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Functional biology of sympatric krill species

METTE DALGAARD AGERSTED[1]* AND TORKEL GISSEL NIELSEN[1,2]

[1]NATIONAL INSTITUTE OF AQUATIC RESOURCES, SECTION FOR MARINE ECOLOGY AND OCEANOGRAPHY, TECHNICAL UNIVERSITY OF DENMARK, KAVALERGÅRDEN 6, 2920 CHARLOTTENLUND, DENMARK AND [2]GREENLAND CLIMATE RESEARCH CENTRE, GREENLAND INSTITUTE OF NATURAL RESOURCES, BOX 570, 3900 NUUK, GREENLAND

*CORRESPONDING AUTHOR: metteagersted@gmail.com

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Here we compare the functional biology of the sympatric krill species, *Meganyctiphanes norvegica* and *Thysanoessa inermis*. For *M. norvegica*, we investigated functional responses on diatoms and copepods, together with prey size spectra on plankton <400 μm and copepods in the size range 500–3220 μm. For *T. inermis*, only prey size spectrum on plankton <400 μm were investigated. The prey size ranges of both species include organisms <400 μm, and they consequently graze on several trophic levels. However, *T. inermis* feed on cells <10 μm equivalent spherical diameter (ESD), whereas *M. norvegica* only feed on cells >10 μm. *Meganyctiphanes norvegica* show maximum predation on 800–1600 μm sized copepods, corresponding to a predator:prey size ratio of 17.0 ± 2.2. Functional response experiments with *M. norvegica* follow a Holling type III functional response, both when feeding on diatoms and copepods, but with an order of magnitude higher ingestion rate on the copepod prey. The two functional groups, *M. norvegica* and *Thysanoessa* spp., overlap in prey size spectra. However, there are differences in their ability to exploit different prey classes. Here, we present clearance rates of both krill species on natural plankton illustrating the two species' wide particle range spectra.

KEYWORDS: *Meganyctiphanes norvegica*; *Thysanoessa inermis*; grazing; predation; prey size spectra; functional response

INTRODUCTION

In northern marine pelagic ecosystems, two functional groups of krill (*Meganyctiphanes norvegica* and *Thysanoessa* spp.) coexist (Einarsson, 1945). Coexistence of sympatric species is only possible if the system is not homogeneous and the species have different ecological niches and have different life strategies, food preferences or distributional overlap (Hutchinson, 1961). In Arctic and sub-Arctic areas, information is available on northern krill species with regard to abundance and distribution (e.g. Einarsson, 1945; Dalpadado and Skjoldal, 1991; Astthorsson and Gislason, 1997), trophic role and feeding behavior (e.g. Mcclatchie,

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1986; Schmidt, 2010; Agersted *et al.*, 2011). However, information is scarce and more knowledge from these regions is needed. Knowledge on feeding by krill provides information on carbon flow, given that krill have an important role in carbon cycling by linking lower and higher trophic levels (Macdonald, 1927; Quetin and Ross, 1991). Furthermore, knowledge on feeding behavior and trophic position is required to understand and model ecosystem functioning.

Krill are omnivorous organisms and able to feed on several trophic levels (Boyd *et al.*, 1984; Mcclatchie, 1985; Agersted *et al.*, 2011). A standard method for studying trophic position in organisms is stable isotope analysis (Peterson and Fry, 1987; Fry, 1988; Hobson and Welch, 1992). Heavier isotopes accumulate from prey to predator over time and consequently give a time-integrated averaged trophic position (Fry and Sherr, 1984; Fry, 1988). However, a constraint is that this will not give information on ingested prey. This information can instead be obtained by gut content analysis (e.g. Båmstedt and Karlson, 1998). Yet, this method is biased toward prey with an exoskeleton (Båmstedt *et al.*, 2000) and therefore ingestion of, for example, naked protozooplankton and phytoplankton is underestimated. As for gut content analysis, grazing experiments only give a snapshot-in-time of the ingested prey. This is nevertheless an accurate method for studying krill prey size preferences as well as grazing- and predation rates on various types of prey.

In the sub-Arctic regions krill is dominated by four species; *Thysanoessa raschii*, *Thysanoessa inermis*, *Thysanoessa longicaudata* and *Meganyctiphanes norvegica* (Einarsson, 1945). In Godthåbsfjord, SW Greenland these species coexist (Agersted and Nielsen, 2014) and stable isotope analyses revealed that these four species have different trophic positions (Agersted *et al.*, 2014). The largest species, *M. norvegica*, has the highest trophic position and is also known to predate on copepods (Båmstedt and Karlson, 1998; Kaartvedt *et al.*, 2002). *Thysanoessa inermis* has the second highest trophic position followed by *T. raschii* and *T. longicaudata*, with the two latter species having similar trophic positions. Grazing experiments with *T. raschii* demonstrated its ability to exploit plankton covering several trophic levels (Agersted *et al.*, 2011). Though, in general, data on grazing rates of the co-existing *T. inermis* and *M. norvegica* is limited.

Here, we investigate the prey size spectra and grazing rates of two krill species, *M. norvegica* and *T. inermis*, on plankton <400 μm. Furthermore, we investigate predation rates on copepods, together with functional responses on diatoms and copepods for *M. norvegica*. Recalculated grazing rates and prey size spectrum for *T. raschii* (data from Agersted *et al.*, 2011) are included for comparison.

METHOD

Feeding experiments

Feeding experiments were conducted with *Meganyctiphanes norvegica* and *Thysanoessa inermis* during various cruises in different regions of the North Atlantic: SW Greenland, Irminger Sea, Iceland Sea and Norwegian Sea (see Figs 1 and 2 and Tables I and II for details). Below is a description of the experimental setup.

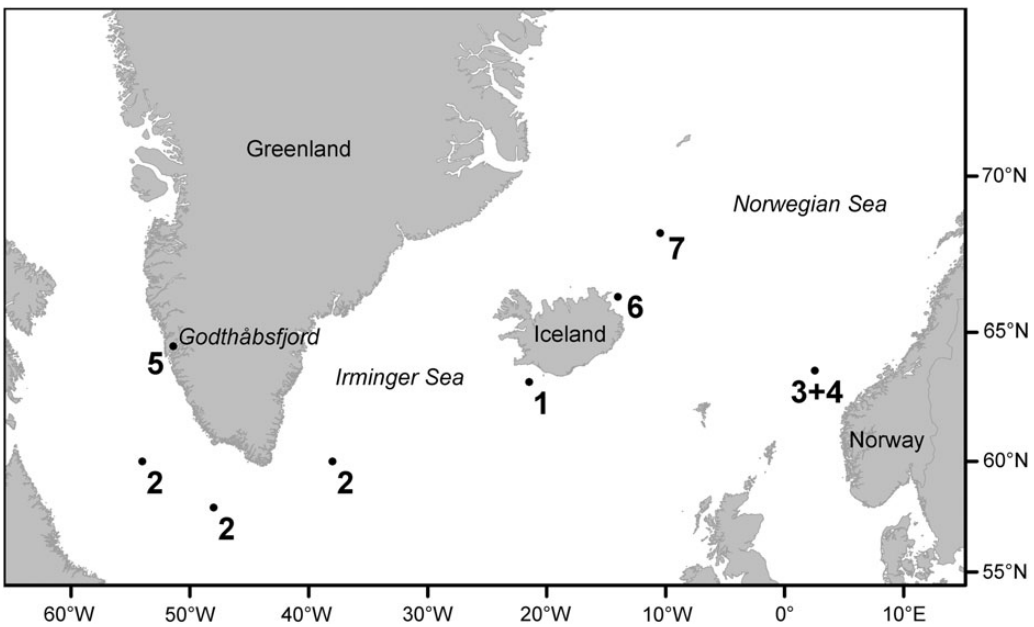

Fig. 1. Map with geographic locations of experimental stations 1–7. See Table I for details on experiments.

