Journal of
Plankton Research

academic.oup.com/plankt

J. Plankton Res. (2020) 42(2): 239–252. First published online March 26, 2020 doi:10.1093/plankt/fbaa012

ORIGINAL ARTICLE

Functional feeding response of Nordic and Arctic krill on natural phytoplankton and zooplankton

JORY CABROL[1,*], ANAÏS FABRE[1], CHRISTIAN NOZAIS[2], RÉJEAN TREMBLAY[1], MICHEL STARR[3], STÉPHANE PLOURDE[3] AND GESCHE WINKLER[1]

[1]INSTITUT DES SCIENCES DE LA MER DE RIMOUSKI/QUÉBEC-OCÉAN, UNIVERSITÉ DU QUÉBEC À RIMOUSKI, RIMOUSKI G5L 3A1, CANADA, [2]DÉPARTEMENT DE BIOLOGIE, UNIVERSITÉ DU QUÉBEC À RIMOUSKI, RIMOUSKI G5L 3A1, CANADA AND [3]INSTITUT MAURICE-LAMONTAGNE, PÊCHES ET OCÉANS CANADA, MONT-JOLI G5H 3Z4, CANADA

*CORRESPONDING AUTHOR: cabrol.jory@gmail.com

Received February 22, 2019; editorial decision February 24, 2020; accepted February 24, 2020

Corresponding editor: Marja Koski

Krill species play a pivotal role in energetic transfer from lower to upper trophic levels. However, functional feeding responses, which determine how food availability influences ingestion rates, are still not well defined for northern krill species. Here, we estimated and compared the functional feeding responses on natural communities of phytoplankton and mesozooplankton of two coexisting species, *Meganyctiphanes norvegica* and *Thysanoessa raschii*. We tested the influence of the presence of phytoplankton on the ingestion rate and the selectivity of both krill species when feeding on zooplankton prey. We performed a series of feeding experiments using increasing concentrations of natural phytoplankton (64 taxa; 2 to >50 μm) and mesozooplankton (28 taxa; ~100–2000 μm) assemblages and the latter in presence and absence of phytoplankton. Results revealed that both krill species exhibited a Holling type III feeding response on phytoplankton. However, *T. raschii* was able to exploit efficiently the highest phytoplankton concentrations. Our experiments highlighted that the presence of phytoplankton modified the functional feeding response on mesozooplankton preys of *M. norvegica*, but not that of *T. raschii*. Similarly, the presence of phytoplankton influenced the feeding selectivity on mesozooplankton preys, although both species showed contrasting selectivity patterns. In addition, we estimated the energy needs in relation to the daily rations. *T. raschii* satisfied its energy needs by feeding either on high phytoplankton concentrations or on low mesozooplankton densities, whereas *M. norvegica* did not cover its metabolic costs efficiently by feeding on phytoplankton only, even at high phytoplankton concentrations.

KEYWORDS: *Meganyctiphanes norvegica*; *Thysanoessa raschii*; functional feeding response; ingestion rate; prey selectivity; daily rations

available online at academic.oup.com/plankt

INTRODUCTION

North Atlantic krill communities are dominated by four species (Einarsson, 1945) that play a significant role in carbon flow (Mauchline and Fisher, 1969; Savenkoff *et al*., 2013). Among them, *Meganyctiphanes norvegica* and *Thysanoessa raschii* coexist and occur in high abundance and biomass (Agersted and Nielsen, 2014; Plourde *et al*., 2014; McQuinn *et al*., 2015). Both are omnivorous species that are able to switch from filter feeding to ambush predation, allowing them to exploit several trophic levels, ranging from small phytoplankton and detritus (>5–10 μm) to large copepods (>3000 μm) (e.g. Mauchline, 1980; Agersted and Nielsen, 2016; Cabrol *et al*., 2019a). However, their functional feeding responses, reflected by their ingestion and clearance rates in relation to food availability (Holling, 1959), are still not well defined. Especially, in *T. raschii* no functional response on carnivorous feeding is available. Furthermore, the presently available functional feeding responses do not provide sufficient quantitative detail to model and predict krill feeding rates in relation to the prey diversity encountered in nature (Benkort *et al*., 2019). Most of the available functional feeding responses are based on a limited number of prey types (McClatchie, 1986, 1988; Beyer, 1992; Agersted *et al*., 2011; Teglhus *et al*., 2015; Agersted and Nielsen, 2016). Moreover, these studies do not consider interactions between different prey types (e.g. phytoplankton and zooplankton) on the functional feeding responses, which is usually the case in nature.

