.63 mg) was not significantly different from the other months. Relative DW to WW was almost constant at 4–6% between months and age groups, whereas relative TL to DW ranged from 27.7 (±5.3)% in 0-group in May to 5.6 (±0.5)% in the 2-group in August (Fig. 6). For all age groups the relative lipid content was highest in May, decreased in July and further in August and increased slightly in September. The relative lipid content in 0-group was significantly higher in May than all other months, in 1-group significantly higher in May than in August and September and in 2-group significantly higher in May than in August (95% CI). Within months, the 0-group always had higher relative lipid content than 1 and 2-groups, and differences were significant in May (age-0 > ages 1, 2), August (age-0 > age-2) and September (age-0 > age-1) (95% CI). Within months, the 1-group always had higher mean relative lipid
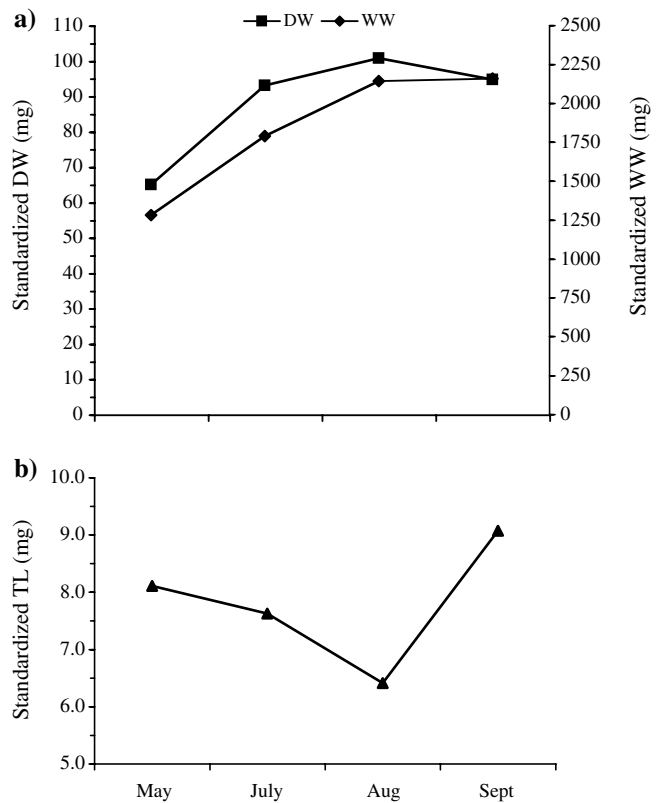
Fig. 4 Length-frequency distribution of *Mertensia ovum* in Kongsfjorden at different times of the year. Data (qualitative and quantitative samples) were pooled in 3 mm length prior to analysis in "Rmix". *Lines* indicate the best-fitted age groups (Chi-square test), with *triangles* marking the mean lengths. Note that the scale on the *y*-axis differs between plots. *Green bar* indicates growth of 0-group throughout summer
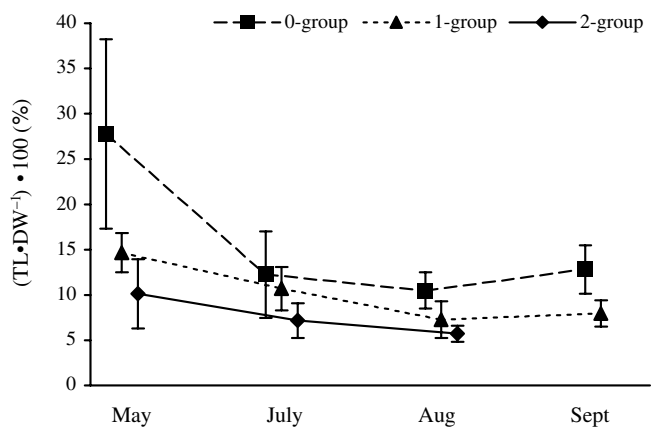
content than the 2-group, although the differences were not statistically significant.