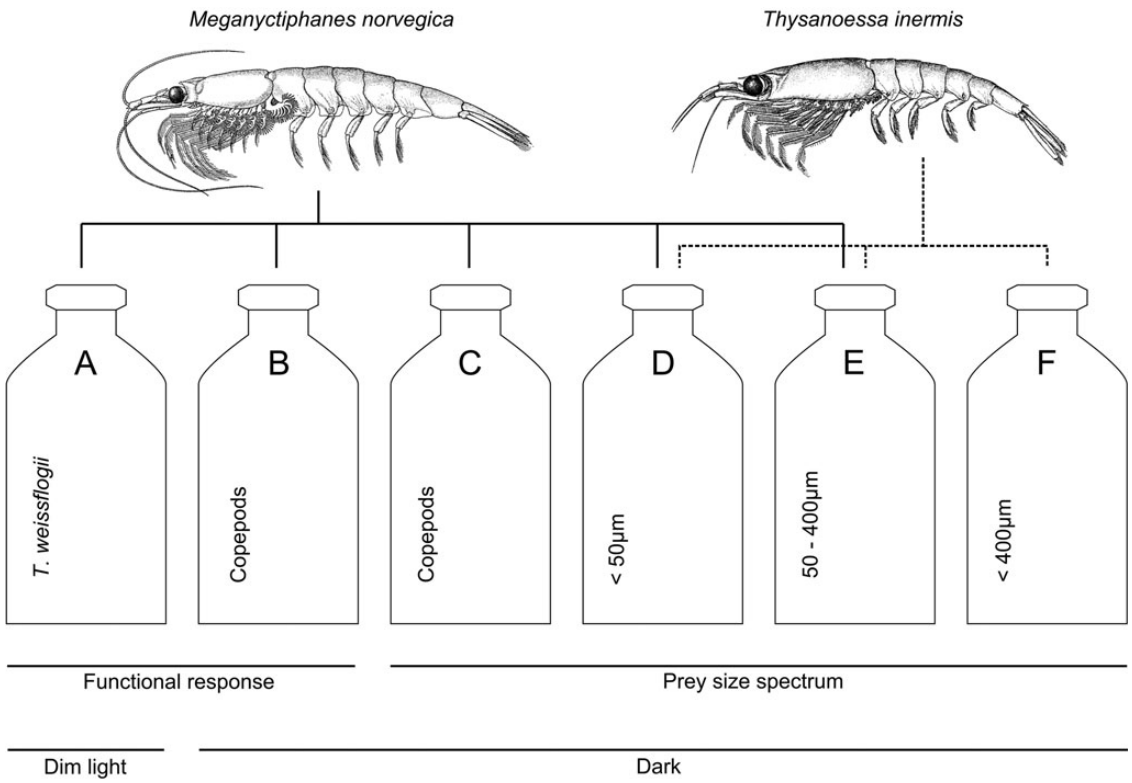

Fig. 2. Cartoon of experiments conducted with *Meganyctiphanes norvegica* and *Thysanoessa inermis*. Krill drawings modified from Einarsson (Einarsson, 1945).

All experiments were carried out with freshly collected animals. Immediately after retrieval, krill were transferred from the cod-end to a 50-L isolated container filled with *in situ* seawater and prey and acclimatized to the experimental temperature prior to experimentation. In the experiment using the diatom *Thalassiosira weissflogii* as prey, *M. norvegica* was kept in 1-μm-filtered seawater and pre-fed with *Thalassiosira weissflogii* daily. Copepods that were used as prey were handled as described for krill. Water used for prey size spectra experiments with prey <400 μm was collected *in situ* and transferred untreated to the incubation bottles.

Males and females were not distinguished and only krill with all limbs and intact antennae were used in experiments. Experiments were conducted in 0.5- to 1-μm-filtered seawater in darkness (except the functional response experiment with *M. norvegica* and *Thalassiosira weissflogii* as prey, which was conducted in dim light) at *in situ* temperature for ∼24 h (Table II). As temperatures differed between regions, results were standardized to 5°C using a Q_{10} of 1.55 for *M. norvegica* (4–8°C; Table III in Saborowski *et al.*, 2002) and 1.9 for *T. inermis* (0–10°C; Table I in Sameoto, 1976). Furthermore, a Q_{10} of 1.9 (1–11°C; Agersted *et al.*, 2011) was used for *T. raschii* grazing rates from Agersted *et al.* (Agersted *et al.*, 2011) for comparison. Due to logistic reasons not all experiments were conducted for both krill species. As a result, the prey size spectrum experiments with 0- to 400-μm sized prey were the only type of experiment conducted for *T. inermis*.

All experiments were conducted with single krill in 13.2-L polycarbonate bottles, except for the prey size spectrum experiment with *M. norvegica* feeding on copepods, which were conducted in 11.4-L bottles. For each experiment, control bottles (prey and no krill) were incubated in parallel ($n = 3–5$). Initial samples were taken for initial prey concentration ($n = 3$). At the end of each experiment, krill were length measured from tip of the rostrum to end of the telson (mm) and length was either converted to carbon (mg C) by a length-weight regression (Agersted and Nielsen, 2014) or the animals were dried for 24 h at 60°C and weighed. Carbon weight was calculated using carbon-dry weight conversions of 53.1% from Agersted and Nielsen (Agersted and Nielsen, 2014) (Table II). Clearance and ingestion rates were calculated by equations from Frost (Frost, 1972).

Cultures of the diatom *Thalassiosira weissflogii* were kept at 14.5°C with a light:dark cycle of 16:8 h. Every day, half of the culture was replaced with filtered seawater and added 1 mL L^{-1} of trace elements, vitamins, silica and

Table I: Locality, gear and sampling depth (m) for krill and prey and type of experiment conducted

Species	Place and time of collection	Gear and sampling depth (m)	Experiment and prey type	Prey collection	Geographic location (see Fig. 1)
M. norvegica	SW of Iceland, May 2012	Bongonet (333 and 500 μm), 0–50 m	Functional response (*Thalassiosira weissflogii*)	Culture	1
M. norvegica	Irminger Sea, June 2013	Krill trawl (3000 μm), 0–50 m	Functional response (copepods)	WP2-net (200 μm), 0–50 m	2
M. norvegica	Norwegian Sea, June 2011	Krill trawl (3000 μm), 0–25 m	Feeding on *C. finmarchicus* (1.2 L^{-1})	WP2-net (200 μm), 0–50 m	3
M. norvegica	Norwegian Sea, June 2011	Krill trawl (3000 μm), 0–25 m	Prey size spectrum (prey <400 μm)	Niskin, Chl *a* max	4
M. norvegica	Godthåbsfjord, SW Greenland, June 2010	2-m ring MIK net (1500 μm), 0–50 m	Prey size spectrum (copepods)	Bongonet (333 and 500 μm), 0–50 m	5
T. inermis	NE of Iceland, May 2012	Bongonet (333 and 500 μm), 0–50 m	Prey size spectrum (prey <400 μm)	Niskin, Chl *a* max	6
T. inermis	Northern Norwegian Sea, June 2013	Krill trawl (3000 μm), 0–50 m	Prey size spectrum (prey <400 μm)	Niskin, Chl *a* max	7

All net types were equipped with a nonfiltering cod-end. Bongonet, krill trawl and MIK were hauled oblique at a speed of 2.5–3 knots, whereas WP2-net was used by vertical hauls (0.2–0.3 m s^{-1}). Water for prey size spectrum experiments was collected by a rosette mounted on a CTD. See Fig. 1 for geographic location of experimental stations.