Numerous factors affect the functional feeding responses (e.g. Frost 1972, 1975; Pilditch and McClatchie, 1994; Kiørboe *et al*., 1996, 2018; Kiørboe, 2008). Among them, prey diversity with the occurrence of alternative prey was shown to drastically affect the type of response, as obtained from laboratory experiments (Kiørboe *et al*., 2018). When offered large mesozooplankton (mostly *Calanus* spp.), *M. norvegica* showed a sigmoidal (Holling type III) functional feeding response (Agersted and Nielsen, 2016), whereas a linear relationship was found when feeding on an assemblage dominated by small copepods (e.g. *Centropages* sp.; McClatchie, 1985). When offered both phytoplankton and zooplankton simultaneously, *Euphausia superba* showed selective feeding (Granéli *et al*., 1993). To date, the only study assessing the effect of phytoplankton on zooplankton predation of northern krill (*M. norvegica*) did not find an effect of phytoplankton on zooplankton ingestion (Agersted and Nielsen, 2016). However, the authors also concluded that the natural phytoplankton community used in their experiments could have been composed of cells, which were too small (<10 μm) to be ingested by *M. norvegica*.

The main objective of this experiment was to determine functional feeding response of the two dominant northern krill species, *M. norvegica* and *T. raschii*, under more realistic *in situ* conditions. The specific objectives were to (1) quantify the clearance and ingestion rates of both krill species in relation to prey concentration of diverse phytoplankton and mesozooplankton communities, (2) evaluate the effect of the presence and absence of phytoplankton on the feeding rates of mesozooplankton and (3) assess the effect of phytoplankton on the feeding selectivity on mesozooplankton for both krill species. Laboratory feeding experiments were carried out using natural phytoplankton (64 taxa, ranging between 2 and >50 μm) and mesozooplankton (28 taxa ranging between ~100 and 2000 μm) assemblages.

MATERIAL AND METHOD

Krill sampling

Sampling took place in October 2015 in the lower St. Lawrence Estuary (SLE) where large krill aggregations occurred (Maps *et al*., 2014; McQuinn *et al*., 2015; Lavoie *et al*., 2017). Three days before the experiments, krill were sampled by successive short oblique tows, using a 1-m-diameter ring net with a mesh size of 303 μm equipped with a strobe light and a large cod end for gentle sampling. *M. norvegica* and *T. raschii* were sorted just after the catch. Krill handling was minimized, and all transfers were performed in water to reduce damage to appendages (Noyon *et al*., 2009). In the laboratory, krill were maintained in 360 L flowing seawater tanks (6°C, ~29 PSU) and fed twice daily using dried phytoplankton (Instant Algae®, N-Rich™ High PRO; Campbell, CA, USA) and a natural assemblage of frozen copepods to acclimate them to laboratory conditions and to recover from potential sampling stress (Ollier *et al*., 2018). Twelve hours before the experiments, krill were kept without food to avoid satiation and to limit disparity between feeding states.

Design of functional feeding response experiments

Two different sets of experiments were performed to assess functional feeding responses of krill on both phytoplankton and zooplankton using food assemblage stock solution, divided into the experiments/controls with various dilutions. In addition, the effect was determined by the presence of phytoplankton on the mesozooplankton ingestion rates and their selectivity. The first set of experiments tested the feeding on six concentrations of the same natural phytoplankton stock assemblage (Fig. 1A), while the second series of experiments tested the feeding on five concentrations of the same natural mesozooplankton stock assemblage, with and without phytoplankton

(Fig. 1B). Note that grazing of krill on phytoplankton in mixed prey experiments was not calculated due to possible food chain effects (Atkinson and Snyder, 1997).