Discussion

The abundances of *M. ovum* recorded in this study were lower than the reports from the Resolute Passage (maximum abundances of 1–12 ind. m^{-3} for the entire water

Fig. 5 Body composition of *Mertensia ovum* standardized to body length 22.62 mm. Mean weights are predicted values from an AN-COVA model: **a** wet weight (WW) and dry weight (DW); **b** total lipid weight (TL). Sample sizes are for May ($n=28$), July ($n=38$), August ($n=67$) and September ($n=50$) in 2001. Note the different scales

Fig. 6 Percentage total lipid weight of dry weight ($\pm$ CI, 95% limit) for different age groups of *Mertensia ovum*. Within months, means are displaced to show the CI bars

column) in late May–early June (Siferd and Conover 1992). If we assume that ctenophore occurrence was restricted to the upper 25 m, where Raskoff et al. (2005) observed 99% of all *M. ovum*, our estimated density would increase to 0–4.7 ind. m^{-3}. Percy (1989) also found higher abundances (0–25 ind. m^{-2}, at stations of 30–600 m depth) in Frobisher Bay, Canada, and at most sta-

Table 2 Mean log weights (± SE) and corresponding anti-log weights (Alog), in mg, of *Mertensia ovum* standardized for length for different months, from ANCOVA model

Month	Log WW	Alog WW	Log DW	Alog DW	Log TL	Alog TL
May	3.108±0.029	1,281.941	1.813±0.029	64.947	0.909±0.031	8.107
July	3.253±0.027	1,790.482	1.969±0.027	93.069	0.882±0.028	7.626
August	3.331±0.019	2,144.653	2.003±0.020	100.807	0.807±0.021	6.410
September	3.334±0.021	2,158.902	1.976±0.022	94.684	0.958±0.023	9.070

WW wet weight, *DW* dry weight, *TL* total lipid weight

tions the abundance was limited to the upper 30 m, similar to previous observations from the same area (Percy and Fife 1985). In the Barents Sea, Søreide et al. (2003) found a mean abundance in Arctic water masses of 1 ind. m^{-2} during winter and spring, when integrated over the water column (100–300 m max. depth).

Rapid changes in abundance are characteristic of gelatinous zooplankton, and many factors could contribute to variable abundance within the fjord and over time. Predation has been suggested to control the abundance of *M. ovum* (Larson 1986), and Falk-Petersen et al. (2002) concluded that *B. cucumis* was its major predator. It was always present in the fjord at times of sampling (M. Lundberg, personal observation). Prey abundances have also been shown to affect the abundance of ctenophores (Deason and Smayda 1982; Larson 1986; Swanberg and Båmstedt 1991) and could indirectly contribute to the peak in abundance in July by creating most favourable conditions for reproduction in summer. Graham et al. (2001) stated in a review that the reproductive life-history characteristics in ctenophores allow populations to respond quickly to increased production, e.g. in frontal areas. *M. ovum* is an indicator of Arctic water masses (Mortensen 1912). Thus, the high abundance of *M. ovum* in Kongsfjorden may be caused by pulses of advected organisms associated with Arctic water masses transported via the South Cape Current into the fjord (Svendsen et al. 2002). The eddy formation in the middle area of Kongsfjorden (Ingvaldsen et al. 2001; Basedow et al. 2004) restricts the outflow of surface water and could concentrate ctenophores advected into the fjord, thereby causing higher abundances in its middle and outer areas. Advection and local winds also influence the abundance of *M. ovum* (Schneider 1987; Falkenhaug et al. 1995). Ctenophores, and other zooplankton, have limited capabilities to cross the physical density borders between different water masses (Mills 1984) and are generally restricted to "go with the flow". In Kongsfjorden, advection of *Calanus* in and out of the fjord has been

documented (Kwasniewski et al. 2003; Basedow et al. 2004). In California, local wind- and current patterns were found to influence the distribution of the boreal ctenophore *Pleurobrachia bachei* (Hirota 1974), and this is probably also the case for Arctic ctenophores in Kongsfjorden based on the locally prevailing winds (Svendsen et al. 2002). "Bands" of high *M. ovum* and *B. cucumis* concentrations were frequently seen along the southern shore of Kongsfjorden. These were probably caused by surface slicks (at low wind speed) or Langmuir circulation (at higher wind speeds) resulting in entrapment of ctenophores (Graham et al. 2001).

