Ctenophora in the Arctic: the abundance, distribution and predatory impact of the cydippid ctenophore *Mertensia ovum* (Fabricius) in the Barents Sea

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The Ctenophora *Mertensia ovum* and *Beroe cucumis*, collected using both conventional sampling gear and scuba divers, were studied in the Barents Sea east of Bjørnøya and North Norway in spring 1987 and summer 1988. Among the gelatinous zooplankton, *Mertensia ovum* was the most consistently abundant copepod predator.

Feeding experiments were conducted to evaluate the predation rate of *M. ovum* in various trophic regimes. This ctenophore can take prey varying in size from small copepods to amphipods and krill, but gut-content analyses from field-collected specimens as well as experimental results showed that the main food source for adults was large-sized copepods (e.g. *Calanus finmarchicus, C. glacialis, C. hyperboreus, Metridia longa*). The robust tentacle arrray of *M. ovum* makes this species effective as a predator on large prey. The high potential predation rate of this ctenophore relative to its estimated metabolic cost of only 1.7% of the body energy content d^{-1} suggests that *M. ovum* may be able to maintain a positive energy balance even in conditions of low prey abundance. It is suggested that a single exploitation of a zooplankton patch may provide energy for survival for a very long time.

The potential impact of *M. ovum* on Barents Sea copepod populations is estimated on the basis of the minimal observed average daily ration in experiments and from field data on gut contents. Using abundances of copepods for the area, and the actual predator biomass collected, it was estimated that an average of 0.7% of the copepod fauna per day could fall prey to this predator.

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Introduction

Fluctuations in copepod populations in the Barents Sea during the recent decade have directed our attention to the roles of the commonest zooplankton predators there. One of the most prevalent large predators is the cydippid ctenophore *Mertensia ovum*, first noticed as abundant during a cruise on G.O. SARS, in August 1985 (Skjoldal et al. 1986).

It is well documented that some ctenophores, particularly lobates, can be significant predators in coastal marine waters (Kremer 1976, 1979; Reeve & Walter 1978; Sullivan & Reeve 1982) but there has been relatively little work done in the open sea. The population dynamics of few species of cydippid ctenophore have been well studied. However, extensive field studies have been carried out where feeding and physiological experiments on *Pleurobrachia*, the most common genus of the Cydippida, give support to the general claim that cydippid ctenophores can also exert considerable predation pressure on the herbivorous zooplankton (Fraser 1970; Greve 1970, 1971, 1972; Hirota 1972; Reeve & Walter 1978; Reeve 1980; Van der Veer & Sadée 1984; Greene et al. 1986). There is a major difference between these two groups. Lobates feed continuously while cydippids, which feed on prey adhering to their tentacles, must normally interrupt their capture cycle and reset their tentacle array each time they feed on captured prey (Greene et al. 1986). This suggests that they may be more inclined to reach saturation than their lobate counterparts.

Gelatinous zooplankters are generally difficult to sample quantitatively. They are usually low in absolute abundance, necessitating a large sample

volume; many species (particularly among the Ctenophora) are very fragile, so that even if they are not damaged by the sampling gear needed for large volume samples, they are often subsequently destroyed in conventional preservatives. By carefully removing and examining the material taken from net hauls before preservation, however, they can be sampled quantitatively; there have been numerous quantitative net studies of gelatinous predators in coastal waters. There have been sporadic efforts to count gelatinous zooplankton in situ (Alldredge 1972; Swanberg 1974, 1979, 1983; Hamner et al. 1975; Harbison et al. 1978; Biggs et al. 1981, 1987) and to count them remotely (Kremer & Nixon 1976) or even from the deck of a ship (Hamner & Schneider 1986). Most of the reports to date of the abundances of gelatinous predators have been based on net samples (Fraser 1970; Greve 1971; Anderson 1974; Hirota 1974; Larson 1986), sometimes including data on gut contents (Fraser 1970; Anderson 1974; Larson 1987).

Unfortunately very few studies have presented much quantitative information on the abundance and distribution of gelatinous zooplankton in the open sea. We know that the species found in oligotrophic ocean waters are usually less abundant in numbers m^{-3} than those found in coastal waters. Harbison et al. (1978) found that ctenophores were present in "abundance" (typically 1 to 40 animals per 10^3 m^3 for three oceanic species) at 70% of their dive stations in the Sargasso Sea. These were typical abundances; many of the species reported did sporadically occur in local abundances as high as 1 m^{-3} even though published zooplankton net records from those same areas gave no indication of their presence.

Based on abundance data of gelatinous zooplankton collected within the Norwegian Program for Marine Arctic Ecology (Pro Mare), we consider one species of cydippid, *Mertensia ovum*, to be of considerable ecological importance in the Barents Sea. There are also predatory ctenophores of the genus *Beroe* which are abundant and may play a role in controlling the population levels of *M. ovum*. There appear to be two forms or species of *Beroe* in the area; one, which we believe to be *B. gracilis*, is rather pale, flaccid, and a sluggish swimmer, while the other, *B. cucumis?*, is firm and robust, often bright red, and swims quite rapidly. The latter form feeds on *M. ovum*, from which it probably derives its red pigmentation.

M. ovum is is a large cydippid. Römer (1903) reported a maximum oral-aboral length of 80 mm and a maximum tentacle length of more than 50 cm in the adult. The extensive secondary tentacles of this species are filamentous, but quite strong and very sticky, rendering it capable of capturing both large and small prey as well as allowing it to cover a large area. For a 4 cm *M. ovum*, Madin (1988) reported the total tentacular length (including its 2000 tentillae spaced every mm along its 60 cm tentacles) as 161 m, the longest of any of those he ranked. Its encounter zone (the volume in which its tentacles are normally deployed) was 113,000 cm^3, representing a sphere of 30 cm radius. Unlike most cydippids, *M. ovum* does not have to completely cease feeding to consume prey caught in a tentacle, but can contract one tentacle while fishing with the other (Madin 1988). The species has a wide distribution (Mortensen 1912), occurring in the Norwegian, Greenland, and Barents Seas, and abundance records from Frobisher Bay, Canada, indicate that it may occur as a key organism in Arctic planktonic ecosystems throughout the year (Percy & Fife 1985; Percy 1989). In this paper we report the results of feeding experiments on small and medium sized *M. ovum*, the aim of these experiments being to elucidate the basic feeding dynamics of the ctenophore. We also report our results on the distribution and quantitative abundance of both this species of ctenophore and its principal predator in the open Barents Sea, and we make an effort to consider the potential importance *M. ovum* might have in this environment.

Methods

General

Ctenophores were carefully quantitatively removed from plankton hauls made during research cruises on the vessels G.O. SARS and R/V ENDEAVOR in the Barents Sea in May 1987 and July and August 1988. Fig. 1 depicts the general study area and the cruise tracks. Detailed descriptions of the general area and standard data on CTD and chlorophyll have been reported elsewhere (see Loeng et al. 1985; Skjoldal et al. 1986).