Experiment duration was 6 h, and all experiments were performed in darkness at 6°C and ~29 PSU to mimic natural conditions found in the SLE (Galbraith *et al*., 2017). According to preliminary tests and the difference of carbon content between both krill species, we used three and six adults of *M. norvegica* and *T. raschii*, respectively, assuming no interindividual competition. Only healthy and active adult krill of similar size were chosen (all limbs and antennae intact). Twelve liters of polycarbonate buckets was used for replicates, controls, space, prey concentrations and time of preparation. At the beginning of each experiment, a subsample was taken (~15% of the initial volume) to determine the initial prey concentration in each replicate.

At the end of the experiments, krill wet and dry (48 h at 60°C) weight was determined and converted to carbon content using carbon-dry weight conversion factors of 50.01% and 44.91% for *M. norvegica* and *T. raschii*, respectively (Cabrol *et al*., 2019a). Total length of krill (in mm, from the tip of the rostrum to the end of the telson) was estimated using the length–weight relationship of krill from the SLE (Fig. S1, see online supplementary data for a color version of this figure). Mean lengths (mean ± SD) were 29.1 ± 2.5 mm for *M. norvegica* and 21.8 ± 2.3 mm for *T. raschii*.

Prey assemblage: phytoplankton community

To mimic phytoplankton community composition of a spring bloom, 16 indoor microcosms (40 L each) were filled with subsurface water from the lower St. Lawrence Estuary (position: 48°N 38′ 34.85″, 68°W 10′ 1.23″). Microcosms were inoculated with natural phytoplankton pre-filtered over a 63 μm mesh size to remove mesozooplankton and left to grow at 6°C with a light/dark cycle of 16:8 h and a photosynthetically active radiation of 997 $\mu mol.m^{-2}.s^{-1}$. The phytoplankton biomass ($\mu gChl\ a.L^{-1}$) was measured fluometrically (Parsons *et al*., 1984) so that six concentrations could be targeted (see Fig. 1). Chl *a* concentrations were converted into carbon content assuming a C/Chl *a* ratio of 42.7 (Juul-Pedersen *et al*., 2006). Samples for taxonomic quantification (~200 mL fixed in acid Lugol's solution) were taken from the initial phytoplankton stock solution before each experiment. Taxonomic identification was performed (Fig. 1) according to the procedure detailed in Cabrol *et al*. (2015).

At the end of each experiment, 200 mL from each container was filtered over a 63 μm to avoid the presence of mesozooplankton in Chl *a* measurement and taxonomic determination.

Prey assemblages: zooplankton community

Mesozooplankton were collected 2 days before the experiments commenced, using a zooplankton net (1 m diameter and 158 μm mesh size) from ~100 m to the surface at the same station where krill were caught. Zooplankton was poured through a 2000 μm sieve to remove potential krill competitors (e.g. Hyperiidae, chaetognaths, gelatinous organisms) and large copepods or advanced stages of as, for instance, *Paraeuchaeta* sp. and *Calanus hyperboreus*. At the laboratory, zooplankton was kept in 500 L tanks and fed once daily with dried phytoplankton. Dead animals were removed before the experiments following the procedure as described in Granéli *et al*. (1993). Then, abundance and composition of zooplankton were determined to the lowest taxonomic level on subsamples of 100 mL ($n = 5$–8), using a stereomicroscope (Leica Mz12.5). Zooplankton assemblage stock solution was gently mixed to homogenize and to keep organisms in suspension and was then divided into various dilutions for the feeding experiments/controls targeting the five planned prey concentrations (10–300 $ind.L^{-1}$).

