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Aggregations of predators and prey affect predation impact of the Arctic ctenophore *Mertensia ovum*

S. Majaneva[1,2,3,*], J. Berge[1,4], P. E. Renaud[1,5], A. Vader[1], E. Stübner[1], A. M. Rao[1], Ø. Sparre[1,4], M. Lehtiniemi[3]

[1]The University Centre in Svalbard, 9171 Longyearbyen, Norway
[2]Department of Environmental Sciences, University of Helsinki, 00014 Helsinki, Finland
[3]Finnish Environment Institute/Marine Research Centre, 00251 Helsinki, Finland
[4]Faculty of Biosciences, Fisheries and Economics, University of Tromsø, 9037 Tromsø, Norway
[5]Akvaplan-niva, Fram Centre for Climate and Environment, 9296 Tromsø, Norway

ABSTRACT: The importance of gelatinous zooplankton in marine systems is increasingly recognized, but little is known about its role in the Arctic pelagic food web or about the way patchiness affects these ecological interactions. We studied the influence of the spatial patchiness of predators and prey on the predation impact of the Arctic ctenophore *Mertensia ovum*, using a combination of feeding experiments, gut content analyses and net sampling, together with aggregation estimations. A nonlinear functional response was detected for *M. ovum* feeding on *Calanus* spp. Ingestion rates at low prey densities were comparable with previous studies (1 ± 0.2 prey predator^{-1} h^{-1}), but increased significantly at higher prey densities (6 ± 2.5 prey predator^{-1} h^{-1}). We estimated that *M. ovum* is capable of consuming on average 1.4 % d^{-1} of the *Calanus* spp. population in the whole water column, or 33 % in the upper 20 m layer, when assuming even distributions of prey and predators. Most importantly, ingestion rates did not significantly decline at high predator aggregations; hence, predation impact increased considerably when predator and prey aggregations were considered. However, feeding saturation was observed at high prey densities, suggesting that copepods may create a refuge by forming dense patches. These are significant consumption rates given that *Calanus* spp. comprises an important part of the Arctic marine food web. Studying the patterns of fine-scale distribution of these gelatinous predators should be emphasized in order to adequately model prey–predator interactions.

KEY WORDS: Predation impact · Patchiness · Comb jelly · Functional response · Gut content analysis · Arctic

INTRODUCTION

Very little is known about the specifics of predator–prey encounter events, since they cannot usually be observed *in situ* and therefore cannot be addressed without a unifying theory. Oceans are not homogeneous, and the process of formulating models for marine populations inevitably involves averaging spatial heterogeneities in some way (Pitchford & Brindley 2001). By ignoring spatial patterns when describing prey–predator interactions the estimated predation impact at the population level may be seriously biased (e.g. Nachman 2006a,b), leading to erroneous conclusions concerning, for example, the ability of the predators to regulate the density of their prey (Hochberg & Holt 1999). Some recent studies have incorporated spatial heterogeneity into their models (e.g. Kareiva 1990, Swanberg & Båmstedt 1991b, Nachman 2006a,b). But much of predator–prey theory and many of the most commonly used

*Email: sanna.majaneva@gmail.com

models assume that populations are homogeneously distributed in space (e.g. Murdoch 1973).

Although patchiness in marine zooplankton populations is common and exhibited over a continuum of scales (e.g. Dagg 1977, Omori & Hamner 1982, Davis et al. 1992), this seems to be particularly pronounced in gelatinous zooplankton (e.g. Graham et al. 2001). Density in swarms is often 100 to 1000 times higher than the average measured population density (Omori & Hamner 1982). Plankton nets may either pass through a number of discrete aggregations or miss these aggregations altogether, leading to biased estimates from net hauls. Video analysis and other optical *in situ* methods have recently proven to be useful tools, revealing considerable structure in gelatinous-plankton distributions that may help reveal aggregation mechanisms and their effects (Graham et al. 2001, Båmstedt et al. 2003, Haddock 2004, Purcell et al. 2010, Raskoff et al. 2010). Patchiness has become a great concern as the number of reports on the intensity and frequency of gelatinous blooms has increased worldwide (e.g. Mills 2001, Richardson et al. 2009).

The gelatinous zooplankton phylum Ctenophora (comb jellies) has a suite of successful adaptations that enable individuals to survive in changing marine ecosystems and to rebound rapidly into high-density blooms as conditions become suitable. These characteristics include fast growth rates, high reproductive output, the ability to lower metabolism when starved and the capacity to fragment and regenerate (e.g. Purcell 2005, Richardson et al. 2009 and references therein). Ctenophores can also be extremely effective predators in the food chains of coastal (Kremer 1979) and open-ocean ecosystems (e.g. Purcell 1985, Swanberg & Båmstedt 1991a,b, Purcell & Arai 2001). Perhaps the most significant aspect of their feeding behavior is that their ingestion rate is proportional to food concentration over a wide range of prey densities. However, the methodology to study this has been under debate. Generally these studies have been made using either laboratory experiments or gut content analysis, both of which include potentially problematic assumptions (e.g. Sullivan & Reeve 1982, Chandy & Greene 1995).

As awareness of the potential increase in the intensity of gelatinous zooplankton blooms has risen (e.g. Mills 2001, Brodeur et al. 2002, 2008, Richardson et al. 2009) and future changes promoting still higher blooms have been predicted (Hay 2006, Purcell et al. 2007, 2010, Richardson et al. 2009), the ecosystem effects of these predators may become even greater. Although evidence concerning gelatinous zooplankton blooms is accumulating (as reviewed in Richardson et al. 2009, Uye 2011, Purcell 2012), it has recently been questioned, due to the lack of long-time monitoring data (Condon et al. 2012). However, the Arctic Ocean is undergoing changes at an unprecedented rate due to climatic change. The dramatic reduction in sea ice thickness and coverage area is predicted to result in a change in plankton community structure (Purcell et al. 2010, Søreide et al. 2010), with some gelatinous species perhaps benefiting from these regime shifts, as seen in other areas of the world's ocean (Brodeur et al. 2008, Purcell et al. 2010). Significant changes in the grazer and predator populations in Arctic areas may, therefore, have important implications for the entire food web. The main aim of our study was to assess the potential effect of the predator *Mertensia ovum* (Mortensen 1912), the most abundant gelatinous zooplankton species in the Arctic (Siferd & Conover 1992, Raskoff et al. 2005, Purcell et al. 2010), on the population of its main prey *Calanus* spp. (Falk-Petersen et al. 2002, Lundberg et al. 2006). Predation efficiency was obtained both from experimental assessment of functional responses and from gut content analysis of field-collected specimens. Even and high patchy distribution of the predator and prey have been taken into account.