Three age groups (0, 1 and 2) were recognized by the MIX analysis, suggesting that *M. ovum* has a 2-year life cycle. All groups were present in May and July. *M. ovum* has been observed under sea ice in late winter west of Spitsbergen, in the outflow from the Arctic Ocean (Swanberg and Båmstedt 1991) and under fjord ice during late winter in Kongsfjorden (H. Hop, personal observation), which supports a multi-year life cycle. Siferd and Conover (1992) proposed that *M. ovum* could live for at least 3 years in the Canadian Arctic.

Prolonged spawning, evident by the continuous presence of small *M. ovum*, has also been reported previously for this species (Percy 1989; Siferd and Conover 1992), and to follow cohorts of ctenophores is therefore difficult (Reeve and Walter 1978). However, even if the length-range of the 0-group is constantly influenced by recruitment of small individuals, the group is still detectable over the course of summer. The April samples are from the following year and fit readily into the general picture with a little shorter mean length than in May. However, growth rates calculated from mean lengths became deflated. The two age groups present in April suggest that the largest group (age-1) had overwintered, as mean length was already 21 mm. The smallest group, however, could be the offspring from early spawning prior to April. Estimated growth rates for the 0-group from April to May (0.10 mm day^{-1}) and July to September (0.15 mm day^{-1}) fall within ranges measured for other cydippid ctenophores, but would be higher if constant recruitment had been left out of the calculation. Growth rate of *P. pileus* in the laboratory at 15°C was 0.13 mm day^{-1} (Greve 1970), and that of *P. bachei* at 13°C in large plastic bags at sea was measured as 0.23 mm day^{-1} (Reeve and Walter 1978). The slow growth from May to July (0.05 mm day^{-1}) is probably caused by increased recruitment to the group, decreasing the mean length in July.

Table 3 Regression equations for different body parameters (weight *W*) against body length (BL), given by the power function: $W(\log+1) = a \times \mathrm{BL}(\log+1)^b$

Body parameter	*a*	*b*	*r*^{2}
Wet weight	0.0004	2.7465	0.94
Dry weight	0.0228	2.6365	0.96
Total lipid	0.0285	1.8051	0.74

The 0-group overwintered and was recognized the next year as 1-group with only a slight increase in mean length. The 1-group increased its mean length over summer with realistically estimated growth rates (0.19 and 0.12 mm day^{-1}, respectively, for May–July and July–September). Slow or no growth would be expected during winter (Clarke 1980), as a result of low prey abundance in the upper water column when *Calanus* spp. generally migrate to depths to overwinter in diapause (Kwasniewski et al. 2003). Negative growth might be caused by shrinkage at times of low food supply, as reported for other ctenophores (Hoeger 1983).

The increases in WW and DW throughout the season mainly represent the summer growth and indicate that the population is in good condition. The lipid contents in this study (5.6–27.7% of DW) ranged higher than in the Canadian Arctic for the same species (5.3–14.4% of DW; Percy and Fife 1981). A large fraction of the sampled individuals in our study had visible prey in their guts, mostly *Calanus*, krill and unidentified materials. Many of the specimens also had well-developed, red "oil sacs" for lipid storage (Larson and Harbison 1989). Total standardized lipid content was highest in September, probably as a result of feeding on the lipid-rich *Calanus*, given their generally higher energy content in the autumn (Falk-Petersen et al. 1987; Scott et al. 2000). The decrease in lipid content in August may be due to high energy demands through extensive reproduction in this period and is supported by a high number of juveniles occurring in the samples. Standardized lipid content in August was even much lower than in May and suggests that lipid is channelled to reproductive effort rather than to energy storage during low-food regimes (Hagen and Schnack-Schiel 1996). The very low proportion of juveniles in September shows that spawning has ceased by September. The high lipid content in the standardized animals in September, as well as in the 1- and 0-groups, suggests that *M. ovum* had built up lipid reserves for winter, feeding on lipid-rich *Calanus*. Higher relative lipid content in the 0-group (27.7% in May) indicates a high fraction of pre-spawners in the group. Higher lipid content in juvenile zooplankton than in adults is uncommon, but has been reported recently for the pteropod *Limacina helicina* (Gannefors et al. 2005).

