

Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum**

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ABSTRACT: The natural history of ctenophores from the Resolute Passage area of the Canadian High Arctic was examined in 1985 and 1986. The seasonal abundance of 3 ctenophore species, *Mertensia ovum*, *Beroë cucumis*, and *Bolinopsis infundibulum*, are reported. *M. ovum* was by far the most abundant, accounting for 88.9 % of all ctenophores collected, and because of its abundance received the most study. The *M. ovum* population developed similarly in both years reaching a maximum abundance of 911 m⁻² in early June 1986. The lipofuscin age-pigment technique suggested that *M. ovum* can live for at least 3 yr. Gut contents showed *M. ovum* to be an opportunistic feeder, but the copepods *Pseudocalanus acuspes*, *Calanus glacialis* and *C. hyperboreus* and the amphipod *Parathemisto libellula* formed most of the diet. *M. ovum* was estimated to consume between 4 and 10 % d⁻¹ of the standing crop of macrozooplankton in Resolute Passage.

INTRODUCTION

In the marine ecosystem, gelatinous predators appear to be important regulators of prey populations and control their own populations by preying on each other and their own offspring (Kremer 1976, Reeve et al. 1978, Greve & Reiners 1988, Purcell 1991). They feed at all levels in the food web, thereby acting both as predators of and potential competitors with fish and other zooplankton (Möller 1980, Shushkina & Musayeva 1983, Purcell & Grover 1990). These predators can have daily rations exceeding 1000 % of their body weight which can be converted into rapid growth rates (Reeve et al. 1978). High feeding rates, combined with rapid growth, show that control of zooplankton populations is within their capabilities (Greve & Reiners 1988). Control of copepod population growth keeps phytoplankton populations from being overgrazed (Greve & Reiners 1988) and algal growth may be enhanced by the return

of dissolved nutrients through excretion into the water column (Biggs 1977, Park & Carpenter 1987).

In the Canadian Arctic, a single ctenophore species, *Mertensia ovum*, makes up 60 to 95 % of the total calories in the macrozooplankton community (Percy & Fife 1985). However, until fairly recently the ecology of this important predator had not been investigated. Percy (1989) found a population in Frobisher Bay that varied little in abundance over the year, although it was considerably smaller than populations offshore in Baffin Bay (Huntley et al. 1983, Percy 1989). Swanberg & Båmstedt (1991) have recently modelled the predation potential of *M. ovum* in the Barents Sea, estimating that this population could consume between 1 and 5 % d⁻¹ of the copepods in the water column.

Here, we examine the role of ctenophores in a high arctic marine ecosystem, first by giving a brief account of the natural history of the ctenophores in Resolute Passage (Northwest Territories, Canada), and second by describing the feeding ecology of the dominant gelatinous zooplankton, the cydippid ctenophore *Mertensia ovum*.

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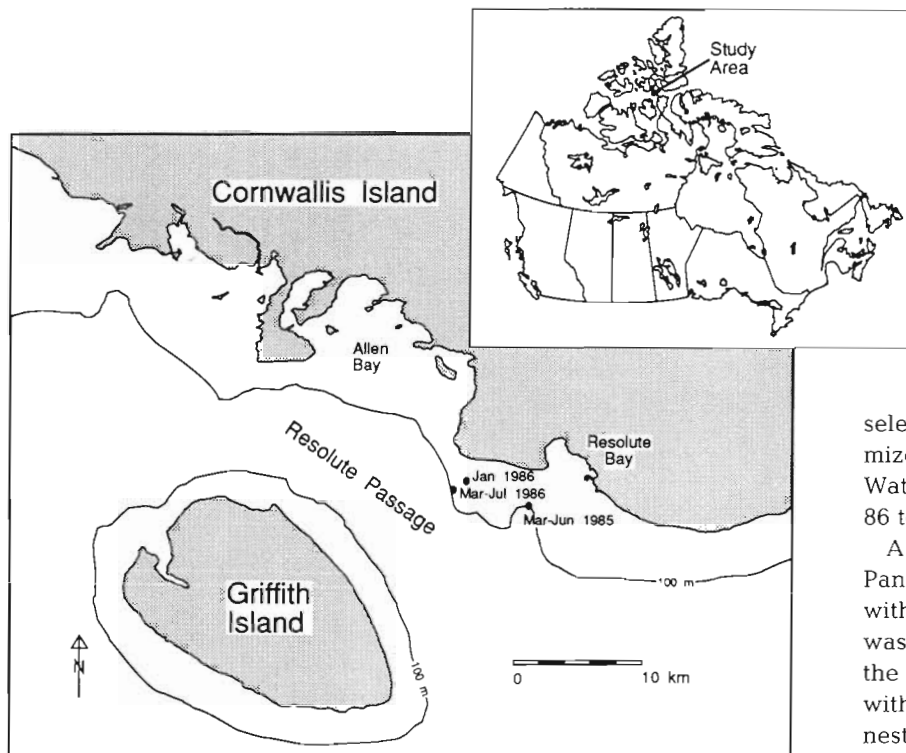


Fig. 1 Sampling locations occupied in the study area during the field seasons of 1985 and 1986

STUDY AREA AND METHODS

Study area. Resolute Passage ($74^{\circ} 40' \text{ N}$, $95^{\circ} 10' \text{ W}$) is located in the central Canadian Arctic Archipelago and separates southwest Cornwallis Island from Griffith Island (Fig. 1). The passage has a maximum depth of 168 m, but water entering from the west must pass over a sill at a depth of 125 m. The physical oceanography of this section of the Northwest Passage is complex. Water from several different sources can enter the passage depending on local meteorological and tidal conditions (Prinsenberg & Bennett 1987). Peak flow in the water column can reach 40 to 50 cm s^{-1} during spring tides (Prinsenberg & Bennett 1987, 1989), but the mean residual current moves water eastward toward Lancaster Sound at about 6 cm s^{-1} (Prinsenberg & Bennett 1987). Land-fast sea-ice up to 2 m thick is a persistent feature in Resolute Passage. The Passage is normally frozen over from November to July. Once frozen, the ice sheet is usually quite solid with few or no leads.

Sampling. Ice season: Sampling during the fast-ice season was conducted during 3 periods: 20 March to 12 June 1985, 8 to 18 January 1986, 20 March to 8 July 1986. The position of each camp (Fig. 1) was influenced by the availability of relatively smooth ice and sufficient water depth. A large, uniformly flat pan of ice as close to the 100 m contour as possible was

selected as a sampling site to minimize turbulence in sub-ice waters. Water depths at the sites varied from 86 to 99 m.