MATERIALS AND METHODS

Study area

Our investigations were carried out onboard RV 'Jan Mayen' (recently renamed RV 'Helmer Hanssen') between 15 and 29 September 2010. Zooplankton (prey) and *Mertensia ovum* (predator) populations were studied at 3 locations in the Svalbard archipelago: Kongsfjord (79° N, 12 to 13° E), Rijpfjord (80° N, 18 to 19° E) and Billefjord (78° N, 16° E) (Fig. 1). For gut content analyses additional *M. ovum* individuals were collected from Smeerenburgfjord (79° N, 9 to 11° E). In contrast to Kongsfjord, where water is periodically influenced by strong Atlantic water intrusion from the West Spitsbergen Current and no fast ice cover has been formed in recent winters, Rijpfjord is predominantly characterized by Arctic Water and is covered by ice for 6 to 8 mo of the year (e.g. Ambrose et al. 2012). Billefjord is an ice-covered (~5 mo of the year) side branch of Isfjord, where the sill at the entrance restricts the exchange of water masses allowing the cold, dense water that forms in the fjord basin to be

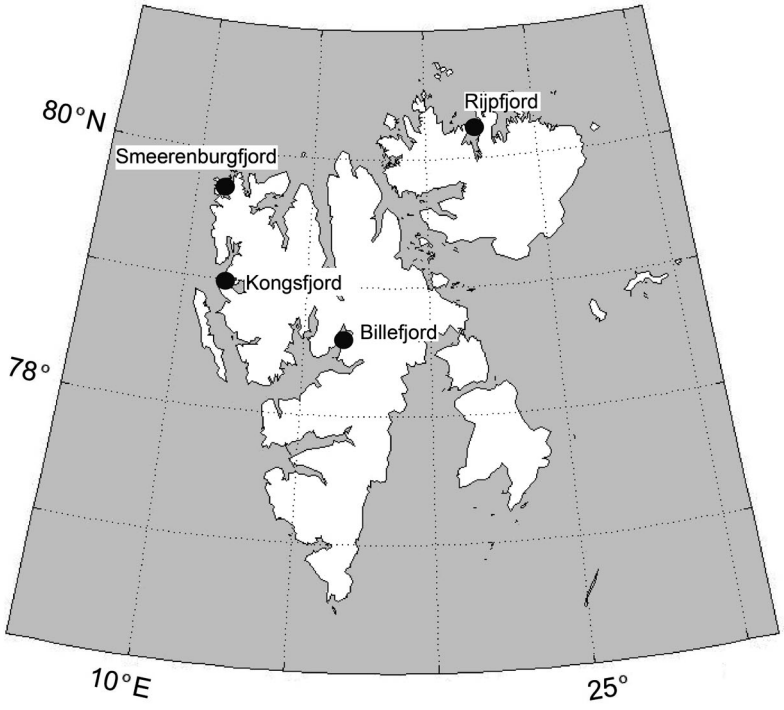

Fig. 1. Study locations around the Archipelago of Svalbard

retained (Walkusz et al. 2009). Smeerenburgfjord is a sound where Atlantic and Arctic Waters meet (Kortsch et al. 2012).

Sampling

Mertensia ovum samples were taken using oblique tows with a MIK-net (1.5 mm mesh size with a filtering cod end, 3.15 m^2 opening, 0.5 m s^{-1} towing speed). We sampled from 3 depth intervals in Rijpfjord and Billefjord (bottom–0, 100–0 and 50–0 m) and from 2 depth intervals in Kongsfjord (bottom–100 and 100–0 m). *M. ovum* individuals were gently removed from the sample and immediately counted and measured for oral–aboral length (Lundberg et al. 2006). *M. ovum* individuals used as predators in the experiments were chosen from the most abundant size class (1.8 to 2.2 cm oral–aboral length). They were hand-collected in 3 l plastic buckets from the surface water. Onboard the ship the samples were sorted, and apparently undamaged specimens were maintained in an incubator at +4°C, and the seawater was changed every 24 h.

The prey community was sampled using a MultiNet (Hydrobios©) equipped with 5 closing nets, 180 µm mesh size, 0.25 m^2 opening, 0.5 m s^{-1} towing speed) deployed in parallel with the MIK-net. Samples were taken from the depth strata of bottom–200, 200–100, 100–50, 50–20 and 20–0 m. All gelatinous zooplankton were immediately removed, counted and identified before the preservation of the remaining sample in 4% borax buffered formaldehyde-in-seawater solution. In the laboratory, subsamples were analyzed under a Leica MZ6 stereo microscope (16 to 40× magnification), and all organisms were identified to the lowest taxonomic level possible. *Calanus* spp. identification was based on the stage-specific length distribution relationships established by Kwasniewski et al. (2003). *Calanus* spp. used as prey in the experiments were collected by vertical hauls with WP-3 nets from the bottom to surface (Hydrobios©; with 1 m^2 opening and 1 mm mesh size) fitted with a 30 l codend to ensure healthy condition of the prey. Prey was diluted in 60 l stock plastic containers and maintained at *in situ* temperature (+4°C) with aeration. The prey used in experiments were sorted by size and immediately transferred to the experimental units. A subsample of the sorted experimental prey stock was identified based on the stage-specific length distribution relationships established by Kwasniewski et al. (2003).

In order to capture the vertical migration during a diel cycle, all net sampling (MIK-net and MultiNet) was carried out at 2 local sun noons (LSN) and 1 local midnight (LM) or vice versa, as described in Berge et al. (unpubl. data). However, samples taken at LSN and LM from all stations were treated as normal replicates (mean ± SD). In addition, temperature, salinity and fluorescence data were collected at all sampling stations from the whole water column with a Seabird SBE9/11+ CTD.

Gut content analyses

From all the *Mertensia ovum* specimens collected with MIK-nets from Billefjord, Rijpfjord and Smeerenburgfjord, a total of 78 individuals were haphazardly selected for gut content analysis. The gastric cavities were immediately dissected and their contents preserved in 96% ethanol. These were then examined for identifiable remains under a Leica MZ6

stereomicroscope (16 to 40× magnification), which were identified to the lowest taxonomic level possible.

In situ clearance rates (F^1, l predator^{-1} h^{-1}) from gut content analysis data were calculated according to the following equation:

$$F^1 = N_{prey} / (T_d C) \quad (1)$$

where N_{prey} is the number of prey in the gut (prey ind.$^{-1}$), T_d is the laboratory-derived gut passage time (h) and C is the prey concentration (prey l^{-1}) based on field data (Sullivan 2010 and references therein). The laboratory-derived gut passage time for *Calanus* spp. was determined by random selection of *Mertensia ovum* individuals used in feeding experiments (Type A, see below). After the experiments were terminated, *M. ovum* were transferred individually to 250 ml containers with filtered seawater and observed frequently until complete gut evacuation. Gut passage time was calculated from the time the first prey item was consumed to complete evacuation. The total number of prey items eaten was considered in calculations to obtain gut passage time per prey.

Prey selectivity of *Mertensia ovum* in natural assemblages of prey sampled with MultiNet was evaluated using a prey selectivity index (*C*; Pearre 1982). Yates' corrected χ^2 values were calculated from the percentage of a prey items ingested and the percentage of the total standing stock in each prey category. Index values range from −1 to 1. Positive and negative values indicate selection for and against a given prey category, respectively, while a value of zero indicates no selection in either direction.