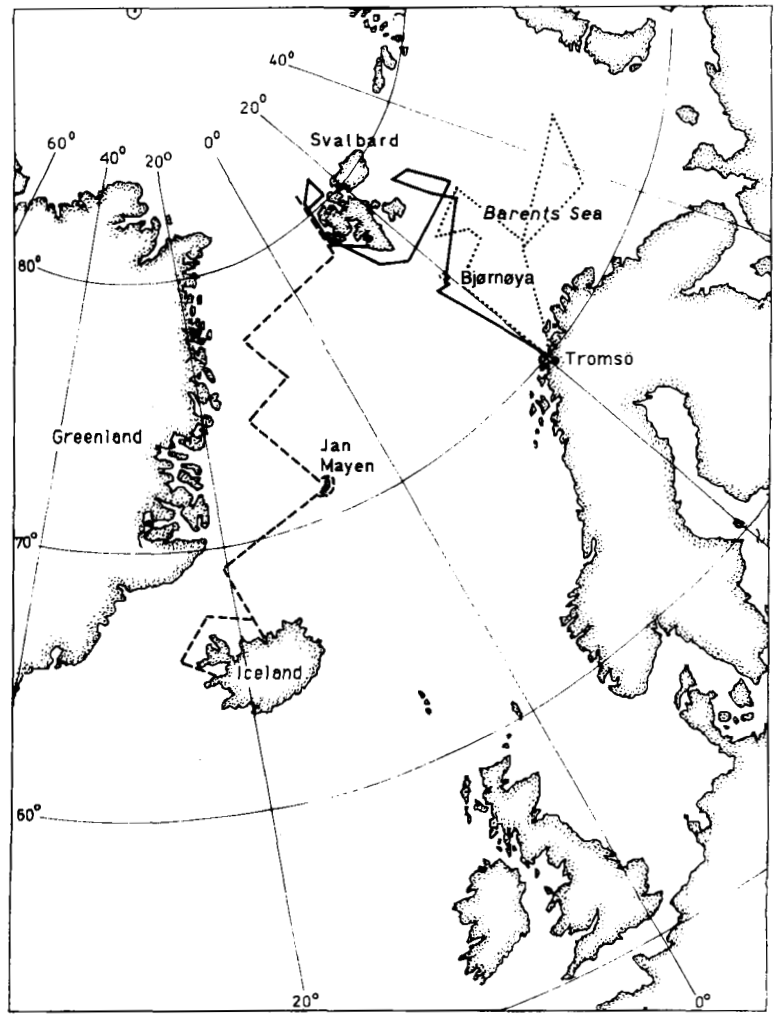

Fig. 1. The investigated area and the tracks of the R/V ENDEAVOR cruise 182 (broken and solid lines) and the G.O. SARS cruise in July 1988 (dotted line). Collections of *Mertensia ovum* for predation experiments were made at 34 stations on ENDEAVOR leg 2 (solid line) between 5 and 16 August 1988.

Collection and Measurement

Plankton samples were collected on all of these cruises using either stratified oblique hauls extending from the bottom to the surface with a 1 m^2 MOCNESS (mesh size of 333 μm), or vertical hauls using a WP-2 net (100 cm diameter, 180 μm mesh). As the Barents Sea is relatively shallow in many areas, not all hauls were of the same length. Live specimens of *Mertensia ovum* and *Beroe cucumis* were removed from the net samples, counted, and measured for size and total biomass before any preservation or freezing. Estimates of dry weight and ash-free dry weight were obtained by using a published regression (Percy 1989) on oral-aboral length.

Gut contents

After collection and measurement, most of those *Mertensia* which were intact and which were not used for experiments were used for gut content analysis. Their gastric cavities were excised and preserved in formaldehyde solution. These were then examined for identifiable remains under the microscope in the laboratory. All the copepods were measured, and, where possible, identified to species and stage.

Experimental methods

Ctenophores were collected by divers on leg 2 of R/V ENDEAVOR 182 (broken line, Fig. 1) using

Table 1. Mertensia ovum. Experimental conditions in the different predation experiments. A = single prey experiments; B = long-term experiments; C = multispecies prey experiments.

Expt. No.	Date	Temp (°C)	Vol. (litres)	Duration (hours)	No. of *Mertensia*	No. of prey	No. of prey types	*Mertensia* length (mm)	Type of experiment
1.	6/8	4–5	4	5	2–3	106	1[1]	8–24	A
2.	7/8	1.5	4[2]	12	1	8–64	1	12–21	A
3.	9/8	4–5	12	6.5	1	4–24	1	23–28	A
4.	10/8	4–5	170	43	2	174	1	15, 18	B
5.	10/8	4–6	2	7	1	20	1	7, 10	A
6.	12/8	4–6	16	12	1	45	3	27–32	C
7.	12/8	4–6	16	15	1	20	2	15–36	C
8.	13/8	4–6	16	65	1	16	1	24, 32	B
9.	13/8	4–6	16	8	1	20	2	31–40	C
10.	14/8	4–6	170	14	3	220	5	40–45	C
11.	15/8	4–6	170	11.5	5	200	5	26–55	C
12.	15/8	4–6	16	13.5	1	60	5	11	C
13.	16/8	4–6	170	10	5	307	6	40–50	C
14.	16/8	4–6	16	10	1	35	3	29–33	C
15.	17/8	4–6	16	20–100	1	16	1	37–45	B

[1] A mixture of small copepods dominated by *Pseudocalanus* sp., *Oithona similis*, *Microcalanus* sp. and young copepodite stages of *Calanus* sp.

[2] Experiment with 8 prey (1 litre^{-1}) was run in 8-l containers

standard methods for blue water diving and collection (Hamner 1975; Madin & Swanberg 1984). During this cruise *Mertensia ovum* was observed and collected on 59 out of 72 stations occupied (Harbison unpubl. data), thus indicating its wide distribution in the Greenland, Iceland, Norwegian, and Barents Seas. The ctenophores were captured in the upper 20 m where the temperature and salinity ranges were −0.2 to +5°C and 31–35‰, respectively. Most of the stations occupied were characterised by an upper layer with warmer, less saline water, separated from a colder, more saline water mass by a strong pycnocline at 15–20 m depth. The experimental animals were refrigerated immediately on collection and usually transferred from their collection containers to larger vessels within 2 hours.

Zooplankton prey were collected in a modified WP-2 net equipped with a large (20-l) cod end which was lined with a plastic bag; the bag could be removed from the cod end of the net and transferred to a larger container without necessitating the pouring of the contents. Plankton collections were diluted and prey organisms were separated from the remainder of the plankton soon after collection and held in 16-l stock containers on deck at 4–8°C until needed. Appropriate types of prey were selected manually under the microscope before each experiment.

Three types of experiments were performed with *M. ovum*. Table 1 summarises the experimental conditions employed. One set of experiments was run with a single prey type to evaluate the significance of prey concentration on predation rate (type A experiments in Table 1). A second set, using Stage V copepodites of *Calanus glacialis* as prey, was used to evaluate sustainability of predation rate (type B experiments Table 1). The third set of experiments was designed to evaluate predation rates in mixed prey populations (type C experiments in Table 1).

The type of experimental containers employed varied. In experiment no. 5, with very small ctenophores (ca. 1–2 ml volume), we used a 2-l beaker. Opaque plastic bags (ca. 4-l volume, 20 cm high, 15 cm diameter) and clear plastic bags (ca. 12-l volume, 32 cm high, 22 cm diameter) were used for small ctenophores in type A experiments (see Table 1). Most of the selectivity experiments (type C experiments in Table 1) were run in 16-l containers, either opaque plastic buckets or clear plastic bags (ca. 42 cm high, 22 cm diameter). One long-term experiment and three selectivity experiments were run in a large, opaque, covered polyethylene tank, filled to 170-l.

The experimental containers were filled with filtered seawater from the uncontaminated sea-

water lines. Initially this was filtered through a 180 μm mesh; we switched to 20 μm mesh when we discovered that there were a few small juvenile copepods in the seawater system which were passing through the 180 μm mesh. Based on replicate counts of these contaminants we determined that the abundance and biomass of potential contaminating prey organisms were too low relative to that of the introduced copepods to significantly affect the results of the early feeding experiments.

The experimental predators were placed in each filled container without prey and allowed to acclimate for 2–6 hours before an experiment was begun. Experiments with the large copepods and the chaetognath were started when a predetermined number and type of prey were introduced to the vessel; they were terminated when the ctenophores were removed. Visual inspection of the experimental vessels during the incubations always showed that the prey organisms were distributed in a relatively homogeneous manner in the vessels. Though the ctenophores were not monitored continuously, as this would disturb them, we did pay considerable attention to their behaviour. *M. ovum* normally sets its tentacles by swimming in a loose spiral and gradually relaxing its tentacles as they trace a path behind it. It then hangs motionless, usually mouth upwards (Madin 1988) in the water, with its ctenes beating rhythmically. This behaviour was observed in all of our experiments and the tentacle array did not appear to be noticeably limited by the vessel.