Table II: Experimental overview

Species	Length and weight (mm, mg C ± SD)	Experiment (capital letters refer to Fig. 2)	Temperature (°C ± SD)	Acclimatization period	Bottles rotated	*n*
M. norvegica	23–28 mm, 14.4 ± 3.1 mg C[a]	A. Functional response (*Thalassiosira weissflogii*)	7.7 ± 0.2	4 d	Every 3–4 h	5–7
M. norvegica	26–37 mm, 34.5 ± 11.4 mg C[b]	B. Functional response (copepods)	2.6 ± 0.2	6–9 h	Every 3–4 h	7–8
M. norvegica	31–35 mm, 41.9 ± 8.1 mg C[a]	B. Feeding on *C. finmarchicus* (1.2 L^{-1})	6.8 ± 0.6	12 h	Every 6 h	6
M. norvegica	32–38 mm, 55.8 ± 12.3 mg C[b]	C. Prey size spectrum (copepods). See Table III in addition.	3.9 ± 0.9	24 h	Every 6 h	8
M. norvegica	21–32 mm, 21.2 ± 8.5 mg C[a]	D and E. Prey size spectrum (prey <50 and 50–400 μm)	6.8 ± 0.6	12 h	Every 5 h	7[c]
T. inermis	20–25 mm, 9.6 ± 3.5 mg C[a]	D and E. Prey size spectrum (prey <50 and 50–400 μm)	5.1 ± 0.3	12 h	Every 6 h	7[c]
T. inermis	25–28 mm, 18.4 ± 3.3 mg C[a]	F. Prey size spectrum (prey <400 μm)	2.6 ± 0.2	12 h	Every 3–4 h	7

Size [length range, mm; mean weight ± SD (mg C)] of experimental animals, type of experiment conducted and experimental temperature (°C). For acclimatization krill were kept in 50-L containers with seawater at experimental temperature. In every experiment bottles were gently rotated to keep prey in suspension. Also shown is the number of replicates (=*n*) in each experiment.
[a]Length–weight regression from Agersted and Nielsen (Agersted and Nielsen, 2014): $mg\ C = (7.25 \times 10^{-5}) \times L^{3.79}$, where L = length (mm).
[b]Carbon-dry weight factor (53.1% carbon of DW) from Agersted and Nielsen (Agersted and Nielsen, 2014).
[c]$n = 7$ for each size fraction experiment (<50 and 50–400 μm).

Table III: Prey size groups and the appertaining copepodite stages (CI–CVI) of the three dominating copepod species Metridia longa, Calanus finmarchicus *and* C. glacialis *from the prey size spectrum experiment with* M. norvegica *(fourth row in Table II)*

Size group (μm)	Prey L^{-1} (=*n* ± SE)	*M. longa*	*C. finmarchicus*	*C. glacialis*
500–800	8.3 ± 0.4	CI–CII	CI	
800–1110	10.8 ± 0.5	CIII	CII	CI
1110–1600	5.9 ± 0.6	CIV	CIII	CII
1600–2250	4.5 ± 0.3	CV	CIV	CIII
2250–2800	2.3 ± 0.4	CVI	CV	CIV
2800–3220	2.5 ± 0.2		CVI	CV

Also stated is the number (=*n*) of prey L^{-1} in start samples.

salt solution (B1 medium, Hansen, 1989) to keep the culture in exponential growth. To estimate the amount of *Thalassiosira weissflogii* to be added in the different experiments, samples were counted under a microscope using a Sedgewick Rafter chamber. An assumed carbon conversion factor of 305 pg C $cell^{-1}$ (Reigstad *et al.*,

2005) was used to calculate how much volume of the culture should be added to the experimental bottles to obtain the intended concentration.

Functional response experiments

For *M. norvegica*, functional response experiments were conducted with two different prey types: (i) *Thalassiosira weissflogii* and (ii) copepods (Fig. 2).

(1) In total, eight different concentrations with *Thalassiosira weissflogii* as prey were conducted. To reduce variability, the same individuals were used for four experiments where they were fed increasing concentrations of *Thalassiosira weissflogii*: batch one with 5–7 replicates for each concentration: 10, 50, 200 and 600 μg C L^{-1}, batch two with 5–6 replicates for each concentration: 25, 100, 400 and 1000 μg C L^{-1}. Hence, two sets of concentrations of *Thalassiosira weissflogii*, with 5–7 replicates for each concentration (Table II), were conducted simultaneously over four sequential times. At termination of each experiment, individual krill were gently transferred to a bottle containing 1-μm-filtered seawater for 2 h, before the next experiment with a higher prey concentration was initiated. From each experimental bottle, triplicates of 50–200 mL (depending on prey concentration) were filtered onto GF/F filters and extracted in 96% ethanol for 12–24 h (Jespersen and Christoffersen, 1987). Fluorescence was measured before and after acid on a fluorometer (Turner TD-700), calibrated against a pure chlorophyll *a* (Chl *a*) standard. The carbon content was calculated using a C:Chl *a* ratio of 45 (Reigstad *et al.*, 2005).

(2) *Meganyctiphanes norvegica* was offered four concentrations of copepods (1, 5, 13 and 17 L^{-1}) dominated by *Calanus finmarchicus* of 1000–3000 μm. An additional experiment was conducted (Tables I and II), where *M. norvegica* was fed a concentration of 1.2 *C. finmarchicus* L^{-1}. For the lowest prey concentrations, the copepods were handpicked by a pipette. For higher concentrations, water including prey was first pre-screened on a 2-mm-sieve, to remove large organism like arrow worms and jellies, to end up with prey dominated by copepods. Next, copepods were kept in a large container and kept in suspension, and a known volume, with a known density of copepods, was then added the experimental bottle for the desired final concentration. At termination, the prey was retrieved on a 50-μm-sieve and fixed in Lugol's solution (2% final concentration) and immediately counted and length measured (prosome length to nearest 100 μm). As *C. finmarchicus* dominated the prey, the carbon content of the prey was calculated based on the weighted mean sized *C. finmarchicus* by the length-weight regression from Hygum *et al.* (Hygum *et al.*, 2000).

An information-theoretical approach was applied, in which AIC values (Akaike's Information Criterion) (Akaike, 1974) for all three functional response types [Type I: a linear increase in predator ingestion rate with prey concentration; Type II: a decelerating increase in ingestion rate with prey concentration and Type III: an S-shaped (sigmoidal) increase in ingestion with prey concentration (Holling, 1959)] were calculated. Calculations were based on the raw specific clearance rate data, in order to determine the best fit of a functional response type for the data. Based on AIC values, clearance (*Cl*, mL mg C^{-1} d^{-1}) and ingestion rates (*I*, mg C mg C^{-1} d^{-1}) were fitted to a Holling type III functional response curve (Schultz and Kiørboe, 2009):

$$Cl = \left(\frac{\alpha \times \beta}{x}\right) \times e^{(1-(\alpha/x))} \quad (1)$$

$$I = \alpha \times \beta \times e^{(1-(\alpha/x))} \quad (2)$$

where α is the concentration of prey (μg C L^{-1}) when clearance rate is maximum, β is the maximum clearance rate (mL mg C^{-1} d^{-1}) and x is the prey concentration (μg C L^{-1}).

To compare the difference in feeding on different food items (*Thalassiosira weissflogii* and copepods), and between krill species (*M. norvegica* and *T. raschii*), the half-saturation constant for ingestion (K_m) was calculated as:

$$K_m = \frac{\alpha}{1 - \ln(e/2)} \quad (3)$$

Prey size spectrum experiments

Two types of prey size spectrum experiments were conducted with (i) *in situ* plankton <400 μm and (ii) copepods >500 μm, respectively (Fig. 2). Both experiments were conducted with *M. norvegica*, whereas the only experiment conducted with *T. inermis* was with prey <400 μm.