Experiments

One set of experiments (Type A experiments) was run with 1 predator and a variety of prey densities (0.2, 1, 2, 4, 5, 10, 20, 30, 50 and 100 prey l^{-1}) to test the effect of prey density on predation. A second set of experiments (Type B) was run at a single prey density (near natural, 2 prey l^{-1}), with varying predator densities (1, 2, 5 and 10 predator experimental vessel^{-1}) to test the effect of predator density. Experiments were run in a cooling room (+4°C, with very low light conditions) for 5 h. The experimental vessels (5 and 20 l for Type A and B experiments, respectively) were filled with filtered (50 µm) seawater collected from the surface layer at the study sites (31.2 to 33.0 psu, 2.5 to 3.5°C) and incubated overnight in the cooling room to stabilize the temperature. Prey items were introduced to the experimental containers and allowed to acclimate for 1 to 2 h. Experiments were begun by introducing the predator(s) and terminated by their removal from the vessel. We observed the behavior of individual predators and prey continuously during the first hour, and the time when the first prey was eaten was recorded (defined as the search time). After the first hour, predation was recorded every 15 to 30 min. After terminating the experiments, the water was sieved and the remaining prey organisms were measured and identified based on the stage-specific length distribution relationships established by Kwasniewski et al. (2003). Controls (no-predator treatments) were not conducted; however, potential prey disappearance due to handling was prevented by checking the sieves and experimental vessels after the trials with a microscope.

To be able to interpret predation efficiency, both ingestion rate (*I*, prey predator^{-1} h^{-1}) and clearance rate (F^2, l predator^{-1} h^{-1}) were calculated. Ingestion rate was calculated according to the following equation:

$$I = N_0 - N_f/t \quad (2)$$

where N_0 is the initial and N_f the final number of prey per experimental vessel and t is the duration of the experiment. Clearance rate was calculated according to the following equations:

$$N_f = N_0 \exp(-mt) \quad (3)$$

$$F^2 = V \times m/P \quad (4)$$

where N_0 is the initial and N_f the final number of prey per experimental vessel, t is the duration of the experiment, m is the instantaneous prey mortality rate, V is the volume of the experimental vessel and P is the number of predators in the experiment. These equations assume constant predation, an exponential decline in prey numbers throughout the experiment and no cumulative change in predator search time while handling the prey (Greene et al. 1986).

Predation impact

Predation impact (%) was calculated multiplying the ingestion rates (*I*; adjusted for *in situ* prey density from the Type A experiments) by the *in situ* predator abundance, and then dividing it by the *in situ* prey density from MultiNet zooplankton samples from the field. While calculating the predation impact full overlap of predators and prey and constant predation

was assumed. Predation impact was calculated separately for each study site.

The potential predation impact of *Mertensia ovum* and prey aggregations were calculated similarly, with the exception of using modeled predator and prey densities. The estimated predator and prey densities were calculated using the densities in natural assemblages (counted from net hauls) and assuming that all individuals collected were concentrated into aggregations of varying size (in 20, 10, 5 and 2 m^3). The sizes of the patches were chosen based on previous observations (e.g. Hutchinson 1961, Hamner et al. 1975, Dagg 1977, Omori & Hamner 1982, Swanberg & Båmstedt 1991a,b, Siferd & Conover 1992, Holliday et al. 1998, Folt & Burns 1999, Raskoff et al. 2010). The potential predation impact of *M. ovum* and prey aggregations was estimated for 3 depth zones: bottom to surface, when all the prey items throughout the whole water column are available for the predator, and 50 m to surface or 20 m to surface, when only the prey items in the surface layers are available for the predator.

Statistical analysis

Due to non-normality of the data set, the non-parametric Kruskal-Wallis test from the open source statistical program R, Version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria) was first applied to establish if there were differences between the individual clearance rates among the prey densities in the Type A experiments and among predator densities in the Type B experiments. The non-parametric analogue of Tukey's test was used in post hoc analyses to determine which rates differed. Calculated selectivity indices were tested for significance with the χ^2 statistic (Pearre 1982), with 1 degree of freedom. The non-parametric Kruskal-Wallis test was also used to compare the number of individual predators in different locations and different net tows.

Table 1. *Mertensia ovum*. Size and vertical distribution based on MIK-net samples. For the size measurements, n = 202 in Kongsfjord, n = 170 in Rijpfjord and n = 310 in Billefjord. nd: no data

Location	Oral–aboral length (cm)			Abundance (ind. m^{-3})		
	Mean ± SD	Min.	Max.	Bottom–0 m	100–0 m	50–0 m
Kongsfjord	1.5 ± 0.5	0.4	3.6	0.07 ± 0.01	0.2 ± 0.1	nd
Rijpfjord	2.1 ± 0.7	0.65	4.1	2.2 ± 0.7	1.2 ± 0.8	2.5 ± 2.0
Billefjord	1.7 ± 0.6	0.4	3.4	0.7 ± 0.6	2.0 ± 1.2	0.8 ± 0.3

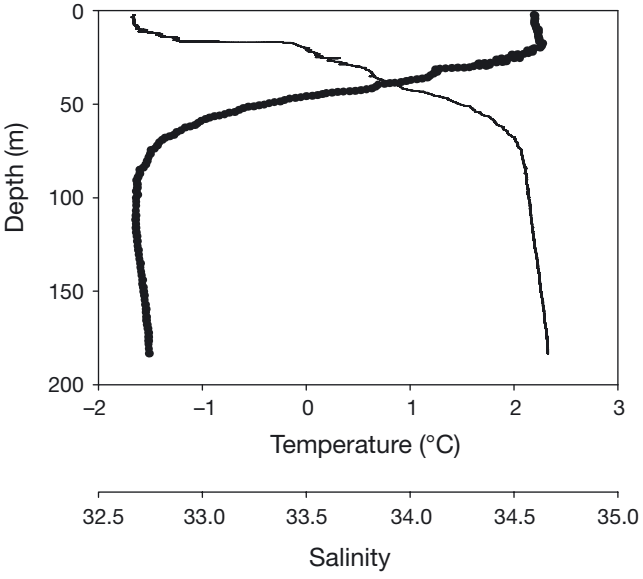

Fig. 2. Typical CTD record of temperature (bold line) and salinity (thin line) from the Svalbard shelf area during autumn 2010. Data are from the Billefjord station (78.39° N, 16.43° E) on 27 September 2010

RESULTS

Physical structure of the water column

At each location, relatively fresh and warm water masses dominated the surface layers (Fig. 2). Salinities varied between 31.2 and 33.0 psu in the upper 20 to 30 m surface water, increasing rapidly with depth and reaching 35.0 psu in the bottom layers. The warmest water was found in the surface layer, with temperatures ranging from 2.5 to 3.5°C. Below 20 to 25 m depth, temperature dropped gradually, reaching 1.5°C at the bottom. In both Rijpfjord and Billefjord, bottom water temperature was ~–1.5°C. The pycnocline was found at ~20 to 60 m depth at all 4 locations (Fig. 2).