After termination of each experiment the water was filtered and the remaining prey organisms counted and dried at 50°C. Controls (containers with prey but without ctenophores) were initially used in all experiments, but as recovery from these containers was reliably 100%, further controls proved unnecessary in all but the experiments with small prey. The Arctic species of *Calanus* are large (frequently 5–10 mm in length) and conveniently pigmented bright red, rendering them easily recovered after an experiment. Recovery by filtration from even a large vessel is not particularly subject to error. A single copepod can readily be seen, and the containers were always carefully rinsed, filtered and examined after each experiment. Moreover the ctenophores' guts could be seen to be full of copepods after the experiments; there is thus every evidence that our values represent the true elimination of the prey by the ctenophores. The prey samples were stored dry and weighed on a microbalance when we returned to our laboratory ashore. Specimens of the chaetognath *Sagitta elegans* that were used as prey were selected as homogeneous size groups of animals for each experiment, differing in total body length between individuals by no more than a few mm. The body lengths of those *S. elegans* remaining after termination of the experiments were measured to the nearest 0.5 mm. Calculation of the dry weight was done by using an equation describing the relationship between body length and body mass (Matthews & Hestad 1977). All prey masses were converted to ash-free dry weight (AFDW) by using conversion factors from Båmstedt (1981). Ctenophore oral-aboral lengths were determined to the nearest mm to calculate the AFDW using the regression equations of Percy (1989). In experiments with small copepods we counted four subsamples of a stock suspension, and a measured volume of this was then added to each experimental vessel. A control without predator was run in parallel and the predation rate was defined as the difference between control and ctenophore vessels. The small copepods were not weighed but their average individual body mass was estimated from the species composition. We consider the procedures with small copepods to be less precise compared to those for larger prey organisms due to the smaller prey size and the subsampling procedure. The calculation of daily rations in the experiments were based upon AFDW of prey and predator. In this paper we use the term daily ration as daily consumption of prey biomass expressed as percentage of predator body mass. Further details of the experimental setup are given in Table 1.

All the experiments were carried out in calm weather, which prevailed during most of the cruise. During the long-term experiments we did not observe any change in predation rate or ctenophore behaviour, suggesting that the effects of ship vibrations and rolls were undetectable.

Results: abundance and distribution

May, 1987

On a cruise aboard G.O. SARS during May 1987 we collected our first detailed data on the distribution of *Mertensia ovum* and *Beroe cucumis*. During this cruise we found *M. ovum* at only 9

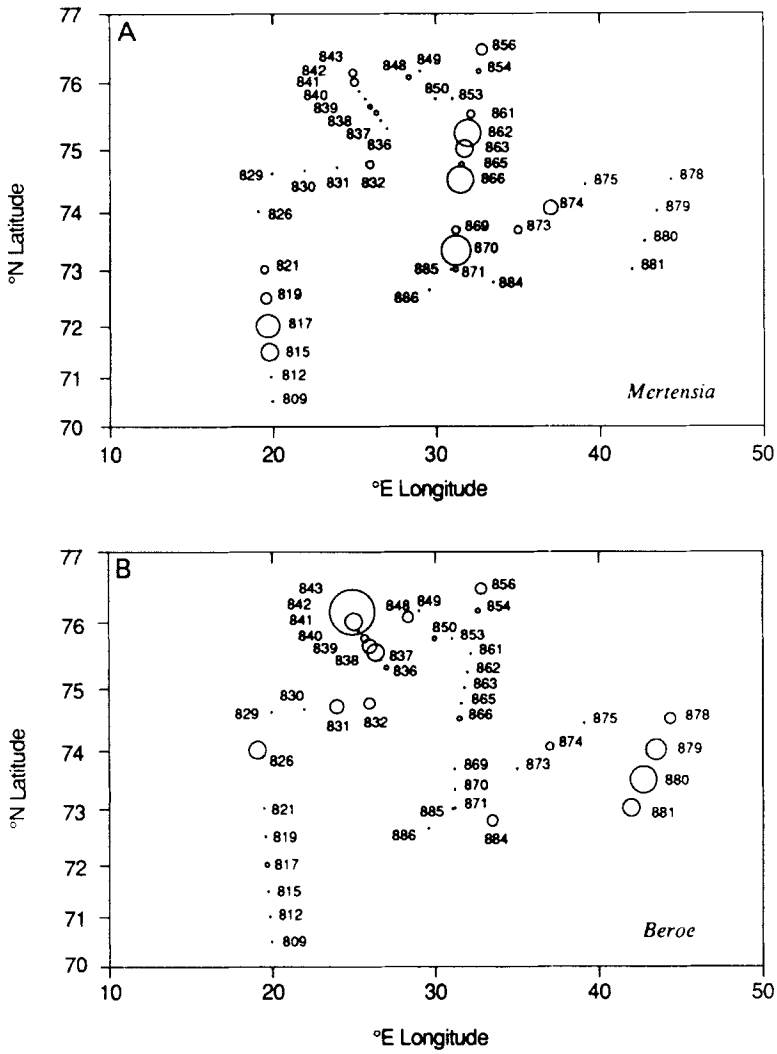

Fig. 2. Mercator Plots showing the horizontal distribution of abundance of ctenophores at stations during the G.O. SARS cruise. A. Numbers of *Mertensia*. B. Numbers of *Beroe*. In both figures the diameters of the circles are proportional to the square root of the numbers of organisms m^{-2}, so that their areas are proportional to numbers m^{-2}.

out of 19 stations where we looked for it, and collected and measured only 103 specimens. *Beroe* was found at 8 stations. Both species were most abundant in the 20–50 m zone. The average number of *Mertensia* collected in 1987 at stations where they occurred was 0.95 m^{-2} (0.003 m^{-3}, 200 mg AFDW m^{-2}). In their peak zone (20–50 m) their average abundance was 0.01 m^{-3} (0.54 mg AFDW m^{-3}). The maximum they attained in their peak zone was 0.14 m^{-3} (13 mg AFDW m^{-3}). The average abundance of *Beroe* at stations where it was encountered in 1987 was 0.29 m^{-2}; the average abundance in its peak depth zone was 0.004 m^{-3}; and the maximum abundance was 0.023 m^{-3}. These and other summarised results of the abundance of *Mertensia* and *Beroe*, including average size at stations where they were collected in both 1987 and 1988 have been presented elsewhere (Swanberg & Båmstedt 1991). Generally, the data suggest that abundances of both *Mertensia* and *Beroe* were lower in 1987 than in 1988. However, during 1987 we were focusing most of our attention on another group, and subsequent diver observations on the frequency of occurrence of ctenophores in the Barents Sea and other Arctic waters, as well as our size distribution data from both years, suggest that we cannot rule out the possibility that we had been missing a lot of small ctenophores of both species in 1987.