(1) *In situ* plankton was collected from the Chl *a* maximum by a Niskin rosette mounted on a CTD system, and water was siphoned by silicone tubes and split into two fractions: <50 μm and 50–400 μm. These two size fraction experiments were conducted simultaneously. However, for the experiment conducted with *T. inermis* in the Norwegian Sea, only one size fraction (<400 μm) was conducted (Fig. 2, Table II). At termination of

experiments with size fraction <50 μm, bottles were gently rotated and 300 mL of the volume was preserved in Lugol's solution (2% final concentration) for later analysis. In addition, Chl *a* was measured in triplicate by the method mentioned above. Prey from the 50 to 400 μm experiments were concentrated on a 45-μm-sieve and preserved in Lugol's solution (2% final concentration) for later analysis. Prey was concentrated by sedimentation in Ütermöhl chambers, counted and identified to genus. However, as prey concentrations were low, all prey was categorized in groups of 10-μm size intervals, with a minimum of 200 cells L^{-1} in each size class, for the calculation of krill clearance rates. Ciliates were corrected for shrinkage (Putt and Stoecker, 1989), whereas dinoflagellates were not (Menden-Deuer *et al.*, 2001). Afterwards, prey cell volume was converted into equivalent spherical diameter (ESD, μm) and an average size was calculated for each specific size group. Prey concentration in the incubations was low and hence, the krill were most likely not food saturated. Therefore, these experiments were only used for identifying the prey size spectra of the krill species, and not their possible ingestion rate and daily ration.

(2) In the feeding experiment with copepods, the experimental bottles were filled with 200 μm prescreened *in situ* seawater with a concentration of 0.5 μg Chl *a* L^{-1}, with the majority (>90%) of the phytoplankton consisting of small cells <10 μm. Copepods were added to the experimental bottles as described for the functional response experiment above. At termination, samples were taken for Chl *a* measurements as described above. The remaining copepods were retrieved on a 50-μm-sieve and preserved in Lugol's solution (2% final concentration) and kept cold and dark until examination 4 months later. Number of individuals was counted and prosome length measured to nearest 50 μm. In a few cases (not significant numbers), we observed copepods with injuries such as lacking antennae or missing limbs, as observed in other studies with different species of krill feeding on copepods (Ohman, 1984; Price *et al.*, 1988; Beyer, 1992; Båmstedt and Karlson, 1998). These copepods were considered eaten according to Ohman (Ohman, 1984). The prosome lengths were corrected for shrinkage using a factor of 16.3% (Jaspers and Carstensen, 2009). Carbon weight was calculated by the length−weight regression for well-fed *C. finmarchicus* in Hygum *et al.* (Hygum *et al.*, 2000). This regression was chosen as *C. finmarchicus* dominated the copepod assemblage and due to the assumption that the copepods in this experiment were in good condition and had a high lipid content. Copepods were pooled into different size groups, based on prosome length and species composition from a biomass sample taken simultaneously (Table III). The size groups were equivalent to copepodite stages of the dominating species *Calanus finmarchicus*, *Calanus glacialis* and *Metridia longa* (Table III). As there were very few copepods >3220 μm (*C. glacialis* CVI; $n = 0.23\ L^{-1} \pm 0.1$ (SE)), this group was ignored.

To calculate predator:prey size ratios (ESD:ESD) for individual krill feeding on copepods, we calculated the average copepod weight in the size group where a given krill had its maximal clearance rate. Biovolume of krill and copepods were calculated by using the conversion factor 0.13 g C cm^{-3} (Hansen *et al.*, 1997). The volumes of krill and copepods were then converted to ESD and the predator:prey size ratio calculated for each krill ($n = 7$).

Statistical analyses

In the prey size spectrum experiments with prey <400 μm, raw data on clearance rates were analyzed to see whether prey size or experiment (for the latter only in relation to *T. inermis*, where two similar experiments were conducted in two different regions) had any effect on the clearance rate of the krill. We used a linear model with clearance rate as dependent factor and prey size and experiment as independent factors (R Core Team, 2013). We chose the appropriate model using stepwise backward deletion and allowed for an interaction between experiment and prey size in the initial model.

RESULTS

Functional response experiments

When grazing on the diatom *Thalassiosira weissflogii*, *M. norvegica* displayed a Holling type III functional response (Fig. 3A and C). The maximum clearance rate at 5°C was 41 mL mg C^{-1} d^{-1} at a prey concentration of 224 μg C L^{-1} (Fig. 3A). The half-saturation constant (K_m) was 413 μg C L^{-1} (=9 μg Chl *a* L^{-1}) and here, *M. norvegica* had an ingestion rate of 14.4 μg C mg C^{-1} d^{-1} (Fig. 3C). For comparison, data for *T. raschii* has been included (Fig. 3B and D) (recalculated from Agersted *et al.*, 2011). *T. raschii* had a maximum clearance rate of 66 mL mg C^{-1} d^{-1} at a prey concentration of 76 μg C L^{-1} (Fig. 3B), and K_m was 100 μg C L^{-1} (=2 μg Chl *a* L^{-1}) with an ingestion rate of 6.2 μg C mg C^{-1} d^{-1} (Fig. 3D). All values are read off the modeled response curves.

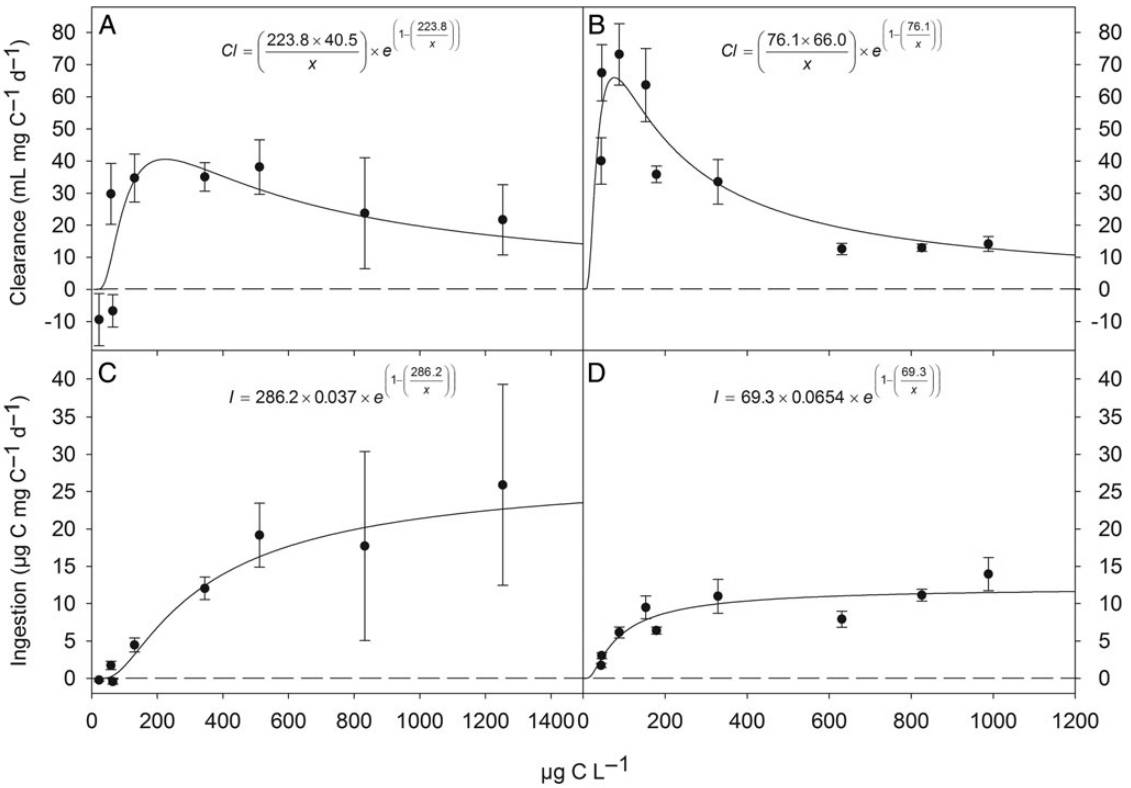

Fig. 3. Clearance (*Cl*, mL mg C^{-1} d^{-1} ± SE) (**A**, **B**) and ingestion rates (*I*, µg C mg C^{-1} d^{-1} ± SE) (**C**, **D**) in *Meganyctiphanes norvegica* (A, C) and *Thysanoessa raschii* (B, D) as a function of prey concentration (µg C L^{-1}) of the diatom *Thalassiosira weissflogii* at 5°C. Data on *T. raschii* have been recalculated from Agersted *et al.* (Agersted *et al.*, 2011). The dashed lines indicate the zero line.