Occurrence of *Mertensia ovum*

Mertensia ovum was present at all sampling locations and in all MIK-net samples. A total of 6476 specimens were collected and subsamples were measured (Table 1). The maximum density was found in Rijpfjord (3.89 ind. m^{-3}), while the minimum was in Kongsfjord (0.07 ind. m^{-3})

(Table 1). However, the number of *M. ovum* specimens in different hauls at the same sampling locality varied widely (Table 1), and there was no significant difference in the total number of *M. ovum* individuals whether the MIK-net was towed from the bottom to surface or just in the surface layer ($p = 1$ in Kongsfjord, $p = 0.28$ in Rijpfjord and $p = 0.28$ in Billefjord). *M. ovum* were also counted and measured from each MultiNet tow at all sites to study vertical distribution; however, the number of individuals was either 1 or 0 in each depth layer. Therefore, the MultiNet samples were not used to study *M. ovum* abundance.

Prey availability

In all sampling locations the zooplankton communities were dominated by copepods, constituting 60 to 99.8% of total mesozooplankton (Fig. 3). *Oithona similis* was by far the most abundant copepod species at all stations, comprising up to 72% of the zooplankton community in the upper layer in Kongsfjord, 59% in Billefjord and 44% in Rijpfjord. *Pseudocalanus* spp. and *Acartia longiremis* were other abundant copepod species. Numerically, *Calanus* spp. abundance varied among locations and was increasingly greater with depth, with *Calanus finmarchicus* being the most abundant *Calanus* species in all depth layers in all study locations (Table 2). Other potential prey groups for *Mertensia ovum* were present in low numbers (Fig. 3), including bivalve veligers, echinoderm larvae and chaetognaths. However, in Billefjord, none of these groups were present in the samples. It is also notable that *Fritillaria borealis* was highly abundant in Rijpfjord (Fig. 3).

Gut content analyses

A total of 78 *Mertensia ovum* individuals (mean length ± SD = 2.1 ± 0.6 cm) were examined for gut contents. Of these, 50 individuals (64%) contained identifiable prey, while the rest (36%) had empty guts (45% in Rijpfjord and 40% in Billefjord, while in Smeerenburgfjord all individuals contained food items in the guts). A total of 306 prey items belonging to 11 taxa and 1 group of unidentified organisms were found (Fig. 3). The mean number of prey items eaten per predator varied between1.4 and 1.5 in Rijpfjord and Billefjord, respectively, and reached up to 19.7 in Smeerenburgfjord. The maximum of 66 prey items was found in 1 specimen from Smeerenburgfjord. *Calanus* spp. were clearly the most abundant prey in the gut (Fig. 3); however, the prey items could not always be identified to species level due to digestion. *M. ovum* individuals exhibited significant positive selection towards *Calanus* spp. according to Pearre's prey selectivity index ($C = 0.153 \pm 0.09$ in Billefjord and $C = 0.23 \pm 0.14$ in Rijpfjord, $p < 0.05$ for both). No significant positive selection towards other prey groups was detected. The laboratory-derived gut passage time (mean ± SD) for *Calanus* spp. at *in situ* temperature was 9.9 ± 4.9 h. The clearance rates (means ± SD) from gut content analysis (F^1) were 0.27 ± 0.16 l predator^{-1} h^{-1} in Rijpfjord, 0.17 ± 0.09 l predator^{-1} h^{-1} in Billefjord and 1.2 ± 0.4 l predator^{-1} h^{-1} in Smeerenburgfjord, when only *Calanus* spp. in the gut were included in the calculations.

Experiments

The prey stock used in the experiment contained mainly *Calanus glacialis* Stage V (mean ± SD =

Table 2. *Calanus glacialis*, *C. finmarchicus*, *C. hyperboreus*. Vertical distribution based on 3 MultiNet samples (mean ± SD), taken at each location at different times; including local sun noon and local midnight at each location to limit the effect of diel vertical migration and, hence, the high SD

Location	Species	Abundance (ind. m^{-3})			
		Bottom–100 m	100–50 m	50–20 m	20–0 m
Kongsfjord	*C. glacialis*	90.9 ± 53.1	5.5 ± 3.9	11.9 ± 7.1	9.6 ± 4.1
	C. finmarchicus	188 ± 114.8	73.7 ± 77.4	53.8 ± 26.3	29.1 ± 19.7
	C. hyberboreus	1.3 ± 2.3	0.0	0.3 ± 0.5	0.2 ± 0.4
Rijpfjord	*C. glacialis*	195.6 ± 163.1	26.9 ± 4.8	7.7 ± 0.8	1.7 ± 2.1
	C. finmarchicus	236.5 ± 103.4	35.1 ± 13.9	11.3 ± 7.0	8.1 ± 5.2
	C. hyberboreus	36.5 ± 31.6	7.1 ± 2.4	1.4 ± 1.1	0.3 ± 0.5
Billefjord	*C. glacialis*	62.4 ± 108.1	21.6 ± 13.6	7.7 ± 4.8	3.1 ± 5.1
	C. finmarchicus	294.6 ± 258.3	24.9 ± 14.1	15.9 ± 15.2	5.3 ± 6.0
	C. hyberboreus	0.5 ± 0.8	5.0 ± 4.2	1.3 ± 1.3	0.1 ± 0.1