A heated portable shelter (Parcol, Panabec Ltd, Montreal, PQ, Canada), with a diesel-generated power source was erected over a $2 \times 1.5 \text{ m}$ hole cut in the sea-ice. Samples were collected with a 1 m diameter, opening/closing, nested, double net (3 mm inner and $202 \mu\text{m}$ outer net) specially rigged for horizontal 'towing' through sea-ice using the tidal currents to stream the net (Siferd & Conover 1992). Approximately biweekly horizontal samples were taken at 2, 10 and additional 10 m intervals to the nearest interval above the bottom, considering the bottom of the ice to be zero depth. All horizontal collections were metered to give the volume of water filtered. The duration (ca 15 to 25 min) of the tow varied with current speed so that ca 150 to 200 m^3 of water was sampled. Since currents were necessary for sampling, collections were made opportunistically without regard to time of day or tidal stage. However, an entire set of tows from top to bottom was attempted with the tide running in a single direction, either ebb or flood. When this was not possible, the set was completed on the returning tide. Inner course-net samples were enumerated as they were removed from the net. *Mertensia ovum* were removed and individually frozen (-20°C) for further analyses. Other ctenophores were counted and then discarded; individuals of any species $< 3 \text{ mm}$ in diameter and ctenophore eggs were enumerated from a subsample of the outer net sample after preservation in 3 to 4 % formalin.

Open-water season: Open-water samples were collected from a 7 m vessel for the periods 20 July to 30 August 1985 and all August 1986 near the depth and position of the ice station of that year. Samples were collected at approximately 20 m depth intervals from the surface to the bottom, using the same double net rigged for towing with a bridle to keep the mouth

vertical. However, because phytoplankton often clogged the outer, finer, net, only the inner net was towed horizontally to collect large specimens and a choke line was added to close it at depth. The water volume filtered was estimated from a flowmeter suspended at 10 m, assuming net efficiency was 100 %. Samples for ctenophores <3 mm during the summer were collected at 10 m intervals from top to bottom with a vertically hauled, 0.5 m closing net of 202 μm mesh. In this paper abundance describes the number of individual ctenophores m^{-2} , assuming a water column of depth to the bottom, and density indicates the number of ctenophores m^{-3} of water.

Digestion rate. Paired, glass aquaria were constructed to maintain live ctenophores utilizing the principle of the 'Doppelkuvette' (Greve 1970) as modified by Bell (1989). Each aquarium had 2 chambers, measuring $90 \times 60 \times 15$ cm (height \times length \times width) and each held ca 80 l of water. Each had an airlift pump which circulated the water in a slow clockwise direction. The aquarium was placed in a 225 l polyethylene tank, cooled by water pumped directly from the sea, but, as only about one-quarter of each aquarium was submerged, the equilibrium temperature was 0.0 to 1.5 $^{\circ}\text{C}$, ca 1.5 to 3 $^{\circ}\text{C}$ above ambient (ca -1.5 $^{\circ}\text{C}$).

Digestion rate was determined on SCUBA-diver-procured *Mertensia ovum*. Individuals were collected in 75 mm diameter \times 160 mm PVC tubes closed with rubber stoppers. The tubes were kept in a pail of seawater to help maintain their temperature until they could be transferred to the aquaria, usually within 30 min. Ctenophores were released directly into an aquarium, previously filled with 50 μm screened seawater. No more than 3 individuals were placed in one chamber of an aquarium. Ctenophores generally resumed active swimming and extended their tentacles within 15 min of their release. Specimens were allowed to acclimate for 24 h prior to experimentation. A 'prey' aquarium was stocked with copepods between 250 and 500 μm screened from a net tow. Ctenophores were carefully dipped from the holding tank in a large plastic beaker and placed in the prey aquarium until they were observed to feed. They were then placed in a prey-free aquarium. With larger prey (>1 mm), ctenophores were fed by pipetting individual copepods of known size and species directly to the tentacles. The behavior of the ctenophores was observed and times of ingestion and removal of the tentacle from the mouth noted. Individual ctenophores were removed at 30 min intervals from 1.5 to 4 h and frozen (-20 $^{\circ}\text{C}$) to stop the digestion process.

Later specimens were thawed and prey examined for state of digestion under a dissecting microscope. In early digestion, the copepod body was softened and

some appendages might be disarticulated. Moderate digestion showed internal tissue loss and many appendages disarticulated. In late digestion body segments were separated and most of the internal tissue was gone. In extreme digestion only the carapace parts remained. Digestion time was taken as time to extreme digestion. Using the same criteria for digestion in gut contents of net-caught specimens, we found no evidence for net feeding.

Gut contents. All *Mertensia ovum* collected in the net tows were examined for gut contents. Before thawing a specimen, the polar (oral-aboral) length was measured with calipers. With the aid of a dissecting microscope, prey remains were identified to species or to nearest taxon. Size of prey was estimated with an eyepiece micrometer using prosome length for copepods and total length for other prey species. Prey were subsequently classified into 3 size categories.

Daily ration. Daily ration was calculated from gut contents assuming gut turnover was the reciprocal of digestion rate; prey were categorized into large, medium, small and unidentifiable size classes. Feeding was assumed to be continuous over 24 h. The average number of prey items consumed per ctenophore per day was calculated as:

$$TPC = \sum_{PC=1}^4 \frac{ANPC \times 24}{SDT},$$

where TPC = total prey consumed summed over all size classes; PC = prey size class (small, medium, large, and unidentified); $ANPC$ = average number of prey in the size class per ctenophore; and SDT = size-specific digestion time (Bajkov 1935). Daily ration was converted into carbon daily ration by summing the size-specific daily ration multiplied by the mean carbon content for each prey size class (large 0.42 mg C, medium 0.06 mg C, small 0.005 mg C, unidentified 0.16 mg C; Conover unpubl. data).

Maintenance ration (MR) was calculated from respiration, assuming the respiratory quotient (RQ) was 0.8 (Larson 1987a, b). Summer and winter respiration rates for *Mertensia ovum* were estimated from seasonal dry weight/length and weight-specific respiration equations from Percy (1988) and expressed as the percentage of total body carbon. Total body carbon was estimated from regressions of polar length on total body carbon for specimens from 7 April, 12 May, 7 June and 24 June 1986. Body carbon of individual ctenophores was determined with a Perkin-Elmer® model 240 B elemental analyzer.