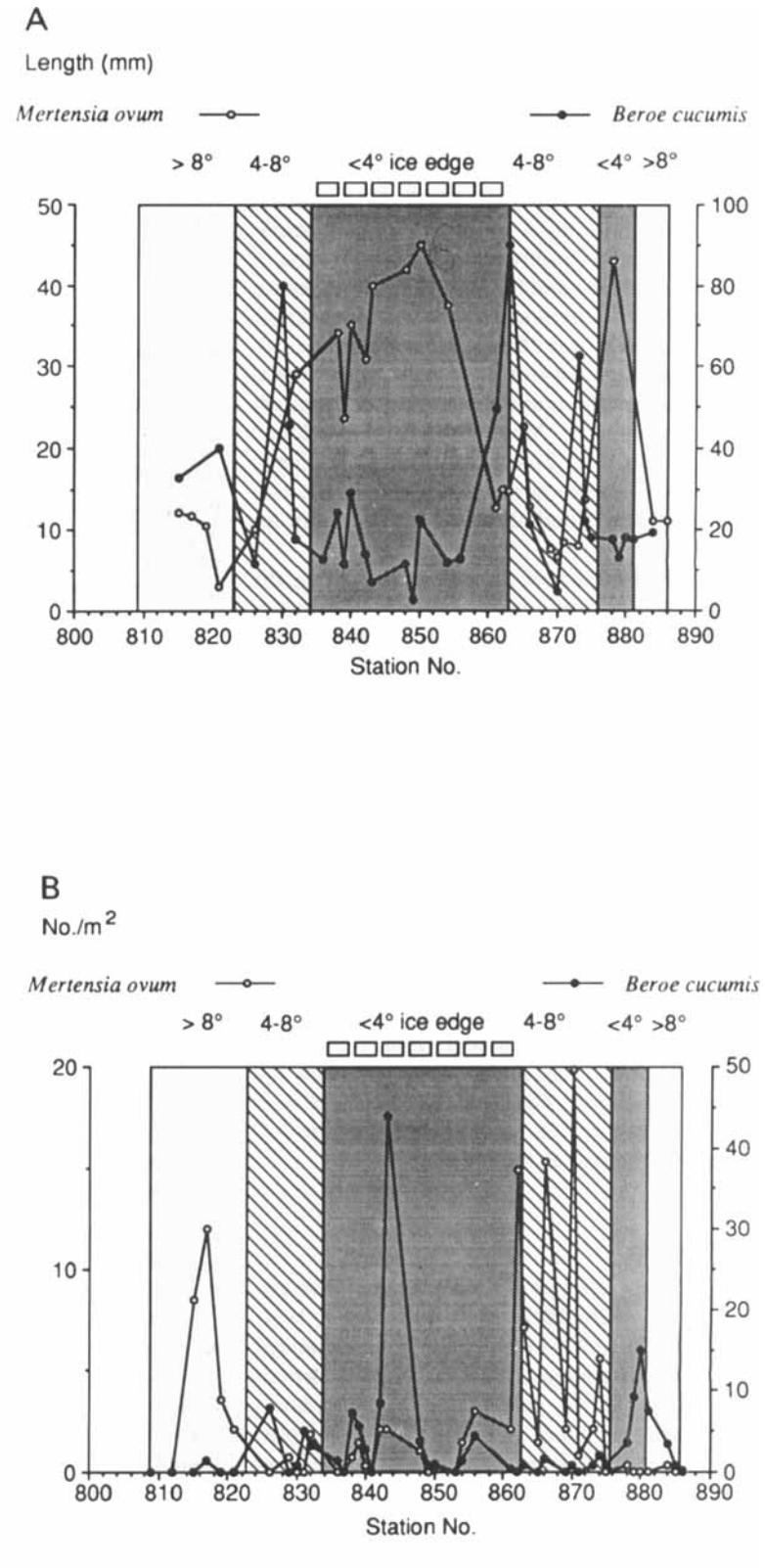

Fig. 3. A. Average size of *Mertensia ovum* (open circles, scale on left) and *Beroe cucumis* (solid circles, scale on right) plotted as a function of station number during G.O. SARS cruise. B. Abundance of *Mertensia ovum* (Symbols and scales as in A) and *Beroe* plotted as a function of station number on the G.O. SARS cruise. Various hydrographic portions of the cruise are denoted by shaded blocks, with the average local surface temperature and ice cover, as determined from satellite data, given above the graph.

July, 1988

In 1988 considerably more effort was devoted to quantifying the distribution of *Mertensia ovum* and that of its principal predator, *Beroe cucumis*. The vertical abundance of *Mertensia* nearly always reached its peak in the upper 50–100 m (see Swanberg & Båmstedt 1991). *M. ovum* was most abundant in a small group of stations (815–819) in the southwest and at a collection of stations (840–843 and 854–871) and along the ice edge mostly to the north and west. The average sized *M. ovum* was 16 mm, from which the calculated average ash-free dry weight for individual *Mertensia* for the cruise (Swanberg & Båmstedt 1991) was 14.0 mg. Most of the *M. ovum* found to the south (Fig. 2A) were juveniles (<15 mm oral-aboral length) however, so most of the biomass was distributed along the northwestern ice edge.

The distribution of *Beroe cucumis* along the cruise track is shown in Fig. 2B. The maxima of its distribution did not coincide with those of *Mertensia* (Swanberg & Båmstedt 1991), except at Stations 842 and 843 where they co-occurred in moderate abundance. Its vertical distribution was very similar to that of *Mertensia*. Similarly to *M. ovum*, the sizes of *Beroe* were inversely related to their abundance. The average abundance of *Beroe* at stations where it occurred (Swanberg & Båmstedt 1991) was 5.91 m^{-2} (0.021 m^{-3}).

There appeared to be a complicated inverse relationship between the size and occurrence of *Beroe* and *Mertensia* (Fig. 3A, B). Most of the small *Mertensia* were located in a rather large patch in an area in the southwest Barents Sea (Fig. 2A), where the largest numbers of the ctenophore were also found. *Beroe* was most abundant but smallest at the ice edge and largest in the 4–8° water; *Mertensia* was most abundant in the >4° water, but largest at the ice edge.

Gut contents

Ctenophores selected at random from 7 dive stations (nos. 1826, 1827, 1828, 1829, 1830, 1832, 1837) on the ENDEAVOR cruise were examined for their gut contents. A total of 73 copepods were found in the guts of the 32 ctenophores examined, 9 of which were empty. Of the copepods, 29 were *Calanus hyperboreus* Stage V or adult, 12 were *C. finmarchicus*, 1 was a *C. glacialis* female 10 were *Oithona* sp. and the remainder were unidentifiable. The overall average was 2.3 copepods per ctenophore (s.d. = 2.7), and the average in those which had eaten was 3.2; the maximum number found in any ctenophore was 10. The average number of copepods in the guts of ctenophores examined on any given dive (not including two dives where only one ctenophore was examined) ranged from 0.2 to 4.8 copepods per ctenophore.

Results: experimental

Predation rate in relation to prey abundance

Predation experiments 2 and 3 (in which Stage V copepodites of *Calanus glacialis* were used as prey) were designed to evaluate the importance of prey abundance (Fig. 4). The first experiment, with 1 to 16 prey l^{-1} and ctenophores varying in length from 12 to 21 mm, was run at 1.5°C in 4-l containers (except for one run with 1 prey l^{-1} in 8-l containers). This gave a non-linear response curve, with a probable saturation level of around 1 prey h^{-1}. Predation rates expressed as daily ration (again as ingestion of prey biomass as percentage of predator body mass, based on ash-free dry weight of predator and prey) indicated a saturation level around 150%. In the second experiment we used 12-l containers and prey concentrations from 0.3 to 2 prey l^{-1}, with the ctenophores varying in size from 23 to 28 mm. This experiment was run at 5°C, and showed the same non-linear response curve as in the other experiment, but this time with an apparent saturation level of 2–3 copepods h^{-1} (Fig. 4). However, expressed as a daily ration this corresponded to ca. 150%; the same value as in the first experiment.

Sustainability in predation rates

Long-term experiments were run in order to evaluate the sustainability of high predation rates in *Mertensia ovum* (experiment type B in Table 1). The prey abundances in experiments 8 and 15 were kept at 1 Stage V copepodite of *Calanus glacialis* l^{-1} (0.9–1.0 mg dry weight $individual^{-1}$) by regularly adding the same number that had been removed by the ctenophore during the preceding experimental period (2–11 hours). Animals varied in size from 24 to 45 mm body length and most of them showed a tendency towards

decreasing predation rate with time (Fig. 5). The average predation rate for the whole experimental period varied between 0.64 (38 mm ctenophore) and 1.16 (32 mm ctenophore) prey h^{-1}. The overall average predation rate in these experiments (based on 54 observations) was 1.0 prey h^{-1} (s.d. = 0.77). In experiment no. 4 we used 2 small (15 and 18 mm body length) *M. ovum* in a 170-l tank with 1 Stage V copepodite of *C. glacialis* l^{-1}, and these ctenophores had an average predation rate over a 43-hour experimental period of 0.55 prey h^{-1}. The predation rate, expressed as the daily ration, showed the same tendency of decreasing values during the long-term experiments (Fig. 5) and the average daily ration for the whole experimental period varied between 16% (45 mm ctenophore) and 58% (24 mm ctenophore). The overall average daily ration for the 5 animals was 35.7% (s.d. = 30.3). The two small ctenophores in experiment no. 4 showed an average daily ration of 76.8% over the whole 43-hour period.