When offered different concentrations of copepods, *M. norvegica* displayed a Holling type III functional response with a maximum clearance rate of 179 mL mg C^{-1} d^{-1} at a food concentration of 494 µg C L^{-1} (Fig. 4A). K_m was 631 µg C L^{-1} with an ingestion rate of 96.9 µg C mg C^{-1} d^{-1} (Fig. 4B). All values are read off the modeled response curves.

Ingestion rates of *M. norvegica* were an order of magnitude higher when feeding on copepods compared with diatoms. From an energetic perspective, the highest concentrations of diatoms correspond to a daily ratio of ~2%. Yet, when feeding on the highest concentration of copepods, the daily ratio was ~14% (read off Fig. 3C and D).

Prey size spectrum experiments

Meganyctiphanes norvegica cleared prey in the range 10–160 µm ESD, corresponding to a length of 14 µm (=10 µm ESD; *Gymnodinium* spp.) and 625 µm (=160 µm ESD; tintinnids), respectively (Fig. 5). The grazing rates on the different sizes of prey were not significantly different (ANOVA; $F_{1,123}$= 0.1476; P= 0.7016). However, clearance on prey <10 µm was negative and therefore the clearance rate of prey cells >10 µm ESD was described as an average clearance rate of 525 ± 95 mL mg C^{-1} d^{-1}.

Meganyctiphanes norvegica fed on copepods in the size range 500–2250 µm with a maximum predation on 800–1600 µm sized copepods, corresponding to copepodite stages CI–CII, CII–CIII and CIII–CIV for *C. glacialis*, *C. finnmarchicus* and *M. longa*, respectively (Fig. 6, Table III). The clearance rate was 47 ± 12 and 46 ± 7 mL mg C^{-1} d^{-1} on prey group 800–1100 and 1100–1600 µm, respectively. The average grazing on the larger copepods was negative and only few individuals of *M. norvegica* predated on larger copepods (>2250 µm), which was a group dominated by *M. longa* CVI stages. In addition, *M. norvegica* did not graze on the available phytoplankton (concentration of 0.5 µg Chl *a* L^{-1}) (Fig. 6). The predator:prey size ratio was 17.0 ± 2.2 (SD) (n = 7). When calculating the total ingestion of the different sizes of copepods, we chose to leave out the negative values for clearance on the largest copepods, and only add together ingestion for the copepods from 500 to 2250 µm in size. This resulted in ingestion rates ranging from 5.3 to 32.5 µg C mg C^{-1} d^{-1}, with an average of 15.4 ± 9.9 µg C mg C^{-1} d^{-1}. This corresponds to daily ratios ranging from 0.5 to 3.3%.

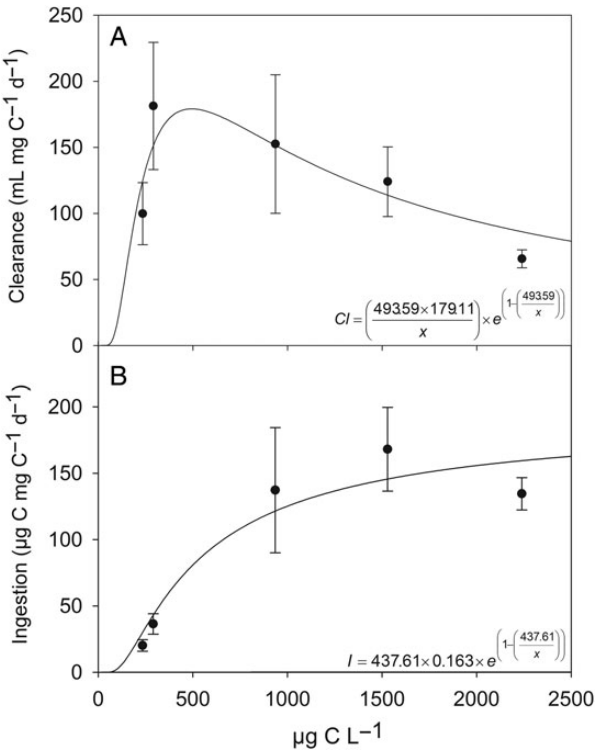

Fig. 4. *Meganyctiphanes norvegica* Type III functional response on copepods (dominated by *Calanus finmarchicus*). (**A**) Specific clearance rate (*Cl*, mL mg C^{-1} d^{-1} ± SE) and (**B**) specific ingestion rate (*I*, µg C mg C^{-1} d^{-1} ± SE) at 5°C as a function of food concentration (µg C L^{-1}).

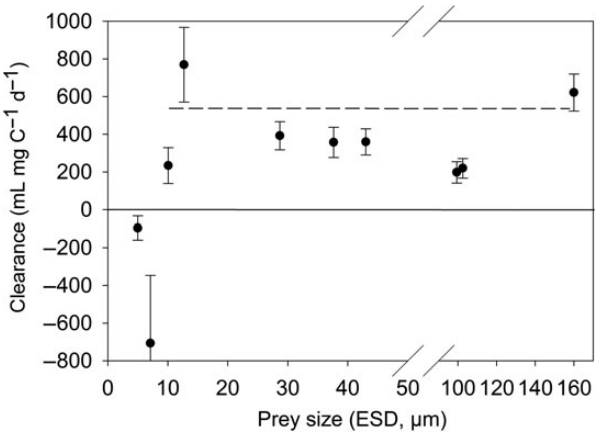

Fig. 5. Prey size spectrum for *Meganyctiphanes norvegica* on microzooplankton at 5°C. Specific clearance rate (mL mg C^{-1} d^{-1} ± SE) as a function of prey size (ESD, µm). The dashed line represents the average clearance rate 525 mL mg C^{-1} d^{-1} on all prey sizes >10 µm ESD.