Determination of *Mertensia ovum* age classes. *M. ovum* at 20 m depth were collected on 6 April and 8 June 1986 for age determination by the lipofuscin age-pigment method (Ettershank 1983, 1984). All

specimens had been previously thawed, examined for gut contents and then refrozen at -20°C . Whole individuals were thawed and rinsed into 15 ml centrifuge tubes with distilled water, frozen and lyophilized. The procedure of Ettershank (1983, 1984) was followed except that the samples were not sonicated (Nicol 1987) and 4 ml of the chloroform:methanol mixture was added to extract each sample. Quinine sulphate in 1 N sulphuric acid was used as the standard. To determine age groups, the fluorescence data were analyzed for polymodal frequency distributions using the methods of Harding (1949).

RESULTS

Four species of Ctenophora, *Mertensia ovum*, *Beroe cucumis*, *Bolinopsis infundibulum* and *Pleurobrachia pileus*, were collected in Resolute Passage during this study. *M. ovum* accounted for 88.9 % of all ctenophores collected and 71.4 % of all gelatinous zooplankton (ctenophores, hydromedusae and scyphomedusae) caught. *Beroe cucumis* made up 11 % and *Bolinopsis infundibulum* 0.1 % of the ctenophores collected. Only a single specimen of *P. pileus* was collected.

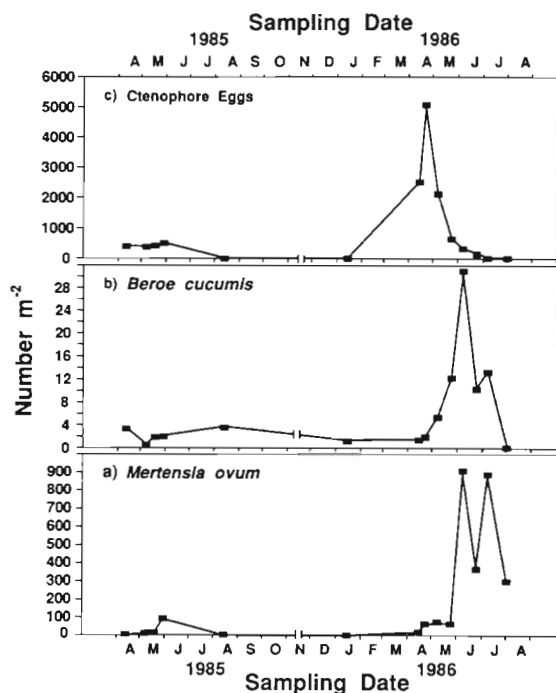


Fig. 2. Seasonal population abundance of the ctenophores (a) *Mertensia ovum* and (b) *Beroe cucumis*, and (c) ctenophore eggs

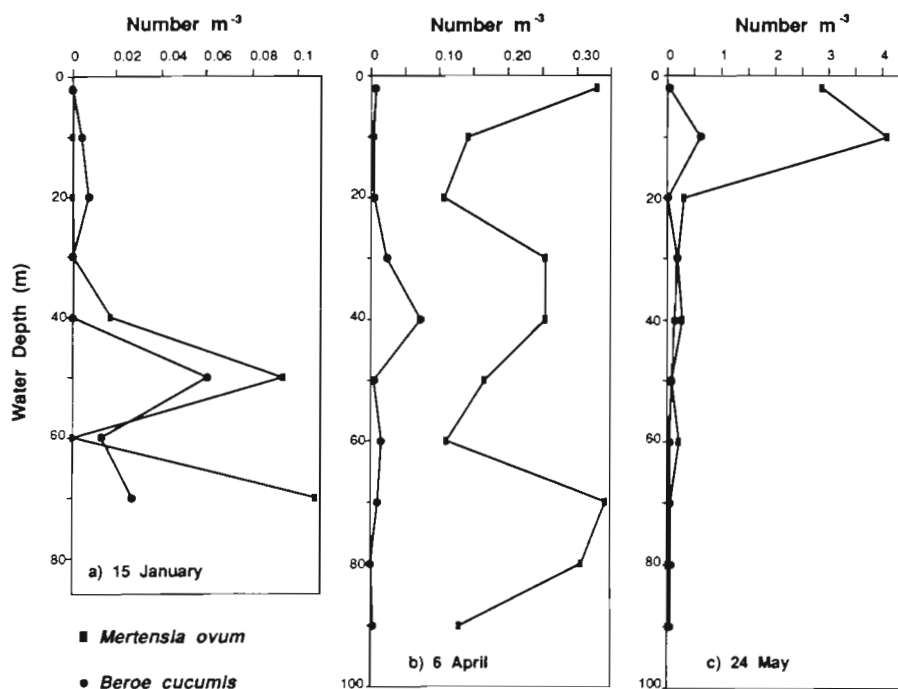


Fig. 3. *Mertensia ovum* and *Beroe cucumis*. Depth distributions of the 2 dominant ctenophores on (a) 15 January 1986, (b) 6 April 1986 and (c) 24 May 1986. The time periods were selected to illustrate changes in depth distributions through the year

Seasonal abundance of *Mertensia ovum* and *Beroe cucumis*

In 1985, the population of *Mertensia ovum* was low with maximum abundance of 94.4 m^{-2} at the end of May (Fig. 2a). *Beroe cucumis* numbers peaked in mid August at 3.57 m^{-2} (Fig. 2b). At the maximum, *M. ovum* had a mean water column density (\pm SE) of $1.02 \pm 0.30 \text{ m}^{-2}$ and *B. cucumis* $0.02 \pm 0.01 \text{ m}^{-2}$. In 1986, ctenophore numbers increased from near zero in January through the spring, reaching a maximum abundance of 911 m^{-2} during the first week of June for *M. ovum* (Fig. 2a) and 31.1 m^{-2} for *B. cucumis* (Fig. 2b). The corresponding mean density over the entire water column was $12.3 \pm 7.60 \text{ m}^{-3}$ for *M. ovum* and $0.36 \pm 0.13 \text{ m}^{-3}$ for *B. cucumis*. The highest density recorded for *M. ovum* was 70.4 m^{-3} from the surface waters (2 m) on 7 June 1986. *B. cucumis* at 10 m depth reached a maximum recorded density of 1.03 m^{-3} also on 7 June 1986. The yearly mean density for 1985 was $0.35 \pm 0.09 \text{ m}^{-3}$ for *M. ovum* and $0.02 \pm 0.01 \text{ m}^{-3}$ for *B. cucumis*. In 1986 yearly mean density increased to $4.05 \pm 1.29 \text{ m}^{-3}$ for *M. ovum* and $0.10 \pm 0.02 \text{ m}^{-3}$ for *B. cucumis*.