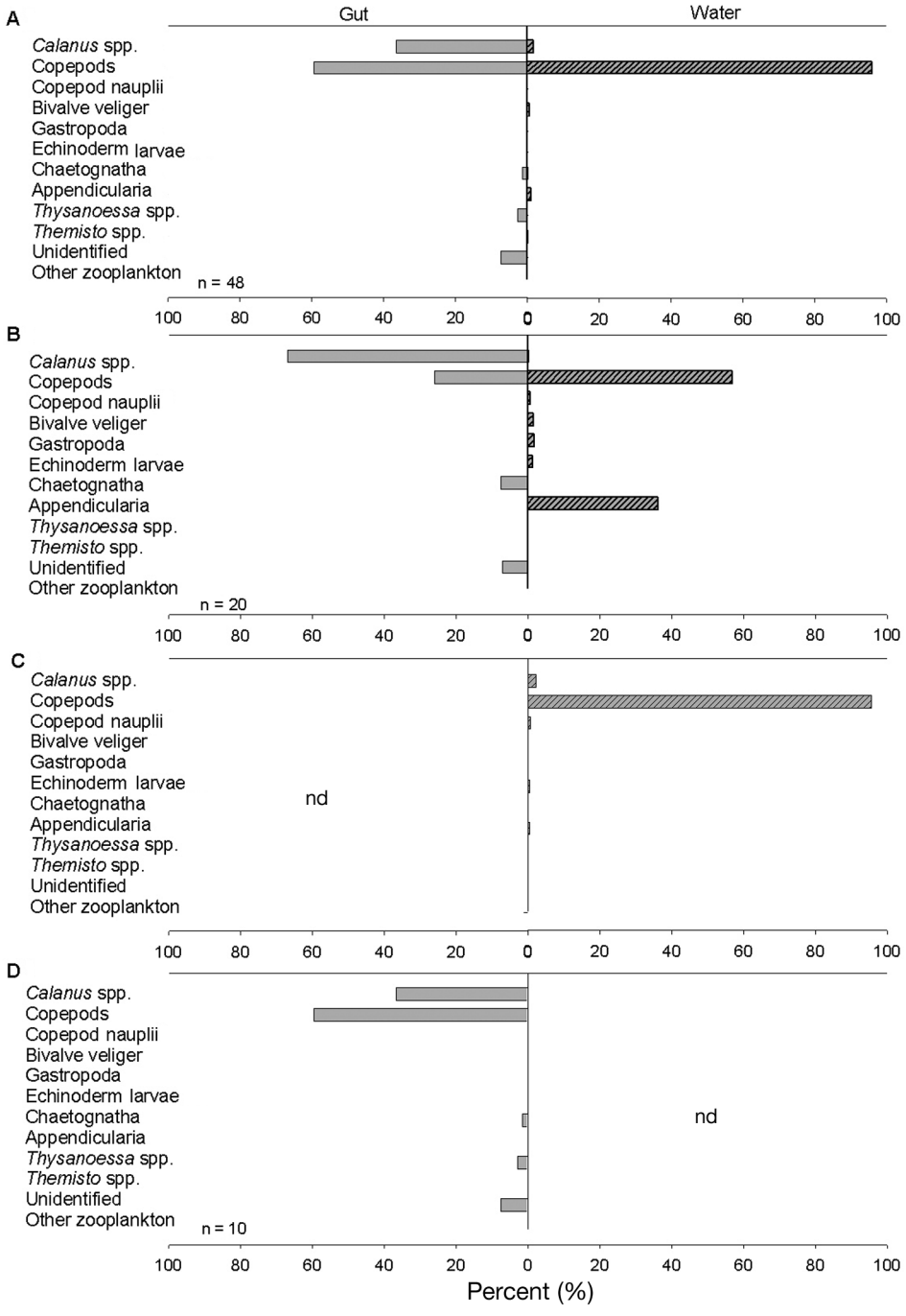

Fig. 3. *Mertensia ovum.* Composition of mesozooplankton in the guts of *M. ovum* (grey bars, left side of axis) and in ambient water (hatched bars, right side of axis) from our study locations around Svalbard, September 2010: (A) Billefjord, (B) Rijpfjord, (C) Kongsfjord and (D) Smeerenburgfjord. nd: no gut content analysis data exist for Kongsfjord, and no ambient zooplankton data exist for Smeerenburgfjord

71 ± 11.8%). Other *Calanus* spp. species and copepodite stages were present in low quantities (*C. glacialis* stage adult female [AF]: 6.5 ± 5.5%, Stage CIV: 7.5 ± 3%; *C. finmarchicus* stage AF: 3 ± 3.4%, Stage V: 6.5 ± 3%; and *C. hyperboreus* Stage CIV: 5.5 ± 3.4%). At the end of the experiments, *C. glacialis* Stage V (83.7 ± 5.2%) was still the most abundant prey item among those remaining. The non-parametric Kruskal-Wallis test showed no significant differences in *Calanus* species or stages between the start and end of the experiment ($p > 0.05$).

The functional response (Type A) experiments with prey densities from 0.2 to 100 *Calanus* spp. ind. l^{-1} and 1 *Mertensia ovum* resulted in a nonlinear response curve (Fig. 4A; $r^2 = 0.51$, $p = 0.0001$), with an apparent saturation level at a prey density of 50 ind. l^{-1} and an ingestion rate of 6 ± 2.5 prey predator^{-1} h^{-1} (144 ± 61.1 prey predator^{-1} d^{-1}). The highest clearance rate (F^2) for predators was measured at a density of 5 prey l^{-1} (mean ± SD: 1.1 ± 0.06 l predator^{-1} h^{-1}), while the lowest measured clearance rate was at a density of 100 prey l^{-1} (0.04 ± 0.02 l predator^{-1} h^{-1}) (Fig. 4B). There was high individual variation within the 10 replicates at each prey density. The non-parametric Kruskal-Wallis test showed statistically significant differences in individual clearance rates among prey densities ($p < 0.01$). The non-parametric analogues of Tukey's tests were used in post hoc analyses in order to determine which of the densities differed (Zar 1999 and references therein). Pair-wise comparisons (Eq. 11.26 in Zar 1999: p. 224), with a significance level of 0.05, showed that the clearance rates in prey densities of 2, 4 and 5 ind. l^{-1} were significantly higher ($p < 0.05$) than at other prey concentrations.

In the second set of experiments (Type B), the clearance rate (l predator^{-1} h^{-1}) was calculated as a mean ± SD of all individuals in each vessel. The highest clearance rate (0.67 ± 0.48 l predator^{-1} h^{-1}) was measured when 2 predators were present. However, in these experiments the mean clearance rates varied between 0.2 and 0.7 l predator^{-1} h^{-1} (Fig. 4B), with no significant differences in clearance rates (F^2) among predator densities ($p > 0.05$).

Predation impact — even distribution

By using the ingestion rate from Type A experiments, the *in situ Mertensia ovum* populations have the potential to consume between 0.7 and