Neither the interaction nor the single factors (prey size and experiments) alone, significantly affected the clearance rate of *T. inermis* on prey <400 µm (ANOVA, size × experiment: $F = 0.0033$, $P = 0.95$), and data were pooled in corresponding prey size groups. *Thysanoessa inermis* grazed

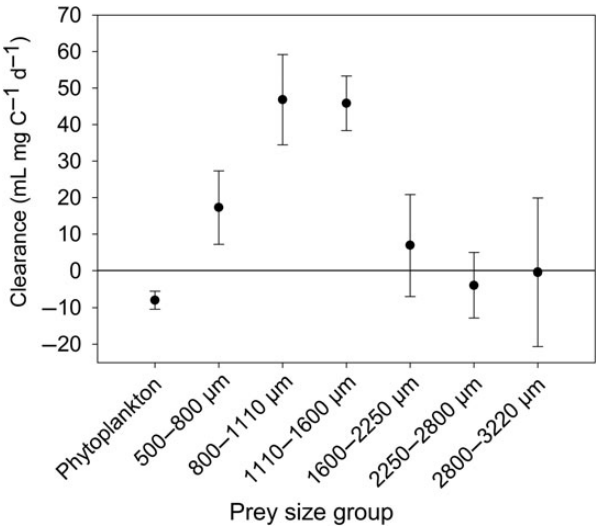

Fig. 6. Specific clearance rates (mL mg C^{-1} d^{-1} ± SE) and prey size spectrum for *Meganyctiphanes norvegica* at 5°C on copepods dominated by *Calanus finmarchicus, C. glacialis* and *Metridia longa*. See Table III for the different stages within the size groups. Also shown is grazing on phytoplankton (0.5 µg Chl a L^{-1}).

all particles from 5 to 200 µm ESD, corresponding to a length of 5 µm (flagellates) to 290 µm (*Oithona* spp.), respectively, at an average rate of 328 ± 36 mL mg C^{-1} d^{-1} (Fig. 7A). A similar experiment has been conducted for *T. raschii* (Agersted *et al.*, 2011), with an average clearance rate on prey >10 µm of 102 mL mg C^{-1} d^{-1} (Fig. 7B). The average clearance rate on microzooplankton by *M. norvegica* was slightly higher than that by *T. inermis*. Yet, clearance rates of *M. norvegica* and *T. inermis* were 3.8 and 3.2 times higher, respectively, than that of *T. raschii*.

DISCUSSION

Here, we document that the two sympatric krill species *Meganyctiphanes norvegica* and *Thysanoessa inermis* exploit a large and overlapping range of plankton prey, despite having different trophic positions (Agersted *et al.*, 2014). In the following, we discuss similarities and differences in their functional biology.

Krill are omnivorous organisms (Mauchline and Fisher, 1969; Berkes, 1973), and *M. norvegica* can detect prey by mechanoreception and by vision (Torgersen, 2001; Patria and Wiese, 2004; Abrahamsen *et al.*, 2010). The attack response on copepod prey is described as 'a pronounced movement of the krill's antennae towards the target, followed by a propulsion and opening of the feeding basket' (Abrahamsen *et al.*, 2010). In addition, krill can localize patches of phytoplankton by chemoreception (Hamner *et al.*, 1983; Price, 1989). By being

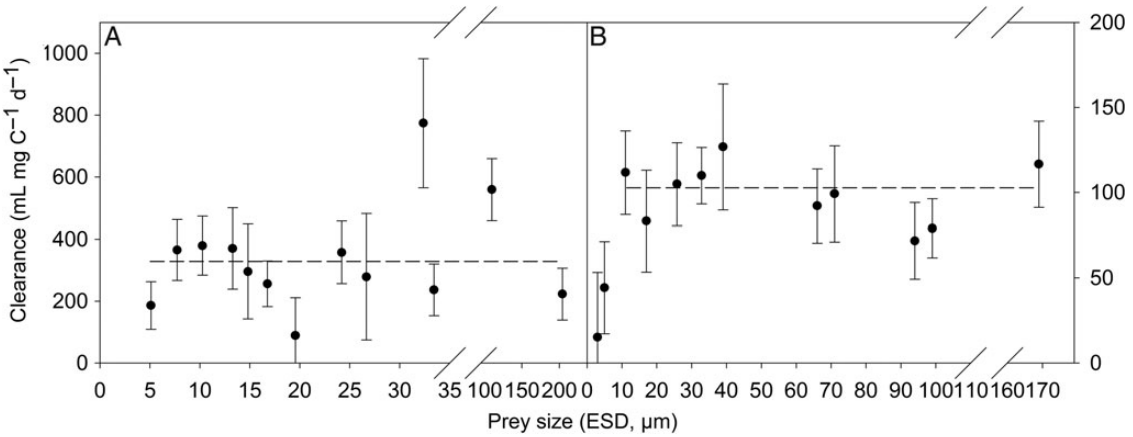

Fig. 7. *Thysanoessa inermis* (**A**) and *T. raschii* (**B**) grazing on *in situ* plankton at 5°C. Specific clearance rates (mL mg C^{-1} d^{-1} ±SE) on different plankton prey size groups (ESD, µm). Data on *T. raschii* is recalculated from Agersted *et al.*, (Agersted *et al.*, 2011). The dashed lines represents the mean clearance rate for all prey sizes for *T. inermis*, 328 mL mg C^{-1} d^{-1} (A), and prey >10 µm for *T. raschii*, 102 mL mg C^{-1} d^{-1} (B). Note different scales on *y*-axis.

able to feed on different prey types, krill possibly switch feeding mode between filter- and predatory-feeding, depending on prey type available. Similar behavior has, for instance, been observed for the copepod *Acartia tonsa*, which uses filter feeding on immobile prey, and ambush feeding on motile prey (Kiørboe *et al.*, 1996). In fish larvae, it has additionally been shown that shifts in feeding mode, from particle feeding to filtering, depend on the size difference between predator and prey (Crowder, 1985). Moreover, the feeding mode in fish larvae will change, from filtering to visual picking of individual prey, when prey concentration decreases (e.g. Crowder, 1985; Gibson and Ezzi, 1985). Nevertheless, there must be an upper prey size on which filter feeding is not possible, as larger prey can more easily detect and escape an approaching predator. Though, from the present experiments we are not able to say anything conclusive about shifts in feeding mode with regard to prey type or size.

Meganyctiphanes norvegica displayed a Type III functional response, when feeding on both the diatom *Thalassiosira weissflogii* and on copepods. This type of functional response indicates that at very low prey concentrations, the cost of searching for prey may be higher than the gain of finding and ingesting the prey (Lam and Frost, 1976). Reduced clearance rates at low phytoplankton concentrations have also been observed in other species of krill; *Euphausia pacifica* (Parsons *et al.*, 1967; Ohman, 1984), *E. superba* (Antezana *et al.*, 1982; Kato *et al.*, 1982) and *T. raschii* (Mcclatchie, 1988; Agersted *et al.*, 2011). In contrast to the present study, Ohman (Ohman, 1984) found *E. pacifica* to display a Type II functional response when feeding on the copepod *Pseudocalanus* sp. Mcclatchie (Mcclatchie, 1985) conducted an experiment, where *M. norvegica* were fed with a copepod prey assemblage consisting of *Centrophages typicus* (75%), *C. finmarchicus* (15%), *Pseudocalanus* spp. (10%) and *Acartia* spp. (<1% of the community) at different concentrations. He found a linear relationship between food concentration and ingestion rate on a log-log scale. However, no functional response type was found for *M. norvegica* in that study.

The daily ratio found in the present study, for *M. norvegica* feeding on diatoms, was similar to the ones found in the prey size spectrum experiment with copepod prey. The daily ratio found in the functional response experiment with copepod prey was higher. Yet, the daily ratios found in the present study, are comparable with daily ratios reported in previous studies (Table 5.6 in Schmidt, 2010). For instance, Båmstedt and Karlson (Båmstedt and Karlson, 1998) conducted five different predation experiments, where *M. norvegica* predated on *C. finmarchicus*, and they found the daily ratio to range from 0 to 33%. Mcclatchie (Mcclatchie, 1985) conducted predation experiments with *M. norvegica* feeding on different concentrations of copepod prey as mentioned above. Here, Mcclatchie (Mcclatchie, 1985) calculated that *M. norvegica* has to ingest >4.6% of its body calories per day to fulfill its metabolic demands. If we use the metabolic requirements as a minimum of 4.6% for *M. norvegica*, it is evident that in our experiments, only in the functional response experiment with copepod prey, was the food intake high enough to meet the metabolic demands of this species. Mcclatchie (Mcclatchie, 1985) also conducted grazing experiments with *M. norvegica* feeding on *Thalassiosira weissflogii*, as in the present study. Here, *M. norvegica* could not fulfill its metabolic demands, and ingested <0.02% of its daily ratio. However, the highest Chl *a* concentration in the experiment was 10 µg L^{-1}, and from the functional response experiment

on diatoms conducted in the present study, it is evident that *M. norvegica* is not food saturated at this food concentration. For comparison, the daily energy requirements for the Antarctic krill, *E. superba*, is ~1% (Atkinson *et al.*, 2002), and so, the 4.6% suggested by Mcclatchie (Mcclatchie, 1985) could be overestimated, as growth rates in *M. norvegica* and *E. superba* are similar (Schmidt, 2010; Tarling, 2010), i.e. food intake and metabolic requirements should not differ too much between these two species (Schmidt, 2010).