At the end of the experiment using zooplankton as feed, mesozooplankton were retrieved using a 63 μm mesh size sieve kept in water to reduce damage to appendages and were fixed in formaldehyde solution (3% v/v final concentration). All remaining zooplankton organisms of all replicates were counted and identified. As krill might only partially ingest their prey, copepods with clear injuries (e.g. lack of antennae or missing limbs) were considered as eaten (Ohman, 1984) although these observations were rare (less than 0.5% of total observations). The carbon content of preys was determined either by direct carbon measurements of mesozooplankton from the study area when available (Table I, see Cabrol *et al*. (2019a) for methods) or was converted from length–carbon regression curves from literature except for juvenile of Temoridae where a weight–length relation was used as the % of carbon was known. Body length (L; μm) was measured of ~20 individuals.

Ingestion and clearance rates

Ingestion rates ($\mu gC.mgC^{-1}.h^{-1}$) were calculated by the difference in prey concentrations between the start and the end of the experiments, corrected by control experiments, expressed in carbon. Clearance rate ($ml.\ mgC^{-1}.d^{-1}$) was determined based on Madsen and Riisgård (2010). The best Holling type response (type I = linear; type II = rectangular hyperbola; type

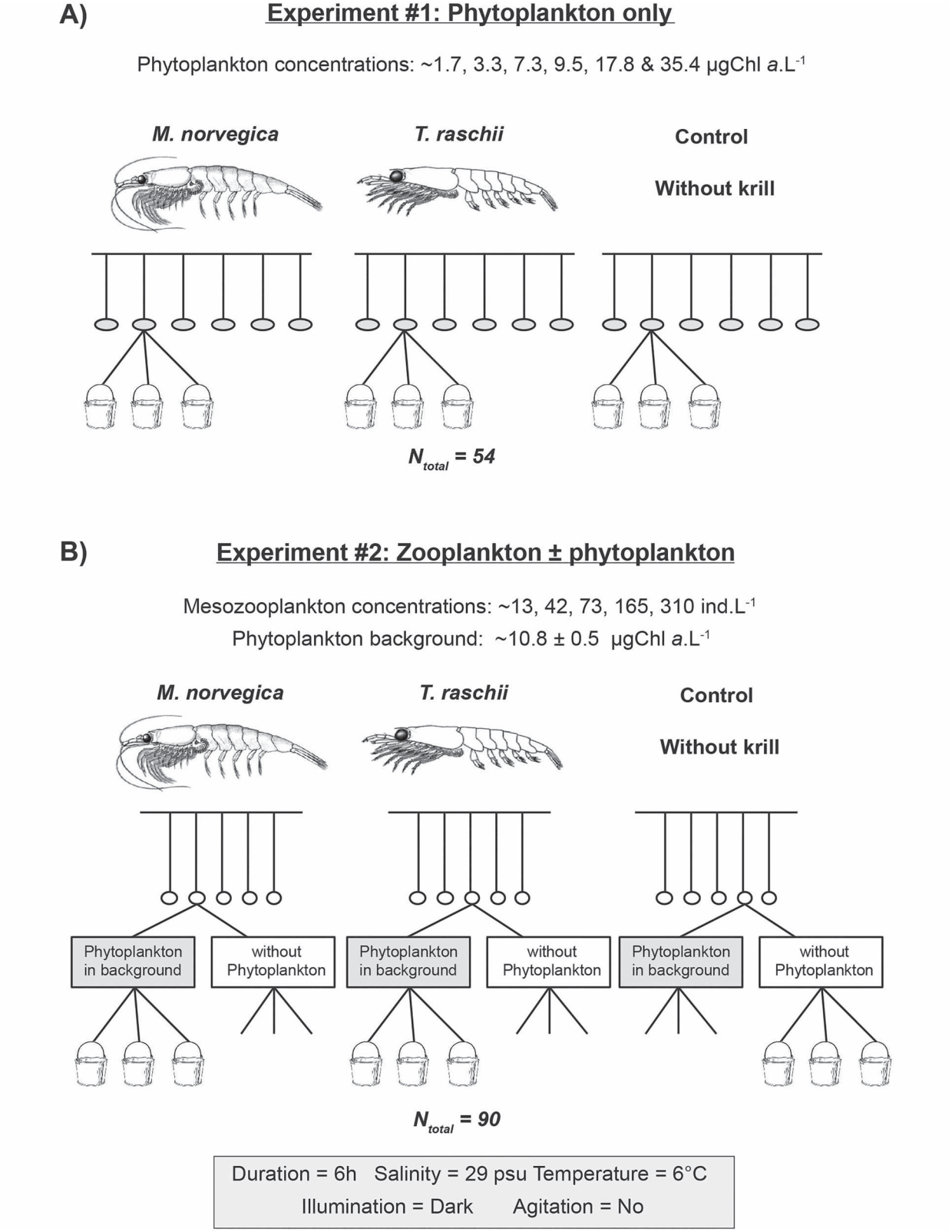

Fig. 1. Experimental design of experiment with phytoplankton only (A) and mesozooplankton with and without phytoplankton (B) conducted with *Meganyctiphanes norvegica* and *Thysanoessa raschii*. Krill drawings modified from Agersted *et al*. (2011 and references included).