Predation rates on multispecies prey assemblages

Table 2 presents a summary of the predation rates obtained in the experiments with different multispecies prey compositions. The experiment with small copepods (experiment no. 1) had the highest abundance of prey in terms of number, but the lowest in terms of biomass. The predation rate of the 4 ctenophores used varied between 2 and 5 prey h^{-1} or 19 and 51 µg AFDW h^{-1}, corresponding to a relatively low daily ration (Table 2). In the other experiments, with prey varying in size from 0.19 to 6.8 mg AFDW and in abundance from 1.2 to 3.8 prey l^{-1}, the daily ration was usually very high. In several experiments we recorded daily rations well above 100%. The highest one (210%) was determined for a ctenophore of 55 mg AFDW (32 mm body length) with a mixture of the three *Calanus* species as prey (experiment 6). The average daily ration for all experiments in Table 2 (n = 31) was 57.9%, with 95% confidence limits of 38.3 and 77.5%.

An index of electivity, E (Ivlev 1961), was calculated for each prey species in these experiments:

$$E = (r_i - p_i)/(r_i + p_i)$$

where r_i and p_i are the proportions of the prey species for the consumed and available prey populations, respectively. The results (Table 3) showed

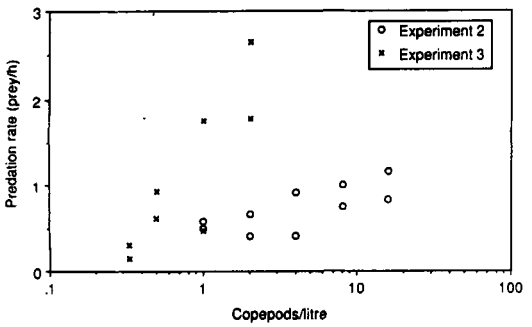

Fig. 4. Mertensia ovum. Predation on *Calanus glacialis* Stage V copepodites as a function of prey abundance. Each point represents one ctenophore. The two experiments differed in experimental conditions (see text).

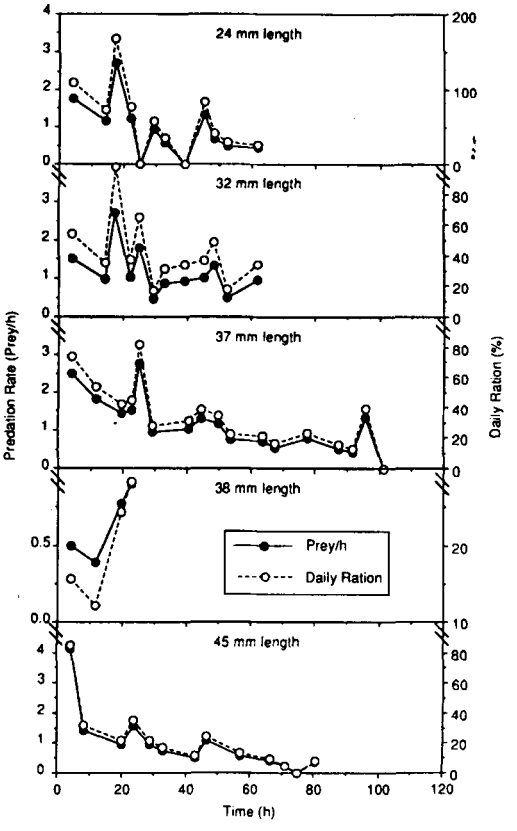

Fig. 5. Mertensia ovum. Predation rate (solid lines and filled circles) and daily rations (broken lines and open circles), based on AFDW of prey and predator, in long-term experiments (type B experiments in Table 1) for 5 ctenophore size categories with regular renewal of prey (Stage V copepodites *Calanus glacialis*).

Table 2. Mertensia ovum. Summary of predation rates in experiments with several types of prey. Weight of prey and predator given as mg ash-free dry weight (AFDW). N = number of *M. ovum* in the experiments; n = number of experimental setups. See also Table 1.

Expt. No	Duration (hours)	N	n	Prey conc./l No.	Prey conc./l mg AFDW	Prey weight	*M. ovum* weight	Predation rate prey ind.$^{-1}$ h^{-1}	Daily ration
1.	5	4	4	27	0.3	0.01	4.3–22.0	1.9–5.1	5.1–17.8
6.	12	4	4	2.8	3.2	0.2–5.3	39.6–55.2	1.8–3.5	79.9–209.5
7.	15	6	6	1.3	1.8	0.4–0.9	12.6–69.5	0.4–1.2	16.4–145.6
9.	8	6	6	1.3	0.8	0.3–0.8	51.9–85.5	1.8–2.5	16.9–52.2
10.	14	3	1	1.3	2.3	0.3–6.8	85.5–107.8	2.9	100.4
11.	11.5	4	1	1.2	1.3	0.3–7.5	36.8–159.3	2.3	117.5
12.	13.5	1	1	3.8	5.8	0.2–6.1	6.85	0.7	94.5
12.*	13.5	1	1	2.5	1.3	0.2–0.7			
13.	10	5	1	1.8	2.3	0.4–3.8	85.5–132.2	3.0	88.5
14.	10	5	5	2.2	1.3	0.2–0.8	45.6–58.7	0.3–1.1	6.5–23.2

* Prey concentration calculated excluding prey species that were not eaten

insignificant deviation of E from zero, and hence no selectivity towards any of the prey species used. This means that predation on each prey species in a mixture was directly related to the prey abundances.

Predation rate in relation to ctenophore size

Although our experiments were not specifically designed for an evaluation of the relationship between ctenophore size and predation rate, a visual impression is obtained by plotting the results from relatively uniform experiments. The results from experiments in 16-l containers were plotted (Fig. 6), and all the high predation rates in terms of prey biomass were found for animals larger than 25 mm body length. Expressed as a daily ration, the very low values were all represented by animals 29 mm or larger in body length. This suggests an increased absolute predation rate with size, in parallel with a decreased daily ration for the largest animals.

Discussion

Sources of Error

Sampling. – Though they may be very common (occur at a large number of stations), Ctenophora and other gelatinous predators usually occur in absolute abundances which are much lower than those of copepods and other crustacean predators. This does not mean they cannot be important predators; their predation rates, for example, and the amounts of water processed can be substantial. It is difficult, however, to sample them with equipment, such as plankton nets, designed primarily for sampling crustaceans. Even in cases where these delicate organisms are not damaged by the physical trauma of capture

Table 3. Mertensia ovum. Summary of the calculated index of electivity (Ivlev 1961) in the predation experiments with several prey species (experimental type C in Table 1).

Prey type	No. of experiments	No. of measurements	Electivity index for prey: Number Mean	Number SD	Number ± 95% C.L.	Biomass Mean	Biomass SD	Biomass ± 95% C.L.
Calanus finmarchius V	1	4	0.044	0.063	0.100	0.075	0.193	0.307
Calanus glacialis V	8	23	−0.139	0.235	0.102	−0.086	0.239	0.103
Calanus glacialis VI	4	4	−0.244	0.440	0.700	0.250	0.442	0.703
Calanus hyperboreus V	4	4	−0.126	0.558	0.888	0.241	0.441	0.702
Calanus hyperboreus VI	5	8	−0.070	0.457	0.382	−0.118	0.354	0.296
Metridia longa VI	7	19	0.028	0.221	0.107	0.201	0.235	0.113
Sagitta elegans	2	6	0.024	0.469	0.492	0.126	0.530	0.556

and preservation, it is rare that a net haul will sample a large enough volume of water to collect a statistically significant number of gelatinous predators; it is not unusual to collect one or a few ctenophores in a net with a thousand copepods. It is obviously because of this apparent low abundance that investigators have either ignored ctenophores or dismissed them as unimportant. Predators are usually lower in abundance than their prey, and a priori there is no reason gelatinous predators should be an exception.