Although ctenophore abundance differed markedly from 1985 to 1986, the population structure changed in a similar way each year. Beginning in January, with only a small number of large ctenophores ($>3 \text{ mm}$) present in the water column, egg numbers began to increase from very low levels early in the year reaching a maximum in late April or early May (Fig. 2c). Egg production then declined rapidly, numbers decreasing by 2 orders of magnitude within 2 mo. Following maximum egg numbers, young ctenophores began to increase, reaching their peak about 1.5 to 2 mo later

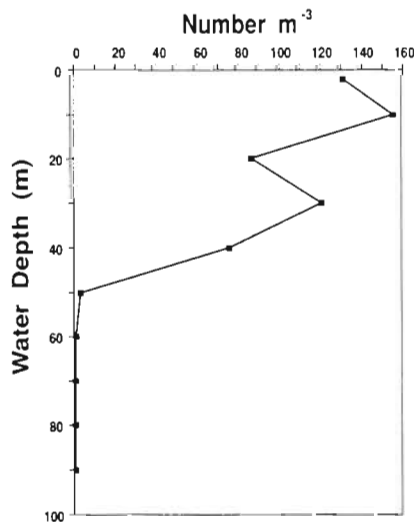


Fig. 4. Depth distribution of ctenophore eggs on 22 April 1986. Time period chosen represents the peak of egg abundance

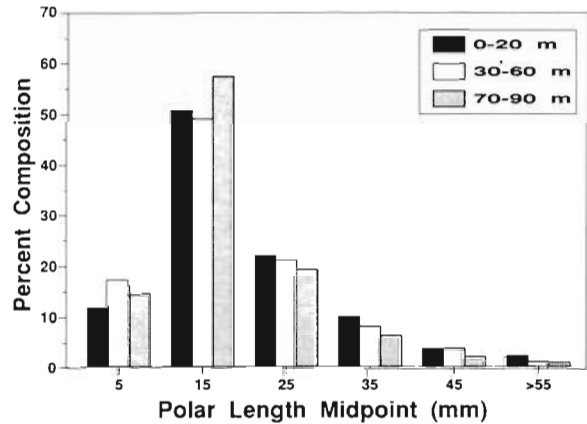


Fig. 5. *Mertensia ovum*. Percent composition of size classes as a function of water column position in 1986

(Fig. 2a, b). From a mid-summer high densities then declined to a mid-winter low.

The 2 dominant ctenophores had similar vertical distributions throughout the year. In January (Fig. 3a) both ctenophores were concentrated near the bottom; by April (Fig. 3b), they were dispersed throughout the water for a short time; however, for most of the year, both species were concentrated in the upper 20 m, as in May (Fig. 3c). Ctenophore eggs were generally found in the upper 30 m (Fig. 4). Through 1986, size distributions of *Mertensia ovum* did not vary significantly with position in the water column (Fig. 5).

Bolinopsis infundibulum occurred at low densities (Fig. 6), but their numbers tended to be highest when *Mertensia ovum* and *Beroe cucumis* populations were at their yearly low (Figs. 2a, b & 6). Maximum abundance for *B. infundibulum*, $12 \text{ ind. } 100 \text{ m}^{-2}$, occurred on 22 April 1986, but highest mean water column density was recorded on 15 January 1986 at $0.2 \pm 0.19 \text{ ind. } 100 \text{ m}^{-3}$. The mean density for 1986 was $0.06 \pm 0.02 \text{ ind. } 100 \text{ m}^{-3}$.

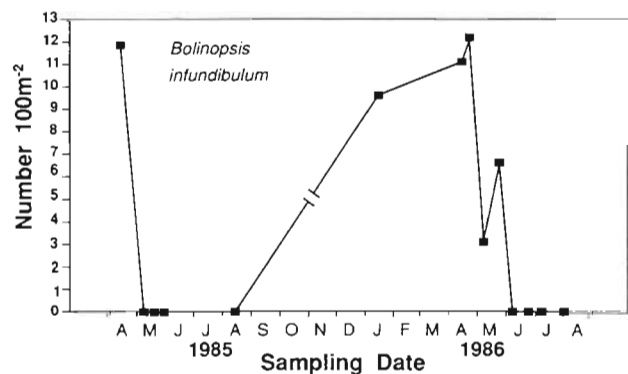


Fig. 6. *Bolinopsis infundibulum*. Seasonal population abundance

Table 1. *Mertensia ovum*. Prey consumed in 1985 and 1986. Number of prey counted with percentage of total prey consumed in parentheses. Prey size classes: Large (L, >5mm), medium (M, 2–5 mm), small (S, <2 mm)

Prey item	Size class	1985	1986
No. of samples		587	1438
Empty stomachs		310 (52.8)	1006 (70.0)
No. prey consumed		624	941
Copepods:		564 (90.4)	525 (55.8)
<i>Calanus</i> spp.	L	81 (12.9)	11 (11.7)
<i>Pseudocalanus acuspes</i>	S	376 (60.3)	21 (29.9)
<i>Metridia longa</i>	M	4 (0.4)	27 (2.87)
<i>Euchaeta</i> sp.	L	2 (0.2)	7 (0.74)
<i>Acartia</i> sp.	S	4 (0.8)	0
<i>Microcalanus</i> sp.	S	1 (0.6)	0
<i>Oncaea</i> sp.	M	0	2 (0.21)
<i>Oithona</i> sp.	M	1 (0.16)	3 (0.32)
<i>Chiridius</i> sp.	M	0	3 (0.32)
<i>Xanthocalanus</i> sp.	M	1 (0.16)	0
Copepodids	S	10 (1.6)	2 (0.21)
Copepod nauplii	S	24 (3.85)	5 (0.53)
Unidentifiable copepods	–	60 (9.62)	85 (9.03)
Other zooplankton:		60 (9.6)	416 (44.2)
<i>Parathemisto libellula</i>	L	37 (5.93)	77 (8.18)
Other amphipods	L	16 (2.56)	23 (2.44)
Barnacle nauplii	S	6 (0.96)	308 (32.7)
Isopods ^a	–	0	6 (0.64)
Ostracods	L	1 (0.16)	2 (0.21)