Table I: Carbon content of zooplankton preys (μgC.ind^{-1}) from direct carbon measurements of mesozooplankton sampled in the study (see Cabrol et al. (2019a) for methods) or from algorithms used to convert body length (L, μm) to carbon content.

Species	Developmental stages	% of Carbon	Dry weight (μg.ind^{-1})	Mean C content (μgC.ind^{-1})	Carbon range observed (μgC.ind^{-1})
Acartia sp.*	C5–C6	34.32 ± 8.64	16.3 ± 3.39	5.59	8.46–3.31
Cypris larvae	Larvae	32.12 ± 4.67	11.02	3.54	4.06–3.03
Bradyodus similis	C5–C6	46.75 ± 2.74	94.5 ± 35	44.2	64.11–26.2
Calanus spp.*	C1–C3	41.43 ± 7.97	34.3 ± 27.63	14.21	30.6–2.23
Calanus spp.*	C4–C6	56.84 ± 5.26	378.9 ± 127.57	215.34	314.5–129.61
Metridia spp.*	C5–C6	45.17 ± 6.30	143.4 ± 38.17	64.76	93.45–40.89
Metridia longa	Copepodite		$y = 5.39e^{-9} \times L(\mu m)^{3.0167}$	(Hirche and Mumm, 1992)	
Microstella norvegica	Adults	13.64 ± 9.71	12.7	1.73	2.97–0.5
Nauplii of copepods	Nauplius	43.07 ± 3.35	3.7 ± 0.96	1.59	2.16–1.09
Oithona spp.*	Adults	29.95 ± 7.21	10.3 ± 1.97	1.97	3.95–0.24
Oncaea spp.*	C5–C6	37.63 ± 5.75	94.9 ± 12.49	3.09	4.57–1.9
Oncaea sp.	Copepodite		$y = 2.51e^{-8} \times L(\mu m)^{2.90}$	(Satapoomin, 1999)	
Ostracode	nd	37.63 ± 5.751	94.9 ± 12.49	35.7	46.58–26.27
Paraeucheta norvegica	C5–C6	47 ± 3.33	783 ± 219	368.04	504.32–246.34
Paraeucheta sp.	Copepodtie		$y = 1.15e^{-23} \times L(\mu m)^{6.92}$	(Tönnesson *et al.*, 2006)	
*Pseudocalanidae**	Adults	45.88 ± 12.32	37.5 ± 17.42	17.22	31.99–6.75
*Temoridae**	Adults	37.46 ± 7.69	15.1 ± 3.42	5.67	8.38–3.48
Temoridae	C1–C3	44.6	$y = 1.4715e^{-8} \times L(\mu m)^{3.064}$	(Ara, 2002)	
Trochophore*	Larvae	45	0.51	0.02	

* Asterix indicate dominant species.