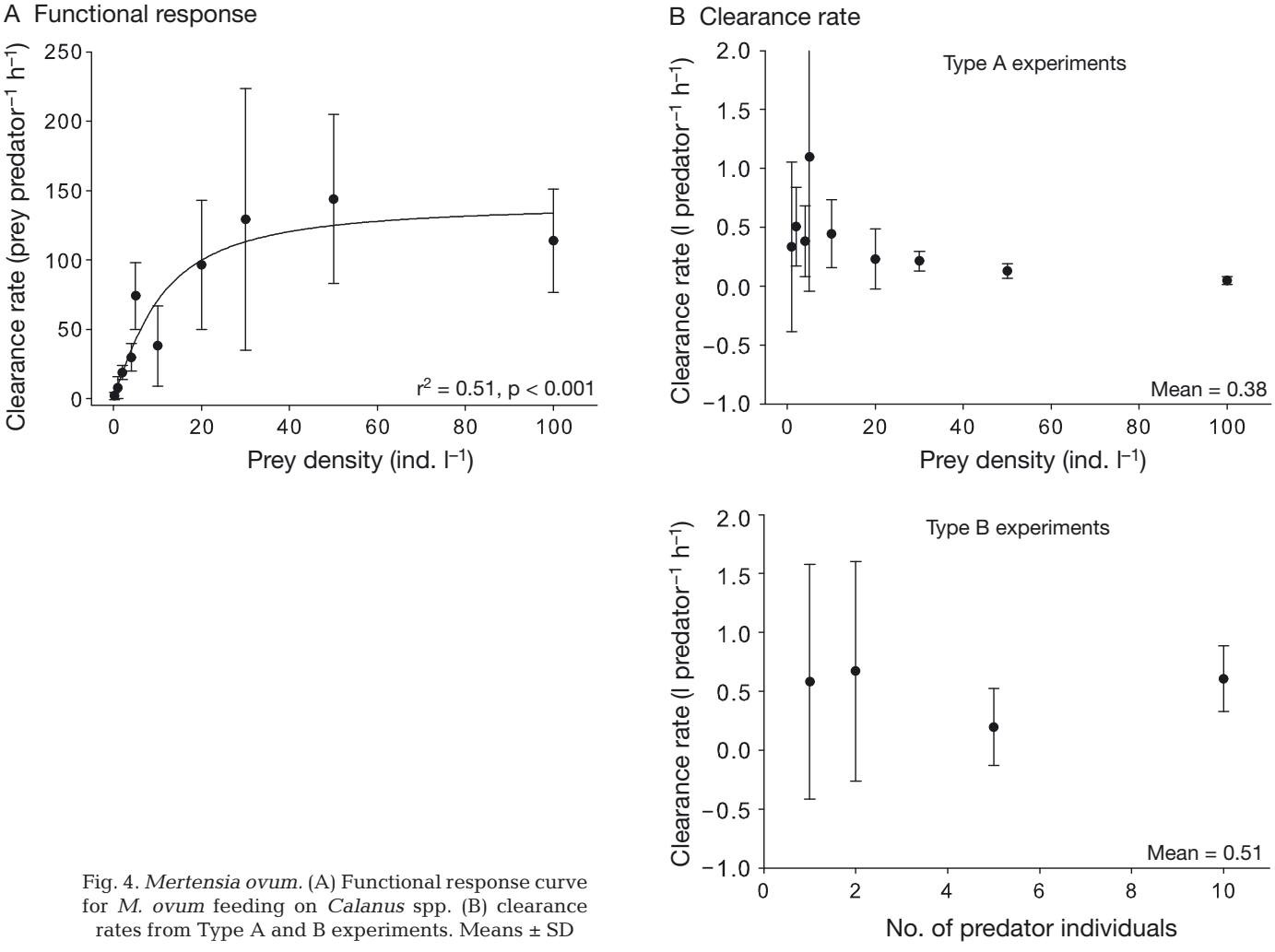

Fig. 4. *Mertensia ovum*. (A) Functional response curve for *M. ovum* feeding on *Calanus* spp. (B) clearance rates from Type A and B experiments. Means ± SD

9.9 prey d^{-1}, when adjusted to the *in situ* prey densities at the study sites. This corresponds to 0.1 to 4.2% of the available *Calanus* spp. standing stock per day assuming an even distribution of predators and prey throughout the water column (Table 3). If we assume that all *M. ovum* were caught in the upper 50 m layer, the potential consumption of the available *Calanus* spp. standing stock increases, reaching up to 1.1% in Kongsfjord, 45.3% in Rijpfjord and 45.9% in Billefjord. In the surface layer (top 20 m), where density of *Calanus* spp. was low, the potential predation increased up to 100% (Table 3).

Table 3. *Mertensia ovum*, *Calanus* spp. Predation impact of *M. ovum* on *Calanus* spp. Field counts (mean ± SD) from MIK-net (*M. ovum*) and MultiNet (*Calanus* spp.). Predation impact range (% d^{-1}) based on field abundances and ingestion rates from Type A experiments. Three groups of depth distribution: from bottom to surface, where all the prey is available to the predator (potential summertime situation), from 50 m to surface and from 20 m to surface

Location	*M. ovum* (ind. m^{-3})	*Calanus* spp. (ind. m^{-3})	Predation impact (% d^{-1})
Bottom to surface			
Kongsfjord	0.1 ± 0.1	802.1 ± 235.9	0.1–0.3
Rijpfjord	2.1 ± 1.1	568.5 ± 151.7	0.7–4.2
Billefjord	0.9 ± 0.5	499.5 ± 260.5	0.2–3.1
50–0 m			
Kongsfjord	0.1 ± 0.1	104.9 ± 51.1	0.1–1.1
Rijpfjord	2.1 ± 1.1	30.4 ± 22.5	4.3–45.3
Billefjord	0.9 ± 0.5	33.3 ± 14.5	1.1–45.9
20–0 m			
Kongsfjord	0.1 ± 0.1	38.9 ± 21.9	0.2–2.7
Rijpfjord	2.1 ± 1.1	10.1 ± 5.9	12.4–100
Billefjord	0.9 ± 0.5	8.4 ± 11.1	2.5–82.1

Predation impact — uneven distribution

By applying the ingestion rate based on Type A experiments and modeled prey densities in the study localities, *Mertensia ovum* individuals have the potential to consume up to 144 ± 61.1 prey d^{-1} (Fig. 4A, saturation level). The predation impact increased with increased prey density in the patch (Table 4), until the saturation level was reached. When both predators and prey were assumed to have uneven distributions, the potential predation pressure did not increase linearly or consistently with increasing numbers of predators (Table 4). In Kongsfjord, where predator abundance was the lowest and prey abundance was the highest, the potential predation impact decreased when the predators and prey where modeled into 5 m^3 size patches. A similar phenomenon was detected in Rijpfjord, where predator abundance was the highest. High variation of predation impact was detected between study locations when focused only on the upper 20 m layer; predation reached up to 100% of the available *Calanus* spp. standing stock in all patch sizes in Rijpfjord and in Billefjord and between 1.6 and 6.4% in Kongsfjord (Table 4), depending on the size of the estimated patch.

Table 4. *Mertensia ovum*, *Calanus* spp. Predation impact of *M. ovum* on *Calanus* spp. Predation impact (% d^{-1}) based on field abundances and ingestion rates from Type A experiments. Predation impact was based on estimated patch sizes of *M. ovum*, of *Calanus* spp. and of both *M. ovum* and *Calanus* spp. Three groups of depth distribution: from bottom to surface where all the prey is available to the predator (potential summertime situation), from 50 m to surface and from 20 m to surface

Location	Predation impact (% d^{-1})											
	Predator patchiness				Prey patchiness				Predator and prey patchiness			
	20 m^3	10 m^3	5 m^3	2 m^3	20 m^3	10 m^3	5 m^3	2 m^3	20 m^3	10 m^3	5 m^3	2 m^3
Bottom to surface												
Kongsfjord	0.6	1.2	2.5	6.2	0.1	0.2	0.0	0.1	0.7	2.9	1.5	4.4
Rjpfjord	10.2	20.3	40.6	100.0	1.3	2.6	0.7	0.9	7.7	30.6	15.7	53.4
Billefjord	4.3	8.6	17.2	43.0	0.6	0.7	1.4	0.4	3.0	7.2	28.4	21.0
50–0 m												
Kongsfjord	1.9	3.8	7.5	18.9	0.2	0.1	0.1	0.1	5.1	5.1	5.1	12.7
Rjpfjord	75.9	100.0	100.0	100.0	9.8	4.9	2.5	2.5	56.9	56.9	56.9	100.0
Billefjord	25.8	51.6	100.0	100.0	4.1	2.1	1.0	1.0	20.3	20.3	20.3	50.7
20–0 m												
Kongsfjord	5.1	10.2	20.3	50.9	0.7	0.3	0.2	0.2	1.6	1.6	4.0	6.4
Rjpfjord	100.0	100.0	100.0	100.0	39.4	19.7	9.8	3.9	100.0	100.0	100.0	100.0
Billefjord	100.0	100.0	100.0	100.0	20.7	10.4	5.2	2.1	100.0	100.0	100.0	100.0