^a Isopods (microniscus) are often found as external parasites on amphipods and copepods and were probably captured incidentally with ingestion of other prey

Feeding ecology of *Mertensia ovum*

In 1985, half of the *Mertensia ovum* examined had empty guts. In 1986, the percentage of empty guts rose to 70.0 % (Table 1). Copepods were numerically domi-

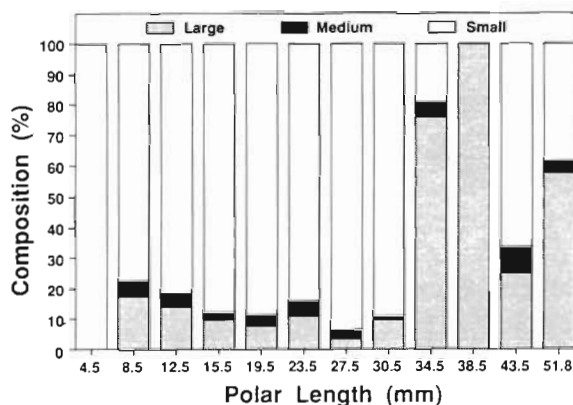


Fig. 7. *Mertensia ovum*. Percent composition of prey size groups (large, medium, small) consumed by *M. ovum* size groups (mm) in 1986

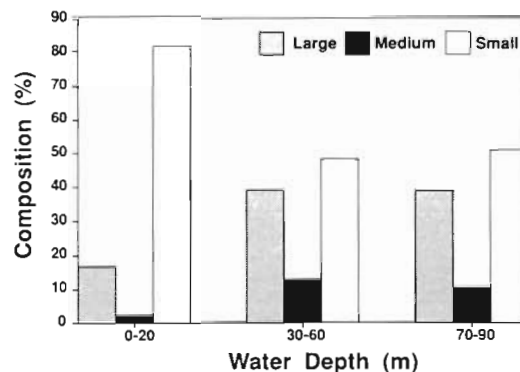


Fig. 8. *Mertensia ovum*. Percent composition of prey size groups consumed by depth in 1986

nant as prey in both years, except during a brief period in late spring 1986, when large numbers of barnacle nauplii were consumed. Of the copepods, *Pseudocalanus acuspes* were numerically dominant, comprising 30 to 60 % of the diet. Next most common were *Calanus* copepods, not easily separated to species in ctenophore guts, forming 12 to 13 % of the prey consumed. The third most common prey were juvenile hyperiid amphipods *Parathemisto libellula*, forming 6 to 8 % of the diet.

In 1986, small *Mertensia ovum* tended to consume a greater portion of small prey, while large prey dominated the diet of larger *M. ovum* (Fig. 7). The size composition of the diet also varied with the depth of the predator (Fig. 8). *M. ovum* in the upper 20 m fed mostly (80 %) on small prey. Below 20 m the size distribution of prey consumed was approximately 50 % large, 10 % medium and 40 % small prey.

Digestion rate

At temperatures of 0 to 1.5 °C *Mertensia ovum* extremely digested 6 mm (large size class) copepods in 4 h, 3 to 3.5 mm (medium size class) copepods in 3 h and <1 mm (small size class) copepods in 1.5 h (Table 2).

Daily ration

The average daily ration for 1985 was 1.40 ± 0.14 (mean \pm SE) large, 0.12 ± 0.04 medium, 11.4 ± 1.22 small and 0.86 ± 0.15 unidentified prey. In 1986, the average daily ration was 0.93 ± 0.10 large prey items, 0.27 ± 0.04 medium, 7.04 ± 0.83 small and 0.32 ± 0.04 unidentified prey items. Converted to carbon, the daily ration was 0.80 ± 0.06 and 0.50 ± 0.04 mg C during 1985 and 1986 respectively. However, feeding varied

Table 2. *Mertensia ovum*. Digestion times when fed various prey size groups. Experiments performed at water temperature of 0 to 1.5°C. Prey size group in brackets. n: number of digestion series run

Prey type	Body length (mm)	Digestion time (h)
<i>Calanus hyperboreus</i>	6 (large)	4 (n = 4)
<i>Metridia longa</i>	3–3.5 (medium)	3 (n = 4)
<i>Calanus</i> sp. (immature)	3 (medium)	3 (n = 4)
<i>Pseudocalanus</i> sp.	1–1.5 (small)	1.5 (n = 4)
Unidentified prey	–	2.8 ^a

^a Mean of digestion times from 3 size classes

greatly among days and among water depths on the same day (Table 3).

All *Mertensia ovum* consumed more than the maintenance ration estimated from metabolic rates (Fig. 9). Small ctenophores ingested a much higher weight-specific ration than the large ctenophores (Fig. 9a). However, monthly averages of daily ration decreased over the spring of 1986, perhaps indicating increasing competition for food. On the other hand, large *M. ovum* increased their ingestion over the same time period.

Ration in *Mertensia ovum* was found to be directly affected by their position in the water column regardless of size (Fig. 9b). Small individuals at 10 m had, on average, double the ingestion ration over those at 80 m, while large ones showed an opposite but weaker trend.

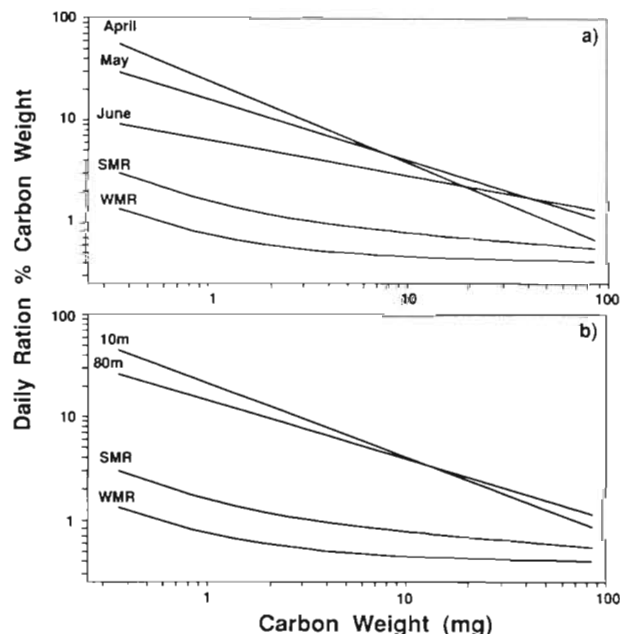


Fig. 9. *Mertensia ovum*. Least squared regression lines of daily ration expressed as percent total carbon weight of *M. ovum* for (a) April (n = 696, $r^2 = 0.91$), May (n = 507, $r^2 = 0.67$) and June (n = 235, $r^2 = 0.13$) 1986, and (b) at 10 m (n = 338, $r^2 = 0.82$) and 80 m (n = 294, $r^2 = 0.68$). Estimates of summer (SMR) and winter (WMR) maintenance rations (based on metabolic rates of Percy 1988) are expressed as % total body carbon for comparison