III = sigmoidal; Holling, 1959) was determined by fitting clearance rate raw data. Once the Holling type was determined, equations were fitted according to equations presented in detail in Agersted *et al*. (2011) and Schultz and Kiørboe (2009). The half-saturation (K_m) constant, corresponding to the prey concentration at which the ingestion rate is half of the maximum ingestion rate, was used to compare potential differences in ingestion rates between species (*M. norvegica* and *T. raschii*) and treatments (with and without phytoplankton). Finally, maximum ingestion rates were converted to daily carbon rations (DR = % bodyC.d^{-1}). All calculations were performed for each species and treatment using the NLS2 package (V.1.1.456; R Core Team, 2017; Grothendieck, 2013).

Feeding selectivity

To detect selectivity of mesozooplankton prey of each krill species, the relative contribution of each mesozooplankton prey ingested (% prey ingested) was plotted against the relative contribution at the start of the experiment (% prey available). Prey positioned above the 1:1 diagonal was positively selected as it was eaten in higher proportion compared to the relative contribution in the initial prey assemblage. Negatively selected preys are below the diagonal. Only mesozooplankton species that contributed more than 1% to the total abundance or total carbon content were included in the analyses. Data are presented as means ± standard error ($n = 3$).

RESULTS

Functional feeding response: phytoplankton ingestion

Phytoplankton communities used during experiments were composed of 64 taxa dominated up to 75% by diatom species (Fig. 2). When offered an increasing concentration of this phytoplankton assemblage, both krill species displayed a Holling type III functional response (Fig. 4). The threshold to trigger feeding response was similar in both species (~62 μgC.L^{-1}). However, *M. norvegica* clearly showed lower clearance and ingestion rates than *T. raschii*. The half-saturation constant (K_m) was reached by *M. norvegica* at 304 μgC.L^{-1} (~7.1 μgChl *a*.L^{-1}) and at an ingestion rate of 0.04 μgC.mgC^{-1}.h^{-1}. In comparison, *T. raschii* reached K_m at a phytoplankton concentration of 555.9 μgC.L^{-1} (~12.9 μgChl *a*.L^{-1}), showing an ingestion rate of 0.24 μgC.mgC^{-1}.h^{-1}. Daily rations (DRs), at maximum ingestion rates of phytoplankton, corresponded to 0.19 and 1.15% DR for *M. norvegica* and *T. raschii*, respectively.

Functional feeding response: zooplankton ingestion

The zooplankton prey assemblage was composed of 28 taxa dominated by intermediate-sized zooplankton varying between 500 and 1500 μm (almost 70%; Fig. 3). When offered increasing concentrations of this assemblage in