There is another problem, however, in that we were usually sampling a three-dimensional environment with a one dimensional linear haul. These predators are often very patchy, both vertically and horizontally, a fact which became painfully obvious as soon as people started going into the environment either as divers or in submersibles. A plankton haul long enough to sample a considerable water volume has a relatively small probability of transecting a patch of zooplankton. While a vertical will necessarily pass through a stratified layer of predators, if this layer is very thin (as diver observations suggest they often are), it will only sample a very small volume of water in such a layer. Similarly an oblique haul will sample both horizontally and vertically, but the probability of its landing directly in a patch is relatively low. A horizontal haul, unless it happens to be at the exact depth of a layer of predators, may completely miss the patch of gelatinous predators. Some devout net samplers have argued, perhaps correctly, that given a sufficient number of lengthy hauls, this problem will disappear. Unfortunately, we rarely have a sufficient number of long hauls at any given place and time. More often we have one disappointingly short haul designed to sample copepods. The result is that occasionally (when these hauls happen to transect a patch) we encounter a large number of gelatinous predators in a net, upon which the haul is often judged to be a statistical fluke and either ignored or discarded as an unreliable sample. Unfortunately, this tends to reinforce the preconceived notion that these organisms are not important. In this project we have tried to avoid this problem by sampling as many hauls as possible and using the largest nets available. We were extremely fortunate in collaborating with a zooplankton research group which was aware of these problems and cooperated to the fullest. Nevertheless, many of our hauls were not as long as we might have wished

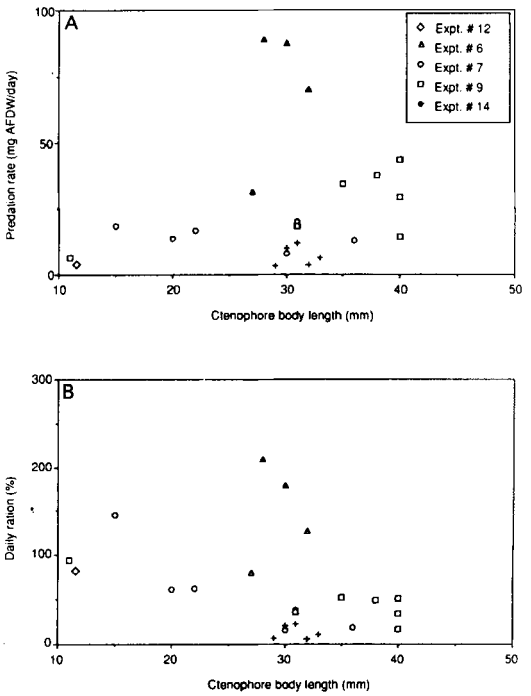

Fig. 6. Mertensia ovum. Predation rate (A) and daily ration (B) (based on AFDW of prey and predator) as a function of ctenophore body length in experiments carried out in 16-l containers.

to properly sample ctenophores; the average MOCNESS haul we had in May 1987 was 153 m^3; the average of all our hauls in 1988 was 96 m^3. It is reassuring that the average abundances obtained from the large number of hauls we made agrees between MOCNESS (oblique) and WP2 (vertical) nets, and we think the numbers per m^{-2}, may be fairly accurate, though a considerable source of error due to the small sample sizes affects the precision. Based on what divers have seen in the same area, it is our judgement that there are no stations where *Mertensia* is completely absent, and that the maximum values per m^{-3} are much higher than the nets indicate, while the average values per m^3 at a given station are likely somewhat lower because the nets tend to either sample patches of or no ctenophores.

The significance of experimental volume. – Most cultivation work with ctenophores has been done in vessels of around 20-l volume (Paffenhöfer & Harris 1979). Hirota (1972) used 1–18-l containers for *Pleurobrachia* of various sizes; Greve (1970)

reared *Pleurobrachia* to adult stage in 20-l vessels. In fact, most predation experiments with ctenophores have been done in containers ranging from 2 to 20-l, usually with several predators per container. Reeve et al. (1978) used 3-l vessels for small *Pleurobrachia* and cydippid larvae of lobates; Greene et al. (1986) used vessels smaller than 4-l for *Pleurobrachia*, and Reeve (1980) used vessels as small as 2-l for small *Pleurobrachia*. Aside from in situ enclosure experiments (Reeve & Walter 1976; De Lafontaine & Legget 1987) and deep vertical tanks, the largest experimental vessel size we have heard of was 120-l, used by Reeve et al. (1989) for experiments on *Mnemiopsis* with low prey concentration. The large container size was used to prevent prey concentration from being significantly reduced during the experiment. Even though fully grown adult *Mertensia ovum* are large ctenophores, the specimens we used were not larger than most of the ctenophores used in the above studies. Larger specimens, which have a tentacle spread similar to that of *Pleurobrachia* were used in 16-l containers. Ctenophores larger than 40 mm body length were almost exclusively studied in the 170-l container.

There is an obvious risk in using even these enclosures in predation experiments with cydippid ctenophores since any spatial confinement affects the behaviour of the prey as well as the radius of swimming possible in setting the tentacles. The latter may prevent total extension of the tentacles and thereby alter the predation capacity either up or down (Madin 1988). We therefore consciously used small ctenophores in most experiments, except in experiments with 170-l volume. We also inspected the experimental animals during the precondition period in order to detect any abnormal behaviour. The few specimens that did not adopt a typical "fishing" behaviour (see above) during the acclimation period were not used further. No ctenophore experiment was used where the predator was observed to be lying on the bottom of the vessel. When the predation rate (expressed as the daily ration) was plotted against the prey concentration, separately for each different container volume, there was no clear indication of an effect of container volume in our experiments (Fig. 7) in any but the smallest container sizes. Therefore, while we recognise that container size is probably a source of error in this and all other investigations of ctenophores (De Lafontaine & Legget 1987), we consider it minor here.

The relevance of the results for situations in natural habitats

We estimated the digestion rate of *M. ovum* in one of the predation experiments (experiment no. 11 in Table 1). Between 27 and 33% of the consumed prey remained identifiable in the guts of the ctenophores after an incubation period of 11.5 hours. If we assume constant predation and digestion rates throughout the experiment this indicates that the gut turnover time was between 3.1 and 3.8 hours, a turnover rate of 0.26–0.32. If this rate were applied to the field-collected ctenophores, then they would have a maximum predation rate of 2.4–2.9 *Calanus* h^{-1}, a value which corresponds startlingly well with the highest rates observed in our experiments. Moreover, the frequent occurrence in the field of ctenophores with empty guts enhances the credibility of our results for predation response in low concentrations of prey. Based on net samples, the maximum abundance in vertical profiles of *Calanus* spp. in the Barents Sea only exceptionally exceeds a few hundred individuals m^{-3} (Rey et al. 1987; unpubl. cruise report data from the Institute of Marine Research, Bergen) and the predation rate at such low abundance of prey indicate that *M. ovum* with empty guts should be common in the field. This does not mean that our experiments, which were normally run at higher abundances, are invalid. We were specifically interested in the potential behaviour of the ctenophore in dense patch situations where the local

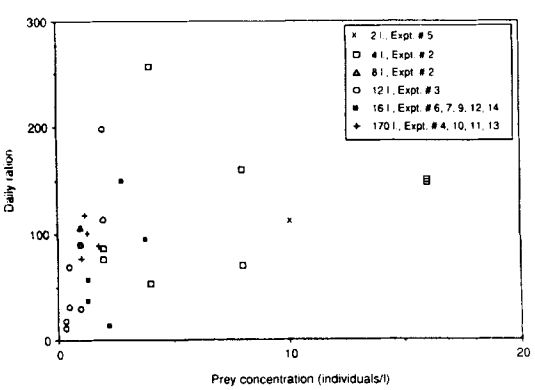

Fig. 7. Mertensia ovum. Scatter diagram of the predation rate (expressed as the daily ration, based on AFDW of predator and prey) as a function of prey concentration for various volumes of experimental container. Each plot for the experiments in 16- and 170-litre containers represents the average value for 2–6 *M. ovum*.

abundances exceed even those of our experiments.