Table 3. *Mertensia ovum*. Ingestion rates on various dates and at various depths for the different prey classes in 1985 and 1986. DR: daily ration; Unid.: unidentified prey

Date	Depth (m)	DR (mg C d ⁻¹ ind. ⁻¹)	Prey size ingested (no. prey d ⁻¹)			
			Large	Medium	Small	Unid.
1985						
All days	0–99	0.72	1.43	0.10	12.1	0.28
All days	≥30	0.37	0.73	0.09	10.1	0.35
All days	30–60	0.65	1.37	0.10	3.86	0.31
All days	≥60	0.82	1.90	0.19	1.46	0.31
< 18 May	0–99	0.49	0.87	0.05	9.42	0.55
> 18 May	0–99	0.95	2.20	0.18	2.77	0.00
14 May	0–99	1.63	3.49	0.56	24.9	0.00
22 May	2	0.81	0.95	0.00	14.9	0.52
27–28 May	2	0.37	0.56	0.00	10.1	0.15
1986						
All days	0–99	0.51	0.91	0.18	6.73	0.00
24 April	10	0.72	1.51	0.07	0.29	0.46
24 April	80	0.40	0.76	0.45	0.34	0.34
12 May	10	0.83	1.40	0.00	10.9	1.15
12 May	70	0.42	0.73	0.11	5.05	0.51
14 May	70	0.61	1.31	0.61	3.31	0.00
8 June	12–20	0.61	0.98	0.23	35.6	0.00

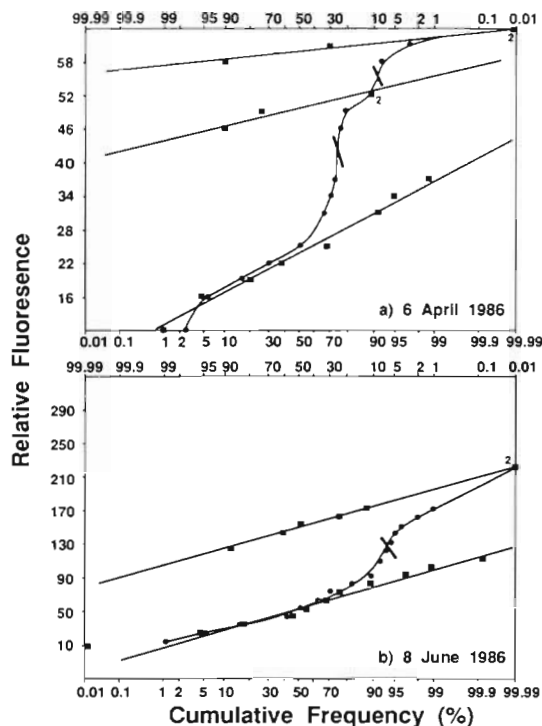


Fig. 10. *Mertensia ovum*. (●): Probability plot of frequency data based on the relative fluorescence of lipofuscin contained in specimens collected from 20 m on (a) 6 April 1986 ($n = 36$) and (b) 8 June 1986 ($n = 99$). Heavy bar indicates an inflection point in the curve. (■): Resolved normal modes making up the sample; (2): circle and square occupy same point

Mertensia ovum age classes

Lipofuscin data for 6 April 1986 clearly show 2 inflection points in the initial plot (Fig. 10a). Therefore, 3 distinct age groups are believed to be present. The sample from 8 June 1986, however, showed only 1 inflection point (Fig. 10b), suggesting 2 age groups only in this sample. Probability plots of size-frequency information from polar length of *Mertensia ovum* showed only 2 modes for each date, however.

DISCUSSION

Seasonal distribution of *Mertensia ovum* and the factors affecting their abundance

Mertensia ovum in Resolute Passage showed a similar seasonal pattern each year. Beginning with a low overwintering population, numbers peaked in spring and then decreased toward winter levels during the summer and autumn. A similar seasonal pattern of abundance has been shown for ctenophore species

from temperate water locations. *Pleurobrachia pileus* from the Dutch Wadden Sea (van der Veer & Sadee 1984) and *P. bachei* from Saanich Inlet (Larson 1986a) both exhibit similar spring population peaks.

In sharp contrast with Resolute Passage, *Mertensia ovum* from Frobisher Bay showed no marked seasonal change in abundance (Percy 1989). There the population-mean abundance was only 3.4 m^{-2} (0.07 m^{-3}) and the maximum abundance ca 25 m^{-2} in the upper 50 m of a water column up to 600 m deep. In Davis Strait, Huntley et al. (1983) reported a mean abundance of *M. ovum* of 1.03 m^{-3} during 7 cruises between April 1977 and May 1978, an order of magnitude higher than in Frobisher Bay and one-third of the 1985 concentration in Resolute Passage. In 1986, Resolute Passage concentrations were 4 times those in Davis Strait and 60 times those in Frobisher Bay. Apparently conditions in Frobisher Bay prevent *M. ovum* from developing abundances as high as those seen outside the bay. These studies and our data demonstrate that there can be large variability in *M. ovum* abundance over the Arctic.

Rapid changes in abundance are characteristic of gelatinous zooplankton populations (Kremer & Nixon 1976, van der Veer & Sadee 1984, Larson 1986a). Such changes also occur in Resolute Passage. In a 2 wk span between 24 May and 7 June 1986 the mean abundance of *Mertensia ovum* in the water column increased by 150 %. This peak abundance was nearly 3 orders of magnitude greater than the mean overwintering population. In the surface waters, numbers increased by 245 % during the same period, a change in population rivalling those reported from southern temperate waters (Kremer & Nixon 1976, van der Veer & Sadee 1984).