DISCUSSION

Abundance and patchiness of predator and prey populations

In our study, the abundances of the Arctic ctenophore *Mertensia ovum* (0.07 to 3.9 ind. m^{-3} when integrated over the entire water column) were comparable to those reported in previous studies conducted in the same area (0.02 to 9.5 ind. m^{-3}; Swanberg & Båmstedt 1991a,b, Falk-Petersen et al. 2002, Lundberg et al. 2006). Reports on the occurrence of gelatinous zooplankton from the Arctic Ocean are widely scattered over the past century (e.g. Bigelow 1920, Sirenko 2001), but usually do not provide information on their abundance or ecology. Due to the scarcity of early reports and lack of long-term monitoring on gelatinous zooplankton, it remains unclear if the abundance and distributional patterns of *M. ovum* have changed in recent decades in the Arctic.

In addition to the lack of historical survey data, abundance estimates of gelatinous zooplankton made from plankton surveys are widely acknowledged to underestimate both the total densities and densities in aggregations (e.g. Swanberg & Båmstedt 1991b, Båmstedt et al. 2003, Purcell et al. 2010). A good example of this inaccuracy is the high variation of *Mertensia ovum* abundance between samples taken with the MultiNet and MIK-net, even though the samples were taken as simultaneously as possible (see above and Table 1). Also, the high variation between the numbers of individuals caught in each MIK-net tow points to patchy distribution. Most *M. ovum* occurred in the upper 50 m, since there was no significant difference in individual numbers whether the tow was taken from 300 m to surface or from 50 m to surface. Therefore, our data support the concept that net sampling in general can lead to severe underestimates, if the densities are calculated as an average, and that this species is not evenly distributed through the whole water column. Plankton nets often have too small an opening to collect these fast swimmers, and the nets often pass through aggregations or collect only parts of fragile gelatinous organisms, leading to poor estimates of their real population sizes. Sampling is also often conducted over depth scales that are too large to evaluate patchiness in different depth layers (Graham et al. 2001, Purcell et al. 2010, Raskoff et al. 2010).

High-resolution patchiness of *Mertensia ovum* was observed both from the ship and during multiple dives at all sampling locations, with *M. ovum* individuals concentrated in the upper 10 to 20 m of the water column, where densities in patches were estimated to be >500 ind. m^{-3} by visual counts (B. Gulliksen & J. Berge pers. obs.). Unfortunately, these observations could not be substantiated by net sampling, as the observation area was not accessible by ship. Diving observations are restricted to the surface layers of the water column. Nevertheless, *M. ovum* has been present primarily in Arctic surface water (salinity < 34 psu and temperature between 0.5 and 5°C) during this time of the year in this area (S. Majaneva et al. unpubl. data from Svalbard Archipelago 2009 to 2011). In all our study locations the Arctic surface water was mainly restricted to the upper 20 m. Similar observations from ROVs and traditional net sampling have been reported from several locations around the Arctic where up to 99% of *M. ovum* have been found to occur in dense patches in the upper 25 m (Swanberg & Båmstedt 1991a, Purcell et al. 2010, Raskoff et al. 2010). As a consequence, it seems reasonable to use an estimate of the *in situ* density of *M. ovum* in patches, instead of an even distribution throughout the water column, to produce a more realistic estimate of their natural density and predation impact.

The prey population densities observed during our study were similar to those found in previous studies (e.g. Walkusz et al. 2003). We focused on the 3 *Calanus* species known from Svalbard waters and — also seen in our study — to be the main prey for *Mertensia ovum* and key species in the Arctic ecosystem (e.g. Falk-Petersen et al. 2002, Kwasniewski et al. 2003, Purcell et al. 2010). At these latitudes, the population structure and vertical distribution of these 3 copepod species change throughout the year depending on the species' reproductive cycles. At the time of our study, *Calanus* spp. had started their seasonal migration to greater depths for overwintering, with low *Calanus* spp. densities in the upper layers compared to the earlier summer season (Falk-Petersen et al. 2008, Walkusz et al. 2009). In addition, *Calanus* spp. have been reported to perform distinct diel vertical migration (DVM). They descend into deeper depths during the LSN and come closer to the surface during the LM in our study area at this time of the year (Cottier et al. 2006, Falk-Petersen et al. 2008). However, from our data, it can clearly be seen that *Calanus* spp. had not descended into complete diapause and performed DVM (high SD values in Tables 2 & 3). To limit the effect of DVM we used either the average number between samples taken during the LSN and LM or the range between the LSN minimum and LM maximum from each study location.

Feeding experiments and gut content analysis

The type of functional response is fundamental to understanding any predator–prey interaction (Solomon 1949). For *Mertensia ovum*, experiments with *Calanus* spp. prey showed a nonlinear Type II functional response (Holling 1959). However, the lowest prey concentration used was 0.2 prey l^{-1}, which may be 10 × higher than natural prey densities if an even distribution is assumed. Thus, a Type III sigmoidal curve or Type I linear curve at low prey densities cannot be totally excluded. Type I and II functional responses have been calculated for lower latitudes from similar experiments for other cydippid ctenophores, whereas Type I has been shown for lobate ctenophores like *Mnemiopsis leidyi* (e.g. Greene et al. 1986, Gibbons & Painting 1992, Chandy & Greene 1995, Jaspers et al. 2011). The low slope of a Type III curve at low prey concentrations is commonly attributed to a delayed response as the prey can find refuges and the predator learns to search for prey (Solomon 1949). Because of the mechanisms involved in ctenophore feeding (passive capture of food items in mucus-covered tentacles) both in nature and under our experimental conditions, it is difficult to imagine learning as an explanation for a Type III response. Increased search rate at low prey densities could also produce a sigmoidal curve; however, this was not observed in our experiments. At high prey densities, *M. ovum* appears to become handling-limited due to the high numbers of prey attached to the tentacles.

Feeding experiments were conducted only using *Calanus* spp. as prey, and clearance rates from gut content analysis were also calculated only for *Calanus* spp. Naturally, as an opportunistic feeder, *Mertensia ovum* is capable of consuming other prey species (Fig. 3), and, therefore, gut passage time is affected by the type and size of the prey, similar to that in other ctenophores (Granhag et al. 2011). For *Mnemiopsis leidyi*, the size of prey affected gut passage time, with larger items having a longer gut passage time than smaller ones. Furthermore, a high number (10 to 50) of prey items implied more prey carbon in the gut and increased gut passage time (Granhag et al. 2011). Even though some prey items are impossible to detect in the guts and the selectivity index used for indicating prey selection does not take into account different gut passage times for different prey types, unidentifiable copepods and *Calanus* spp. were clearly a numerous prey item in our samples (Fig. 3).