Studies of the zooplankton community in Kongsfjorden were carried out simultaneously with our study in May 2001 and reported nauplii of *Calanus* spp. and nauplii of other calanoid copepods to be the most abundant groups, followed by larvae of polychaetes and echinoderms (Basedow et al. 2004). Of the later developmental stages, *C. glacialis, C. finmarchicus, Oithona similis, C. hyperboreus* and *Pseudocalanus* spp. were dominant. Altogether, a variety of prey was available at high abundances in May. Stoecker et al. (1987) determined in feeding experiments that larval ctenophores feed on ciliates in addition to nauplii, and this alternative food source is likely present in Kongsfjorden prior to the spring bloom. Siferd and Conover (1992) showed that *M. ovum* is in condition to spawn just as its *Calanus* prey starts to

spawn. However, *C. finmarchicus* in Kongsfjorden spawns during or after the spring bloom (Scott et al. 2000), which normally takes place in early May, depending on the ice conditions (Falk-Petersen et al. 1999; Hop et al. 2002), so this could not support the early development of juvenile *M. ovum*. The larger *C. glacialis* and *C. hyperboreus*, on the other hand, have greater lipid deposits built up over two or more years, which facilitates their reproduction prior to feeding on the spring bloom. This together with advection of prey from outside the fjord could fuel the development of young *M. ovum* as early as in April.

Conclusions

We conclude that the abundance is variable and high in summer in central areas of Kongsfjorden, probably caused by advected organisms trapped by an eddy formation. *M. ovum* has a 2-year life cycle in the fjord, as is evident by the three age groups recognized. Reproduction starts early, probably prior to the spring bloom, and continues throughout summer, peaking in July–August, as shown by high numbers of small individuals (< 5 mm) and a marked decrease in lipid content. The 0 and 1-groups rebuild their lipid stores after spawning, feeding on lipid-rich *Calanus*, which ensures energy supply for overwintering in low-food regimes, but more importantly facilitates early pre-bloom spawning to take full advantage of the short, but intense Arctic summer. Relative lipid content is highest in the 0-group early in the year. With a multi-year life cycle and relatively high lipid content, *M. ovum* has adapted a typical Arctic life strategy.

References

Basedow SL, Eiane K, Tverberg V, Spindler M (2004) Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). Estuar Coast Shelf Sci 60:113–124

Clarke A (1980) A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol J Linn Soc 14:77–92

Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res 110:C12005. DOI 10.1029/2004JC002747

Deason EE, Smayda TJ (1982) Ctenophore-zooplankton–phytoplankton interactions in Narragansett Bay, Rhode-Island, USA, during 1972–1977. J Plankton Res 4:203–217

Falkenhaug T, Nordby E, Svendsen H, Tande K (1995) Impact of advective processes on displacement of zooplankton biomass in a North Norwegian fjord system: a comparison between spring and autumn. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 195–217

Falk-Petersen S (1985) Growth of the euphausiids *Thysanoessa inermis, Thysanoessa raschii*, and *Meganyctiphanes norvegica* in a subarctic fjord, North Norway. Can J Fish Aquat Sci 42:14–22

Falk-Petersen S, Sargent JR, Tande KS (1987) Lipid composition of zooplankton in relation to the sub-Arctic food web. Polar Biol 8:115–120

Falk-Petersen S, Pedersen G, Kwasniewski S, Hegseth EN, Hop H (1999) Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. J Plankton Res 21:1249–1264

Falk-Petersen S, Dahl TM, Scott CL, Sargent JR, Gulliksen B, Kwasniewski S, Hop H, Millar R-M (2002) Lipid biomarkers and trophic linkages between ctenophores and copepods in Svalbard waters. Mar Ecol Prog Ser 227:187–194

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipides from animal tissues. J Biol Chem 226:497–509

Gannefors C, Böer M, Kattner G, Graeve M, Eiane K, Gulliksen B, Hop H, Falk-Petersen S (2005) The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. Mar Biol 147:169–177

Graham WM, Pages F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212

Greve W (1970) Cultivation experiments on North Sea ctenophores. Helgoländer Wissenschaftliche Meeresuntersuchungen 20:304–317

Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? Deep-sea research part I. Oceanogr Res Pap 43:139–158

Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton—sampling problems, feeding biology, and behavior. Limnol Oceanogr 20:907–917

Harrison NM (1984) Predation on jellyfish and their associates by seabirds. Limnol Oceanogr 29:1335–1337

Hirota J (1974) Quantitative natural history of *Pleurobrachia bachei* in La-Jolla Bight. Fish Bull 72:295–235

Hoeger U (1983) Biochemical composition of ctenophores. J Exp Mar Biol Ecol 72:251–261

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalzuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-Å, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208

Ingvaldsen R, Bø Reitan M, Svendsen H, Asplin L (2001) The upper layer circulation in Kongsfjorden and Krossfjorden—a complex fjord system on the west coast of Spitsbergen. Mem Natl Inst Polar Res 54(special issue):393–407

Kwasniewski S, Hop H, Falk-Petersen S, Pedersen G (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. J Plankton Res 25:1–20

Larson RJ (1986) Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British-Columbia. Mar Ecol Prog Ser 33:89–98

Larson RJ, Harbison GR (1989) Source and fate of lipids in polar gelatinous zooplankton. Arctic 42:339–346

Macdonald PDM, Pitcher TJ (1979) Age-groups from size-frequency data—versatile and efficient method of analyzing distribution mixtures. J Fish Res Board Can 36:987–1001

Mills CE (1984) Density is altered in hydromedusae and ctenophores in response to changes in salinity. Biol Bull 166:206–215

Mortensen T (1912) Ctenophora. In: Hagerup H (ed) The Danish Ingolf expedition. Copenhagen, pp 1–95

Omori M, Hamner WM (1982) Patchy distribution of zooplankton—behavior, population assessment and sampling problems. Mar Biol 72:193–200

Percy JA (1989) Abundance, biomass, and size frequency distribution of an Arctic ctenophore, *Mertensia ovum* (Fabricius) from Frobisher Bay, Canada. Sarsia 74:95–105

Percy JA, Fife FJ (1981) The biochemical composition and energy content of arctic marine macrozooplankton. Arctic 34:307–313

Percy JA, Fife FJ (1985) Energy distribution in an arctic coastal macrozooplankton community. Arctic 38:39–42

Pianka H (1974) Ctenophora. In: Giese A, Pearse J (eds) Reproduction of marine invertebrates. Academic, New York, pp 201–265

Purcell JE (1991) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216:335–342

Raskoff KA, Purcell JE, Hopcroft RR (2005) Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Polar Biol 28:207–217

Reeve MR, Walter MA (1978) Nutritional ecology of ctenophores—a review of recent research. Adv Mar Biol 15:249–287

Reeve MR, Walter MA, Ikeda T (1978) Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. Limnol Oceanogr 23:740–751

Schneider G (1987) Role of advection in the distribution and abundance of *Pleurobrachia pileus* in Kiel Bight. Mar Ecol Prog Ser 41:99–102

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2000) Lipids and life strategies of *Calanus finmarchicus, Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. Polar Biol 23:510–516

Siferd TD, Conover RJ (1992) Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. Mar Ecol Prog Ser 86:133–144

Søreide JE, Hop H, Falk-Petersen S, Gulliksen B, Hansen E (2003) Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring. Mar Ecol Prog Ser 263:43–64

Stoecker DK, Verity PG, Michaels AE, Davis LH (1987) Feeding by larval and postlarval ctenophores on microzooplankton. J Plankton Res 9:667–683

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther J-G, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133–166

Swanberg N, Båmstedt U (1991) Ctenophora in the Arctic—the abundance, distribution and predatory impact of the cydippid ctenophore *Mertensia ovum* (Fabricius) in the Barents Sea. Polar Res 10:507–524

Venables W, Ripley B (2002) Modern applied statistics with S. Springer, Berlin Heidelberg New York

Venables W, Smith D, Team RDC (2002) An introduction to R. Network Theory Limited, Bristol

Walkusz W, Storemark K, Skau T, Gannefors C, Lundberg M (2003) Zooplankton community structure; a comparison of fjords, open water and ice stations in the Svalbard area. Pol Polar Res 24:149–165