Spawning of ctenophores can be prolonged, but tends to have a peak period; some temperate species spawn year round (Pianka 1974). Although ctenophore eggs can be found in Resolute Passage over most of the year, large numbers are found only between April and June. For the remainder of the year spawning appears to be nil. The co-occurrence of *Mertensia ovum* and *Beroe cucumis* and the restricted period of high egg abundance suggest nearly simultaneous spawning.

Factors affecting *Mertensia ovum* abundance

Population dynamics of zooplankton determined from sampling from a single location situated in a complex hydrological environment can lead to inaccurate conclusions. The change in abundance of a species at a given site may not have anything to do with biological processes, but rather may be a consequence of an exchange of water mass containing different populations (Schneider 1987).

During the ice season, the usual easterly current in Barrow Strait/Resolute Passage produces an upwelling of more saline water along the southern coast of Cornwallis Island because of the Coriolis effect. Under these conditions there is net southerly transport of cold, more saline water across Barrow Strait (Prinsenberg & Bennett 1987). But in 1986, with much of Barrow Strait ice free, meteorological events apparently caused a breakdown in upwelling circulation, current reversals and intrusions of less saline water from the south into the Resolute Passage area persisting for at least 2 wk (Bedo et al. 1990). Transects across adjacent Barrow Strait have shown differences in the zooplankton composition on opposite sides (H. E. Welch unpubl.), presumably related to differences between water masses. Major changes in the distribution of these different water masses could produce different estimates of total abundance and/or composition in Resolute Passage. A significant change in water properties, including change in population structure of *Pseudocalanus acuspes*, occurred in mid May 1986 (Bedo et al. 1990), which might also have influenced the ctenophore population (Fig. 2). On the other hand, we believe that the overall pattern of population development in *Mertensia ovum* in the Resolute Passage largely reflects biological dynamics, for the following reasons: first, no large-scale changes in population concentrations or composition were observed when sampling at the same depth on consecutive days, even with a change in current direction; and second, a regular progression of ctenophore size classes from adult to eggs to adult was observed during the study. If different water masses were being sampled, then at least *M. ovum* in the same developmental stages were occurring simultaneously in all water masses.

The factor most often cited as affecting the seasonal abundance of gelatinous predators is prey abundance (Greve 1971, Kremer 1976, Larson 1986a). Condition has been shown to be an important factor in the timing of their egg production (Larson 1986b). In Resolute Passage, there would seem to be sufficient large prey in the water column over winter to support predator populations (Conover unpubl.). In the case of *Mertensia ovum*, it is in condition to spawn just as its prey begins to spawn. Hence, small ctenophores are present in the water column when small prey are most abundant. In early spring under the ice of Resolute Passage, copepod nauplii increase by 2 orders of magnitude between April and June (Conover & Harris unpubl.). Microzooplankton are required by larval ctenophores for efficient growth (Stoecker et al. 1987). The 'catchability' (ratio of capture per encounter) of prey has been shown to be an inverse function of prey size in other gelatinous predators (Greve 1977, Bailey & Batty 1983, 1984, Greene 1986, Greene et al. 1986,

Purcell et al. 1987). Preliminary observations indicate that this relationship also holds for *M. ovum* (Siferd unpubl.). The strategy would ensure that young ctenophores are present when both the encounter rate and catchability are optimized.

The factor most often associated with the decline of a population of gelatinous predators is predation. Greve & Reiners (1988) demonstrated a linked, negative feedback loop between the seasonal peaks of *Pleurobrachia pileus* and their predators *Beroe gracilis*. In Narragansett Bay (Rhode Island, USA), the seasonally abundant butterfish was a major factor responsible for the decline of *Mnemiopsis leidyi* (Kremer 1976, Kremer & Nixon 1976). A second predator, *Beroe ovata*, although only sporadically abundant in that Bay, also had a clearly negative influence on *M. leidyi* when present.

Species of *Beroe* have been found to feed exclusively on gelatinous zooplankton and may specialize on a particular prey species (Purcell 1991). Contrasting views have been expressed in the literature about feeding of *Beroe cucumis*. Greve (1970) found that *B. cucumis* only fed on *Bolinopsis infundibulum*, while a second species, *Beroe ovata*, only fed on *Pleurobrachia pileus*. Anderson (1974) found that *B. cucumis* fed on either *P. pileus* or *Bolinopsis infundibulum* in aquaria. Swanberg (1974) reported that *Beroe cucumis* would eat any ctenophore contacted. In Resolute Passage, *B. cucumis* are much more abundant than *Bolinopsis infundibulum*, which could then hardly be the only prey source as suggested by Greve (1970). The parallel population abundances of *Mertensia ovum* and *Beroe cucumis* suggest that they might have a predator-prey relationship. Indeed, *B. cucumis* does feed on *M. ovum* by ingesting whole individuals (Siferd pers. obs.), but the extent of feeding has not been quantified.

Our data indicate that *Beroe cucumis* abundance peaked when *Mertensia ovum* did, which is not the normal pattern in a predator-prey relationship. Greve & Reiners (1988) showed the *Beroe gracilis* population to lag behind that of their prey, *Pleurobrachia pileus*, by ca 4 to 5 wk. It may also be that *B. cucumis* is not a specialized predator like *B. gracilis* (Greve & Reiners 1988). There are *Bolinopsis infundibulum*, *Cyanea capillata* and a number of hydromedusae available in Resolute Passage which *B. cucumis* could potentially consume. Therefore their numbers would not be totally dependant on the availability of *M. ovum*.

Other predators known to feed on *Mertensia ovum*, thereby possibly influencing its population levels, include the scyphozoan *Cyanea capillata* (Purcell 1991, Siferd pers. obs.) and arctic cod *Boreogadus saidi* (H. Hop pers. comm.). Two avian predators which are known to feed on gelatinous zooplankton are the

northern fulmar *Fulmarus glacialis* and black-legged kittiwake *Rissa tridactyla* (Harrison 1984), both common in the Resolute area.