Predation impact

We estimated that *Mertensia ovum* may consume an average of 1.4 % d^{-1} of the *Calanus* spp. community in the whole water column, or 33 % d^{-1} in the upper 20 m layer, when assuming even distributions of predators and prey and using the ingestion rates (I) from functional response experiments (Type A). Our estimates are similar to those reported in earlier studies. Siferd & Conover (1992) estimated that average-sized *M. ovum* may consume 3 to 9 % of the copepods per day in the Canadian Arctic, and Purcell et al. (2010) estimated that *M. ovum* could remove ~2 % of *Calanus* spp. standing stock daily. However, when concentrating on the upper 20 m layer, our estimates are clearly higher compared to earlier reports. For example, Swanberg & Båmstedt (1991b) estimated that under the right circumstances *M. ovum* could consume a maximum of 1 to 5 % of the copepods in the water where it occurs.

At the time of our study, *Calanus* spp. had started their seasonal migration to overwintering depths, resulting in low *Calanus* spp. densities in the upper layers compared to the summer season. Hence, the calculated effect of prey in the entire water column may be indicative of summer conditions, when predators and prey both occur at high densities in surface waters (e.g. Siferd & Conover 1992, Lundberg et al. 2006, Walkusz et al. 2009). Our results suggest that the potential predation impact of *Mertensia ovum* may even increase significantly with increased prey density during summer, due to a high saturation level (Fig. 4A; compare Swanberg & Båmstedt 1991a). In addition, the *M. ovum* population has been shown to descend in the winter (Siferd & Conover 1992), suggesting that this tactile predator can continue consuming *Calanus* spp. prey items throughout the year (Purcell et al. 2010).

Many approximations were necessary when estimating the predation impact of *Mertensia ovum* from our data, either due to the logistical limitations of our field work or the assumptions required in the methodological approach (Chandy & Greene 1995, Purcell et al. 2010). One of the important assumptions in our study, and for most published feeding estimates, is that ingestion rate is affected by experimental conditions (Swanberg & Båmstedt 1991b, Gibbons & Painting 1992, Møller et al. 2010). Small containers may limit feeding efficiency by posing physical limitations on predator behavior, e.g. not allowing full extension of tentacles or tentillas (Gibbons & Painting 1992, Purcell 2009, Møller et al. 2010). The vessels in our experiments (Type A) were scaled by the minimum

ratio (1:2500) of container volume to ctenophore volume recommended for ctenophores by Purcell (2009), and no severe signs of physical limitation were observed during our study. Also, potential prey depletion at low prey densities in Type A experiments might result in lower calculated feeding efficiencies than would be realistic. However, in our study, prey depletion was on average 25%, which has been reported to be reasonable (Beddington & Cooke 1982). Another important assumption while calculating predation impact is that *M. ovum* is able to consume constantly (e.g. Madin 1988). Unlike most invertebrates which have to stop hunting while they are feeding (Madin 1988, Matsumoto 1991), *M. ovum* is able to continue 'hunting' while processing its prey. It is a common feature for gelatinous zooplankton to continue eating as long as prey are available (until saturation level), and then to fast for periods during which no food is available (Lundberg et al. 2006, Purcell et al. 2010). This is supported by the behavior observed in our experiments. When *M. ovum* was introduced to unnaturally high densities of prey (100 ind. l^{-1}), more prey items were captured on the tentacles than the individual was able to consume at the time.

Patchiness effects on predation impact

Interestingly, neither ingestion rate nor clearance rate in our experiments decline significantly when predator density increased. Cydippid ctenophores and other tentacle feeders should exhibit a mechanical limitation when occurring in high aggregations (Madin 1988). A high density of predators could limit tentacle extension, thus decreasing predation efficiency (Madin 1988). There were no signs of such intraspecific interference (cf. Nachman 2006 a,b), even at predator densities of 500 ind. m^{-3}, which is equal to the highest density used in the experiments. Therefore, the predation impact at high densities could be modeled directly, multiplying the ingestion rate by predator abundance. Presumably, the absence of intraspecific competition might result from ctenophores adapting efficient avoidance of tentacle interactions due to frequent occurrences.

The most important component of a functional response is the predators' ability to adjust its ingestion rate to changes in prey density (e.g. Solomon 1949). The results from the predation–impact models indicate that prey patchiness may be advantageous for prey at low densities, but an advantage to the predator at high densities, if the predator is able to compensate by adopting a non-random searching behavior (Dagg 1977, Arai 1992). Nachman (2006a,b) suggests that such behavior will lead to a positive aggregative response whereby the majority of predators will cluster in the most profitable prey patches. If the degree of prey aggregation is high, predators may actually be able to achieve a higher ingestion rate, even though the clearance rate does not increase, than they would if the prey were evenly distributed. On the contrary, prey accumulation into dense patches has often been thought to be beneficial to the prey, due to the saturation of predator feeding (Nachman 2006a,b). This was also clearly seen in our study, where the potential predation impact was higher if patchy distributions of both prey and predators were taken into consideration, due to a high saturation level, but was even higher if only predators had uneven distributions.

Conclusions

We have shown that the common Arctic comb jelly *Mertensia ovum* has the potential to dramatically affect the abundance of prey populations. At our study locations, we estimated that *M. ovum* is capable of consuming on average 1.4% d^{-1} of the *Calanus* spp. population in the whole water column, or 33% in the upper 20 m layer where it mainly occurs, when assuming even distributions of prey and predators. Most importantly, ingestion rates did not significantly decline at high predator aggregations; hence, predation impact increased locally to >50% d^{-1} when spatial predator and prey aggregations were considered. We do not propose that our numerical values are globally accurate for all locations, seasons or species. Nevertheless, we show that they are significant proportions in Arctic waters and are especially important as *Calanus* spp. are such a valuable source of energy for higher trophic levels such as fish and seabirds. Furthermore, a proposed increase in the occurrence of gelatinous zooplankton species due to climate shifts (Purcell et al. 2010) suggests an increased importance of these species as regulators of prey communities as well. Under the assumption of spatially homogeneous distributions of both predators and prey, it has been predicted that the rate at which an individual predator consumes prey should depend only on prey density. This, however, gives a biased view of natural conditions, in which patches of high abundance frequently occur and may lead to miscalculated energy flows in food web models. The potential predation impact was even higher when patchi-

ness of both predators and prey was taken into account, and is further affected by extensive spatial and seasonal migration patterns. Since predation did not increase linearly with predator and prey aggregations, it is possible that high-density patches of predators may be refuges for prey. Whereas prey accumulating into dense patches has been thought to be beneficial for the prey (Nachman 2006a,b), our results show that the co-occurrence of predator and prey aggregations can actually increase the potential predation impact due to the high saturation levels of the predator. For adequately modeling prey–predator interactions more emphasis should be placed on the patterns of fine-scale distributions of predators and prey.

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