Our results also show that chaetognaths were preyed upon as frequently as would be expected from their abundance and biomass (cf. Table 3), and visual observations on specimens kept in large deck tanks showed that *M. ovum* was even able to catch large amphipods (*Parathemisto libellula*) and euphausiids (*Thysanoessa* sp.). These experimental results have not yet been confirmed from gut content analyses of field collected animals, although a few specimens collected by a multiple pelagic trawl during an earlier cruise (R/V G.O. SARS, Pro Mare cruise no. 15, July 1988) contained a euphausiid. A plausible explanation for this apparent discrepancy is that we haven't many gut analysis data and these potential prey organisms are considerably less abundant than the copepods; chaetognaths, for example, are usually found in numbers lower than 10 m^{-3} (Tone Falkenhaug pers. comm).

Food utilisation

Our results show that high concentrations of zooplankton can be efficiently utilised by *Mertensia ovum* through extremely high predation rates, corresponding to maximum daily rations of more than 200%, a value comparable to the high values reported for the smaller cydippid, *Pleurobrachia bachei* (Reeve & Walter 1978; Reeve 1980). However, our results from the long-term experiments also suggest that such high predation rates can only be maintained for a restricted time, probably not more than a day, and that satiation causes the animals to reduce their predation rate gradually thereafter. Such a behavioural adaptation to excess food has been reported for ctenophores earlier (Reeve & Walter 1978). Because any food intake in excess of the metabolic requirements will permit growth, it is important to define how much of the daily ration is used for maintenance. Percy (1988) investigated the metabolic rate of *M. ovum* from Frobisher Bay, Canada, during the spring, summer and winter. In summer the average in situ respiration and excretion rates at close to 0°C were 525.6 µl O_2 g^{-1} AFDW h^{-1} and 3.3 µg-at NH_3–N g^{-1} AFDW h^{-1}, respectively (from Percy 1988, and biometric relationships given in Percy 1989). The corresponding energy losses at 5°C are then, respectively, 15.39 and 1.71 J g^{-1} AFDW (1 ml O_2 = 20.2 J, 1 mg ammonium–N = 24. 86 J, from Elliot & Davison 1975; Q_{10} for respiration = 2. 1, for excretion = 1.7, from Percy 1988). Metabolic losses due to respiration and ammonium excretion then amount to 410 J g^{-1} AFDW d^{-1}. The energy content of the ctenophores can be estimated from a general conversion factor between AFDW and joules. Norrbin & Båmstedt (1984) gave a mean value of 23.85 J mg^{-1} AFDW for 42 species of marine invertebrates. If this value is applied, the daily metabolic energy loss of *M. ovum* corresponds to 1.7% of the energy content. The most probable source of error in measuring the respiration of this ctenophore is that in confinement to the very small vessels required to detect a change in oxygen concentration, the animal is put in a situation very different from its normal resting feeding posture. These respiration values are quite possibly overestimates. This means that 1) *M. ovum* can grow or produce eggs even when the prey abundance is rather low, and thereby the predation rate is low, and 2) that after an exploitation of a zooplankton patch it can probably survive for a very long time (Larson & Harbison 1989).

Small copepods were only found occasionally in the guts of field collected specimens (4 out of 32 specimens contained between 1 and 6 *Oithona*), but our experimental results indicate that *M. ovum* may achieve a considerable part of its daily ration from such a prey source, given that they contribute significantly to the total available prey biomass. The discrepancy in the results from deck experiments and field samples is therefore either explained by a low ambient abundance of this prey or by a faster digestion rate for it than for the larger copepods. The largest ctenophore used in the experiment with small copepods was 20 mm (22.0 mg AFDW), corresponding to a predator:prey body-mass ratio of 2200:1.

Our results on predation in mixed prey populations do not provide any strong evidence for selectivity on any of the *Calanus* species or the chaetognath. Hirche (1987) recorded a uniform swimming speed (1 cm s^{-1}) for the four copepod species used in our experiments. The species differed in the proportion of time spent swimming, which was rather small for all three *Calanus* species, higher for *Metridia longa*. Differences in the natural encounter rate for the three *Calanus* species will therefore be determined almost exclusively by their abundance. As our results also indicate a very low critical ratio between prey size and predator size (see Expt. 1, Table 2) we

have assumed that the prey susceptibility is the same for all prey species used in our study, and 100% for the main part of the population of *M. ovum*. Prey vulnerability on the *Calanus* species would then solely be an effect of prey abundance, and high predation rates in the natural habitats probably occur only in prey patches.

Sagitta elegans is considered as an ambush, raptorial predator (Greene 1986) that rests motionless in the water. If this characterisation is valid, then this behaviour would generate a negative electivity index for *S. elegans* as prey (lower encounter rate compared to swimming copepods). This was not confirmed in our experiments. However, the behavioural studies on *Sagitta hispida* by Feigenbaum & Reeve (1977) highlight the importance of a vertical swimming cycle for the occurrence of predator/prey interactions. This species alternated between a slow sinking (4.4 mm s^{-1}) and a fast upward swimming (44 mm s^{-1}), with an average swimming speed for the whole cycle of 8 mm s^{-1}. If such a "hunting" behaviour is common among chaetognath species it challenges the validity of defining chaetognaths as true ambush predators.

Summary and conclusions

Considering the ability of *Mertensia* to feed at high rates in the presence of abundant prey, it would be prudent strategy for prey to minimise the predation from ctenophores by avoiding aggregation entirely, or by maintaining spatial separation between its aggregations and those of its predator, i.e. aggregating away from the peak in the vertical distribution of the ctenophores. In shallow coastal waters a restricted depth may limit the option of vertical avoidance by the prey, and ctenophore predation may significantly reduce copepod populations in such environments (Kremer 1979; Deason & Smayda 1982). In deep environments, where ctenophores may occur in high abundance, the impact from ctenophore predation seems to be less significant (Hirota 1974), and the deep water may therefore function as a refuge for the prey. This might be the reason that *Mertensia ovum* does not eliminate the copepod populations in the Barents Sea. We consider a detailed study of the dynamic vertical distribution of this predator and its prey to be an important goal for the future.

Estimate of potential impact: M. ovum

The problem of assessing the overall impact of the predator in a large area is complicated because it depends on patchiness and size distributions of both *Mertensia* and its prey as well as of *Beroe*, the most probable principal predator of *Mertensia*. If one accepts our coverage of a fairly large area of the Barents Sea to be representative of the area in general, then we can use the actual numbers and sizes of organisms (including those stations examined where they were absent) to calculate the biomass of *M. ovum* at each station in 1988. Using the lowest average value for daily ration obtained from our predation experiments, and measurements for zooplankton biomass for these same stations provided by the Marine Research Institute (Skjoldal et al. unpubl. data), we estimated the impact on copepod populations of *M. ovum* at the stations occupied in 1988 (Table 4). The result, depending on the abundances of ctenophores relative to copepods, ranged from 0.002 to 9.2% of the copepod biomass per day where ctenophores were present, with a mean of 0.69% (N = 44; s.d. = 1.52%). Considering the slow generation turnover rate of the dominant copepod species (Tande et al. 1985), this must represent a substantial part of the copepod production. If these abundance and predation levels were maintained, then the population of these copepods would be halved in approximately 100 days. Even if the copepods were to find refuge in the winter by dropping to levels where *Mertensia* does not occur, during the spring and summer *Mertensia* could account for a substantial proportion of the copepods. Moreover, *Mertensia* is only one among a number of gelatinous predators in the area, each of which also consumes a small portion of the production. We suggest that the sum of these small portions is far from insignificant.