We found that *M. norvegica* had highest clearance rates on intermediate-sized copepods of 800–1600 μm. A selection for this size range has previously been observed by Båmstedt and Karlson (Båmstedt and Karlson, 1998), where about 70% of all mandibles in the stomachs were from *Calanus* CIII (prosome lengths >800 μm). Stuart and Huggett (Stuart and Huggett, 1992) documented similar size selection in *Euphausia lucens*, which preferred slow continuous swimmers, e.g. *E. lucens* nauplii, as opposed to fast intermittent swimmers, such as *Calanus agulhensis*. As mentioned above, *M. norvegica* uses mechanoreception and vision to detect prey (Torgersen, 2001; Kaartvedt *et al.*, 2002; Abrahamsen *et al.*, 2010), and therefore, it is possibly easier for *M. norvegica* to detect more active prey, as found by Torgersen (Torgersen, 2001), where the predation rate of *M. norvegica* on the more active *Metridia longa* was 2.3 times higher than on the slower swimming *C. finmarchicus*, when experiments were conducted in darkness. In our experiment, copepod prey consisted of *Calanus* spp. and *Metridia longa*. As both copepod genera were present in the different size classes, except for the largest size class, which only consisted of *Calanus* spp., we assume that this would not affect prey selectivity between size classes. Furthermore, smaller and maybe slower moving prey could be more difficult to detect than larger prey. In addition to this, *M. norvegica* preferred copepod prey of 1110- to 1600-μm in size, which was present at a lower concentration than smaller 500- to 800-μm sized copepods. Even though *M. norvegica* preferred the intermediate-sized copepods, some of the krill did also feed on larger copepods (dominated by *C. finmarchicus* CV–CVI), and are therefore capable of predating on these larger stages as also observed by Torgersen (Torgersen, 2001). This therefore suggests, that when *M. norvegica* is offered different sized copepods, they prefer the intermediate-sized, probably due to a trade-off between encounter rates and handling time of the prey (Kiørboe, 2008). It should though be noted, that the concentration of largest copepods was lower than for the smaller and intermediate-sized ones, which impact the encounter rate and thereby the ingestion rate. Also, on average there was a negative grazing rate on the largest sized copepods (2250–2800 and 2880–3220 μm), which is due to the low number of copepods in this size range ($n = 2.3 \pm 0.4$ SE and $n = 2.5 \pm 0.2$ SE, respectively), or the fact that *M. norvegica* did not predate on those. For planktonic predators, the assumed predator:prey size ratio is 10:1 (Hansen *et al.*, 1994; Kiørboe, 2008) but the optimum ratio varies between taxonomic groups (Hansen *et al.*, 1994). The optimum predator:prey size ratio for *M. norvegica* feeding on copepods was 17.0 ± 2.2, which is similar to the optimum predator:prey size ratios for copepod nauplii, copepodites and rotifers (Hansen *et al.*, 1994). It is however important to note, that this predator:prey size ratio only applies to the predatory feeding mode. When *M. norvegica* switch to filter feeding, the optimum predator:prey size ratio will be much higher. Thus, when a 36 mm long *M. norvegica* (equaling an ESD of 9455 μm) feed on a cell of 80 μm ESD, which is the optimal cell size when filter feeding (Artiges *et al.*, 1978), it corresponds to a predator:prey size ratio of 118:1. This optimum predator:prey size ratio is higher than for, e.g. *C. finmarchicus* copepodites, which is 80:1 (Kiørboe and Runge unpubl. data, in Table I in Hansen *et al.*, 1994). However the predator:prey size ranges of *M. norvegica* and *C. finmarchicus* copepodites do overlap as the 50%-max predator:prey size ratio for *C. finmarchicus* is reported to be 137:1 (Kiørboe and Runge unpublished data, in Table I in Hansen *et al.*, 1994) and so, they compete for the same food. Yet, *M. norvegica* has an advantage in food competition, as they are also able to feed on *C. finmarchicus* and other copepod species.

In the prey size spectrum experiment with copepod prey, we observed that some copepods were partly ingested, as observed in other studies with *M. norvegica* (Beyer, 1992; Båmstedt and Karlson, 1998), *E. superba* (Price *et al.*, 1988) and *E. pacifica* (Ohman, 1984). Båmstedt and Karlson (Båmstedt and Karlson, 1998) observed that ~ 20% of the *Calanus* were only partly eaten by *M. norvegica* and Ohman (Ohman, 1984) conducted a feeding experiment with *Pseudocalanus* sp. as prey, where *E. pacifica* would injure and not completely consume 22% of the prey. These partly eaten copepods were counted as eaten by the krill, which could lead to an over-estimation of predation rates. However, as we only had few of these observations, this will not have any significant effect on the calculated predation rates.

We observed that krill fed on cells >10 μm (*M. norvegica* and *T. rachii*) and >5 μm (*T. inermis*). We found the prey size spectra of *T. inermis* and *T. raschii* to be similar, except that *T. inermis* was able to feed efficiently on smaller cells than *T. raschii*. The similar prey size spectra is supported by Berkes (Berkes, 1976), who saw similar food items in the stomachs of these two species in the Gulf of St. Lawrence, with food overlap coefficients of 0.98 in August and 0.97 in May (where 1.00 = identical). According to Berkes

(Berkes, 1973), *T. raschii* and *T. inermis* have similar distances between feeding appendages, with 6.5–8 and 8.5–9 μm between setae, respectively. This finding, however, contradicts with the present study, where *T. inermis* are able to feed on smaller cells than *T. raschii*. The distance between adjacent setae on the feeding appendages of *M. norvegica* is 25 μm (Berkes, 1973), and *M. norvegica* is therefore not able to exploit smaller cells as efficiently. In addition, Artiges *et al.* (Artiges *et al.*, 1978) found that *M. norvegica* can efficiently exploit cells from 20 to 140 μm. However, Sameoto (Sameoto, 1980) analyzed stomachs from these three species in the Gulf of St. Lawrence in April, and found that the smallest prey eaten by all the species was 10 μm in diameter, which supports our results. Yet, there was a difference in the number of individuals whose stomachs contained copepod remains, with 90% of *M. norvegica* stomachs containing copepods, compared with 22 and 5% of *T. inermis* and *T. raschii* stomachs, respectively (Sameoto, 1980). Suh and Choi (Suh and Choi, 1998) examined the feeding baskets of five different krill species of the genus *Euphausia* and found three different types of feeding baskets, which were related to different feeding modes, investigated by stomach content analyses. They concluded that a distance between secondary setae of <5 μm correspond to a more herbivorous feeding mode, whereas distances of 10–20 and 20–30 μm indicate a more omnivorous diet. *Thysanoessa raschii* and *T. inermis* are in between the fine mesh (<5 μm) and medium sized (10–20 μm) feeding basket type (Berkes, 1973; Suh and Choi, 1998), and are both found to be omnivorous corresponding to our results. In contrast, *M. norvegica* has a coarse feeding basket (20–30 μm) (Berkes, 1973; Suh and Choi, 1998) and can feed on large copepods (Båmstedt and Karlson, 1998). Additionally, Berkes (Berkes, 1976) found *M. norvegica* to be distinct from the two others based on stomach content. Here, we did not feed the two *Thysanoessa* species with larger organisms than 400 μm ESD. However, they have previously been observed to be able to feed on larger copepods (Sameoto, 1980; Båmstedt and Karlson, 1998). In the Northeast Atlantic, Båmstedt and Karlson (Båmstedt and Karlson, 1998) observed *C. finmarchicus* mandibles (CIII) in *T. inermis*. In contrast, *C. finmarchicus* mandibles were found only a few times in stomachs of *T. raschii*. Due to their smaller size, in relation to *M. norvegica*, the two *Thysanoessa* species will most probably not be able to handle the largest stages of *Calanus* spp. as also suggested by Sameoto (Sameoto, 1980).