Mertensia ovum age classes

Following cohorts of gelatinous zooplankton in field populations has proved difficult (Reeve & Walter 1978). Many reasons exist, including rapid growth when food is optimal (Hirota 1974, Larson 1986a). When food is limiting, gelatinous zooplankton reduce their metabolism (Percy 1988) and survive by 'degrowth', using internal reserves and actually shrinking in size (Hamner & Jenssen 1974, Kremer 1976). Differential changes in size between cohorts distort the size-frequency distribution making cohorts virtually impossible to distinguish.

The 6 April 1986 sample of *Mertensia ovum* represented an overwintering population before spawning began. The presence of 3 groups with distinctly different lipofuscin levels suggests that *M. ovum* can survive for least 3 yr. Percy (1989) predicted that this might be the case from size-frequency data, reasoning '...that *Mertensia* may be similar to other arctic planktonic organisms that live for 2 or more years....' Even though the 8 June 1986 sample contained only 2 age classes, a 3 yr life span for *M. ovum* is not precluded. In this sample, young of the year (<3 mm polar length) were not available for lipofuscin assay, but by June, the oldest group may have spawned and died off.

The fact that ctenophores undergo degrowth when food is limiting presents a potential problem when trying to age populations by either size-frequency or lipofuscin analysis. The basic premise of the age-pigment technique that lipofuscin is accumulated in the cells, and not metabolized during cell shrinkage (Sohal 1981, Wolman 1981), may not be supported in ctenophores where degrowth is related to a decrease not only in cell size but also in number (Hamner & Jenssen 1974). What happens to the lipofuscin in a cell when the cell is resorbed is not known, but presumably cell contents, including age-pigments, are redistributed to the remainder.

If lipofuscin is indeed lost during degrowth, the ageing based on lipofuscin analysis would not be reliable. Ctenophore degrowth itself makes ageing through size-frequency analysis very questionable. That 3 frequency modes were shown in one of the samples using the lipofuscin technique would suggest some promise for this method of ageing. Our lipofuscin results are at least partial confirmation of Percy's (1989) supposition of a multi-year life cycle for *Mertensia ovum*. Obviously, more controlled research is required to validate the lipofuscin technique for ageing ctenophores and gelatinous zooplankton in general.

Digestion rate

Mertensia ovum seem to have a metabolism suited to the pulsed food supply and strong seasonality of the Arctic (Percy 1988). Because their metabolic rate was lower than ctenophores from the tropical and temperate regions (Percy 1988), their digestion rate might also have been slower. However, digestion rates for *M. ovum* were comparable to those for *Pleurobrachia bachei* from Saanich Inlet, British Columbia, Canada (Larson 1987b), even though the experimental temperatures in Resolute Passage were 10 to 12 °C colder. Kremer et al. (1986) found that *Bolinopsis vitrea*, a lobate ctenophore, digested 200 to 330 µm copepods in 1.9 h. Water temperature was not reported, except that the experiments were conducted in warm Florida waters. On similar sized prey, *M. ovum* had a digestion rate of 2 h. Apparently, *M. ovum* have digestive enzymes that can digest prey rapidly even at low temperatures.

Cold adaptation for enzymes regulating intermediary metabolism has been demonstrated for polar fish (Clarke 1991). One mechanism would be to increase the amount of enzyme when needed, as shown for digestive enzymes in cold water zooplankton on several occasions, but usually in response to increased food (Head & Conover 1983, Båmstedt 1988, Hirche 1989). The only published data on digestive enzymes in ctenophores, in this case for *Pleurobrachia pileus* at 15 °C (Hoeger & Mommsen 1984), suggest a modest (<2 times) increase with feeding for several enzymes followed by a decrease to near starting levels after 64 h. A few measurements of digestive enzymes have been made on *Mertensia ovum* from Resolute Passage for protease, averaging 6.4 µg substrate min⁻¹ (mg protein)⁻¹ at less than 0 °C (Siferd unpubl.). The comparable mean for *P. pileus* was 10.8 µg S min⁻¹ mg⁻¹, but the range was large (1.5 to 53.4 µg S min⁻¹ mg⁻¹) and incorporated that for *M. ovum*. Without further experimentation it is impossible to more completely evaluate digestive performance by *M. ovum*.

One potential source of error in our digestion rates could be the higher (≤1.5 °C) temperature in the experimental aquaria over that *in situ*, which might result in higher metabolism and more rapid digestion of prey. However, the experimental temperature falls within range of summer surface-water temperature in Resolute Passage. Therefore, the digestion rates reported here may be too fast for winter, but are probably within the range for summer when most growth occurs. A second source of error is that digestion time was defined as the point at which the digestible copepod tissue had been absorbed by the ctenophore and only an extremely disarticulated indigestible exoskeleton remained. The time of gut evacuation was not

recorded. Gut evacuation time, if used in the ingestion equation, would yield lower ingestion rates.

Impact of *Mertensia ovum* on other zooplankton

Mertensia ovum was found to be an opportunistic feeder, concentrating on 4 species, *Pseudocalanus acuspes*, *Calanus glacialis*, *C. hyperboreus* and *Parathemisto libellula*. It also took advantage of barnacle nauplii when they were abundant in 1986 (Table 1). From the population data for both predator and prey, and the digestion rate of *M. ovum*, the potential impact of feeding *M. ovum* on prey populations can be assessed. Using yearly means for daily ration, *M. ovum* might consume 9.3 % of the large copepod population, 2.8 % of the medium and 3.8 % of the small, but could consume up to 45.4 % for the large, 20.1 % of the medium and 20.7 % of the small prey population (prey densities from Conover & Harris unpubl.). Impact would be lower in January when the ctenophore population is low and much higher in the summer at peak population levels. The daily population ingestion rates for *M. ovum* from Resolute Passage are slightly higher than those determined from a population model for *M. ovum* from the Barents Sea (Swanberg & Båmstedt 1991), which is not surprising since Resolute Passage had a much higher population level than the one modelled.

Mertensia ovum therefore controls to some extent the transfer of energy through the arctic food web through direct competition for food with or by predation on other members. It potentially competes with, and possibly consumes arctic cod *Boreogadus saida*, the key food-web intermediate in the transfer of energy from lower trophic levels to marine mammals in the arctic food web (Welch et al. in press). Indeed, the diet of *M. ovum* overlaps almost completely with that of arctic cod, especially young of the year (Bradstreet et al. 1986, Lønne & Gulliksen 1989), so the presence of large numbers could significantly affect year class strength. We conclude that in the Arctic as elsewhere gelatinous predators can be an important regulator in the food web.

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