Mertensia is capable of storing fairly large lipid reserves (Larson & Harbison 1989). Though relatively unusual for gelatinous predators, this is a common trait for Arctic organisms. This ability to store energy, and its relatively low respiration (Percy 1988) means it can survive for long periods without prey. The evidence (Swanberg & Båmstedt 1991; Ospovat pers. comm.) that *Mertensia* is present under the Arctic ice pack suggests that it may be present when the copepods move up in the spring. It also means we must consider its predatory behaviour as being potentially impor-

Table 4. Calculation of the biomass of *Mertensia ovum* and its consumption of copepods is based on the average size and abundance of *Mertensia* at each station. The calculation includes zero values (blanks in table) and assumes a daily ration of 16%. The biomass of copepods is estimated as the total biomass of three zooplankton fractions (>180 µm, >1000 µm and >2000 µm). These measurements were taken at these stations by the Marine Research Institute (Bergen) as g AFDW m^{-2} in vertical hauls from the bottom to the surface. An average copepod biomass of 0.3 mg AFDW is used to estimate the number of copepods consumed per ctenophore.

Station No.	Abundance *Mertensia* m^{-2}	*Mertensia* measured	*Mertensia* Length	*Mertensia* Individual mg DW	*Mertensia* Individual mg AFDW	*Mertensia* Biomass mg AFDW m^{-2}	Copepod biomass consumed daily	Equivalent No. of copepods	No. copepods per ctenophore	Copepod biomass g AFDW m^{-2}	Percentage consumed daily
809										58.1	
812										12.6	
815	8.51	12	12.0	20.2	8.12	69.0	11.0	36.8	4.33	4.19	1.65
817	12.0	19	11.8	19.3	7.81	94.1	15.1	50.2	4.16	5.49	1.71
819	3.54	5	10.4	14.9	6.14	21.8	3.48	11.6	3.27	3.04	0.72
821	2.13	1	3.00	1.07	0.54	1.15	0.18	0.61	0.29	18.6	0.01
826	0.03	2	10.0	13.7	5.68	0.16	0.03	0.08	3.03	7.14	.002
829	0.71	1	17.0	42.1	16.0	11.4	1.82	6.06	8.55	2.98	0.38
830										0.77	
831										5.15	
832	1.82	4	29.0	130	45.6	83.1	13.3	44.3	24.3	7.69	1.08
836										5.98	
837										6.66	
838	0.76	6	34.2	185	62.8	47.4	7.59	25.3	33.5	15.4	0.31
839	1.42	2	23.5	83.6	30.2	42.8	6.85	22.8	16.1	5.74	0.75
840	0.35	1	35.0	194	65.8	23.3	3.73	12.4	35.1	5.85	0.40
841										4.39	
842	2.10	15	30.9	149	51.5	108	17.3	57.5	27.5	4.61	2.34
844	2.13	3	40.0	258	85.4	182	29.1	96.9	45.6	1.98	9.16
848	1.06	3	42.0	286	94.0	100	16.0	53.3	50.1	13.0	0.77
849										7.76	
850	0.24	2	45.0	330	108	26.2	4.20	14.0	57.4	7.49	0.35
853										8.92	
854	1.42	13	37.5	224	75.2	106	17.0	56.8	40.1	7.51	1.42
856	2.96		20.3[1]	61.3	22.7	67.1	10.7	35.8	12.1	4.68	1.43
861	2.13	6	12.7	22.6	9.02	19.2	3.07	10.2	4.81	9.58	0.20
862	14.9	21	14.9	31.9	12.4	185	29.5	98.4	6.61	14.6	1.26
863	7.09	10	14.7	31.0	12.1	85.6	13.7	45.6	6.44	17.8	0.48
865	1.42	2	22.5	76.2	27.7	39.3	6.29	21.0	14.8	24.1	0.16
866	15.4	35	12.8	23.2	9.25	142	22.7	75.8	4.93	33.7	0.42
869	2.13	3	7.67	7.81	3.38	7.19	1.15	3.83	1.80	9.81	0.07
870	19.8	28	6.75	5.97	2.64	52.3	8.37	27.9	1.41	9.85	0.53
871	0.80	2	8.50	9.72	4.14	3.31	0.53	1.76	2.21	7.46	0.04
873	2.13	6	8.00	8.55	3.67	7.81	1.25	4.17	1.96	13.3	0.06
874	5.57	25	13.8	26.9	10.6	59.1	9.45	31.5	5.66	1.69	3.50
875										15.6[2]	
878	0.33	1	43.0	300	98.4	32.5	5.20	17.3	52.5	9.54	0.34
879										12.0	
880										13.3	
881										6.75	
884	0.30	2	11.0	16.8	6.85	2.09	0.33	1.11	3.65	24.0	0.01
885										4.30	
886	0.11	1	11.0	16.8	6.85	0.73	0.12	0.39	3.65	11.8	0.01
Average:	2.64	231 (total)	20.3	61.3	22.7	37.6	6.03	20.1	11.1	10.8	0.69

[1] As *M. ovum* was present, but no ctenophores were measured at this station, the overall average value for average size at these stations was used here.
[2] At this station the >2 mm fraction was lost after measuring dry weight, so it was estimated from the ratio for the >1 mm fraction DW and added to the other values.

tant year-round. It is generally assumed that overwintering is a refuge for copepodites, but it may be overwintering with predation, depending on the role of vertical stratification. If so, then the principal refuge for the copepods may be in their stratification behaviour.

An effort was made in an earlier paper (Swanberg & Båmstedt 1991) to consider the probable importance of stratification of predator and prey on the feeding potential of *M. ovum*. We still know virtually nothing about the behavioural coupling between *Mertensia* and its prey, either during the peak growing season or during the long winter months. While there are (or will be) data available on the vertical and horizontal distribution of primary production and copepods in the area, our experience suggests that these are not adequate to thoroughly evaluate this factor. On one cruise we had in situ observations which suggested that the relationship between vertical distributions of phytoplankton, larvaceans, pteropods, copepods, chaetognaths, ctenophores, and other large members of the biotic community needs to be resolved on a vertical scale of a metre. Our modelling effort on the role of vertical stratification on *Mertensia* feeding potential seemed to confirm this. Unfortunately, the resolution we have with conventional equipment cannot approach this scale, and until we have this information, we cannot go further in estimating the role played by these and other large predators.

Finally, we have presented evidence that the abundance and distribution of biomass of *Beroe*, the principal known predator of *M. ovum* is inversely related to those of its prey. Other studies (Kamshilov 1955, 1960; Swanberg 1974; Greve 1970, 1971, 1981) have documented that *Beroe* feeds on and controls populations of other ctenophores, and there is no reason to think this does not act as a limiting factor in the Arctic. We have virtually no data of high spatial resolution on the distribution of the two organisms, and neither feeding rates nor gut contents of the predator have been assessed. *Beroe* feeds very differently than other ctenophores, and its predation rate is largely density dependent, though it may employ a chemokinetic search strategy (Swanberg 1974). Obviously we need to understand much more about the biology of the Arctic *Beroe* species before we can go much further in predicting the potential population growth of its prey.

While the large-scale abundance of the principal (most abundant) organisms in the ecosystem is indeed necessary information for estimating stocks and managing fish quotas, it is not sufficient information for modelling the system. The behaviour, feeding processes, population and individual growth rates and reproductive potentials of Arctic predators such as the large ctenophores *M. ovum* and *Beroe cucumis* must be studied in more detail before a more meaningful evaluation of the role of gelatinous organisms in high-latitude environments can be made.

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