In the prey size spectrum experiment with copepods, there was a phytoplankton concentration of 0.5 μg Chl *a* L^{-1} in the experimental bottles. However, *M. norvegica* did not graze on the phytoplankton probably because it was dominated by cells <10 μm, which are too small for *M. norvegica* to ingest efficiently (the present study; Berkes, 1973; Artiges *et al.*, 1978). The size of *Thalassiosira weissflogii* (ESD = 13 μm) is therefore in the lower end of the size spectrum for *M. norvegica* (Artiges *et al.*, 1978). Yet, this does not mean that *M. norvegica* cannot feed on cells smaller than 20 μm; Sameoto (Sameoto, 1980) found prey of 10 μm in diameter in the stomachs of *M. norvegica* as previously mentioned. The distance between setae in the feeding appendages is however smaller in *T. raschii* (6–8.5 μm) (Berkes, 1973), which might explain why we see higher clearance rates and a lower K_m in *T. raschii* than in *M. norvegica* when feeding on *Thalassiosira weissflogii*. Hansen *et al.* (Hansen *et al.*, 1997) found K_m to be independent of body size within each group of zooplankton examined, from heterotrophic nanoflagellates to crustaceans. They therefore described K_m as a general mean value of 240 μg C L^{-1}, which is in between K_m-values found here for *T. raschii* and *M. norvegica* (100 and 413 μg C L^{-1}, respectively).

We observed that microzooplankton (ciliates and heterotrophic dinoflagellates) were grazed with a higher clearance rate by *M. norvegica* and *T. inermis* than by *T. raschii* (latter data from Agersted *et al.*, 2011). The observed difference is most likely caused by bottle effects (Roman and Rublee, 1980; Peters and Downing, 1984; Båmstedt *et al.*, 2000), primarily due to the interaction with the container walls (Price *et al.*, 1988; Båmstedt *et al.*, 2000) as krill are fast swimming animals. In Agersted *et al.* (Agersted *et al.*, 2011), the prey size spectrum experiments with *T. raschii* were conducted in 2.8-L bottles, whereas the experiments in the present study were conducted in 13.2-L bottles, i.e. a factor of 4.7 difference in bottle volume. Price *et al.* (Price *et al.*, 1988) found similar results for *E. superba*, where feeding rates on copepods were 7–10 times higher in 50-L tubs than in 5-L bottles. This is also the case for the functional experiments for *M. norvegica* and *T. raschii*, where the bottles were of same volumes as mentioned above. Therefore, the clearance rates could possibly be higher for *T. raschii* than found. Another issue with bottle incubations could be the effect on the normal escape, or attack ability for prey and predator, respectively. However, we observed that *M. norvegica* had a maximum predation on the same sized copepods as observed *in situ* in stomachs of the same species (Båmstedt and Karlson, 1998). Additionally, due to the possibility of trophic cascades in experimental bottles on plankton assemblages <400 μm, estimating grazing rates on the smallest cells can be difficult. Therefore, this will most likely result in an underestimation of true grazing rates on the smallest cells, as other potential grazers on these cells are eaten by the krill in the experimental bottles but not in the controls. Thus, there is a lower grazing pressure, and thereby a higher growth potential, for the small cells in the experimental bottles.

Regardless of the above mentioned differences, there is an overlap in prey size spectra of these three species, and they therefore potentially exploit the same prey. This could lead to competition if food is limited. Berkes (Berkes, 1976) found a seasonal difference in the dietary overlap between the four species that coexist in the Gulf of St. Lawrence, which are the same species found in SW Greenland (Agersted and Nielsen, 2014). In the autumn, when food was plentiful, the dietary overlap between the species was high. Conversely, in winter when food resources were scarce, there was only little dietary overlap (Berkes, 1976). By stable isotope analyses, we found that these species had different trophic positions in Godthåbfjord in June (Agersted *et al.*, 2014), and that the trophic position of a species differed along the fjord and most likely was reflected in the prey community. *Meganyctiphanes norvegica* had the highest trophic position and *T. inermis* generally had a higher trophic position than *T. raschii*. In addition to this, Berkes (Berkes, 1973, 1976) observed a higher proportion of detritus in the stomachs of *T. raschii* compared with *T. inermis*. Other studies have found varying results for these three species regarding feeding. Falk-Petersen *et al.* (Falk-Petersen *et al.*, 2000) describe *M. norvegica* as a carnivore, *T. raschii* as an omnivore and *T. inermis* as a true herbivore species, based on fatty acids from krill in Kongsfjorden, Svalbard and Balsfjorden-Ullsfjorden, northern Norway. These authors furthermore report, that *T. raschii* seemed to feed on detrital material in Balsfjorden-Ullsfjorden during winter, whereas this was not the case for Kongsfjorden. They explain the observed difference found in *T. raschii* between these two fjords, by the fact that detrital material is not available as food in Kongsfjorden. Contrary to Falk-Petersen *et al.* (Falk-Petersen *et al.*, 2000), Petursdottir *et al.* (Petursdottir *et al.*, 2012) found *M .norvegica* to have a lower trophic position than *T. inermis* in the Iceland Sea. A study by Kaartvedt *et al.* (Kaartvedt *et al.*, 2002) investigated seasonal feeding of *M. norvegica* in Oslofjorden, Norway. Here, they found variations in food intake with regard to type of prey, season and time of day. They observed that *M. norvegica* to a large extent was a herbivore during spring (March and May), whereas it mainly fed on copepods during late summer (August), where abundance of copepods was at its highest, but where also Chl *a* levels were high. Thus, *M. norvegica* actively chose to feed on copepods during late summer. These abovementioned findings support that prey availability affects feeding and trophic position of a given species, and furthermore, that feeding in krill is very complex and dependent on the plankton community they inhabit. As the experiments presented in the present study were conducted at different geographical places and times, and due to the fact that not all experiments have been conducted for both species, we cannot directly compare the results obtained for the two species. Nevertheless, the results contribute to a better understanding of the trophic role of these important but understudied species.

CONCLUSION

The two functional groups, represented by *M. norvegica* and *Thysanoessa* spp., coexist in the Atlantic and sub-Arctic regions. Despite overlapping prey size spectra, we suggest that during food limitation, they have the possibility to switch between different feeding modes to reduce interspecific competition. *Thysanoessa* spp. has an advantage over *M. norvegica* if the prey community is dominated by small prey, e.g. flagellates. In contrast, *M. norvegica* have the advantage in being able to feed on larger prey. These differences in functional biology combined with spatial and temporal environmental patchiness, the wide prey size spectra and the ability of prey-switching, allow the coexistence of these two groups of krill.

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