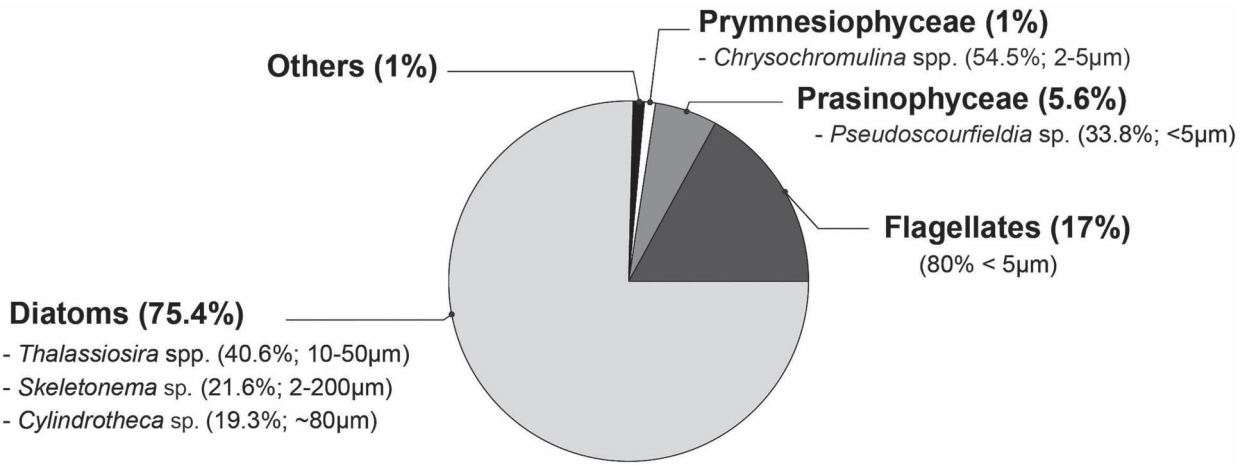

Fig. 2. Composition of phytoplankton assemblage used as prey during phytoplankton and zooplankton feeding experiments. Data are expressed as phytoplankton types in % of total and the dominant species within each type (taxa % by type).

absence of phytoplankton, *M. norvegica* showed a Holling type II response and a Holling type III response in presence of phytoplankton. Furthermore, the K_m of zooplankton ingestion was almost 3.5 times higher when phytoplankton was absent as compared to the one in presence of phytoplankton (584.4 and 168 µgC.L^{-1}, respectively). When converted into DRs, ingestion rates on mesozooplankton with and without phytoplankton present corresponded to 2.97 and 5.1% of body carbon per day, respectively.

In contrast, the differences of the clearance and ingestion rates of *T. raschii* on mesozooplankton with and without phytoplankton were less marked as in *M. norvegica* (Fig. 5). K_m of *T. raschii* was reached at prey concentrations of 775.3 and 1084 µgC.L^{-1} (~120 and 160 ind.L^{-1}) with ingestion rates of 1.54 and 1.29 µgC.mgC^{-1}.h^{-1} in presence and absence of phytoplankton, respectively. The DRs of *T. raschii* in the treatments with and without phytoplankton were comparable, with 6.24 and 7.4% bodyC.d^{-1}, respectively.

Selectivity on zooplankton

Selectivity on mesozooplankton prey varied between krill species and treatments (Fig. 6). In absence of phytoplankton, *M. norvegica* positively selected juveniles of *Calanus* spp., Pseudocalanidae, Temoridae (adults and juveniles) and trochophora larvae but negatively selected cyclopoid copepods (Fig. 6A). When phytoplankton was present, only juveniles of Temoridae and *Calanus* spp. were positively selected (Fig. 6C).

The selectivity patterns of *T. raschii* on mesozooplankton prey were less affected by the presence or the absence of phytoplankton. Only two taxa, Pseudocalanidae and to a lesser extent juveniles of *Calanus* spp., were positively selected (Fig. 6B and D), while other prey taxa were not or negatively selected (e.g. Temoridae; Fig. 6B and D) with and without phytoplankton.

DISCUSSION

Ingestion rates of krill on phytoplankton

Both krill species showed a Holling type III functional response of their ingestion rates, when offered an increasing concentration of a natural phytoplankton assemblage. The Holling type III functional feeding response is typically related to prey switching (Holling, 1959; Kiørboe *et al.*, 1996) or a change in foraging effort with prey concentration (Kiørboe *et al.*, 2018). This sigmoidal curve response was also observed when both species were feeding on a monoculture of diatoms (*Thalassiosira weissflogii*; Agersted and Nielsen, 2016), indicating the presence of a phytoplankton concentration threshold to trigger a more efficient feeding response. The phytoplankton threshold concentration was comparable for *M. norvegica* and *T. raschii* (Fig. 4), indicating that both species started to feed more efficiently at almost similar phytoplankton concentrations. The presence of a sigmoidal response also suggests that energetic costs for searching and handling prey below these algal concentrations are higher than the energy gain obtained (Lam and Frost, 1976).

Ingestion rates found during our experiments for *T. raschii* were similar to those reported by Teglhus *et al.* (2015) for *Thysanoessa* spp. in the Godthåbsfjord (SW Greenland). The maximum ingestion rate was 11.52 µgC.mgC^{-1}.day^{-1} in the present study, as compared to 11.5 ± 4.6 µgC.mgC^{-1}.day^{-1} from *in situ* calculation

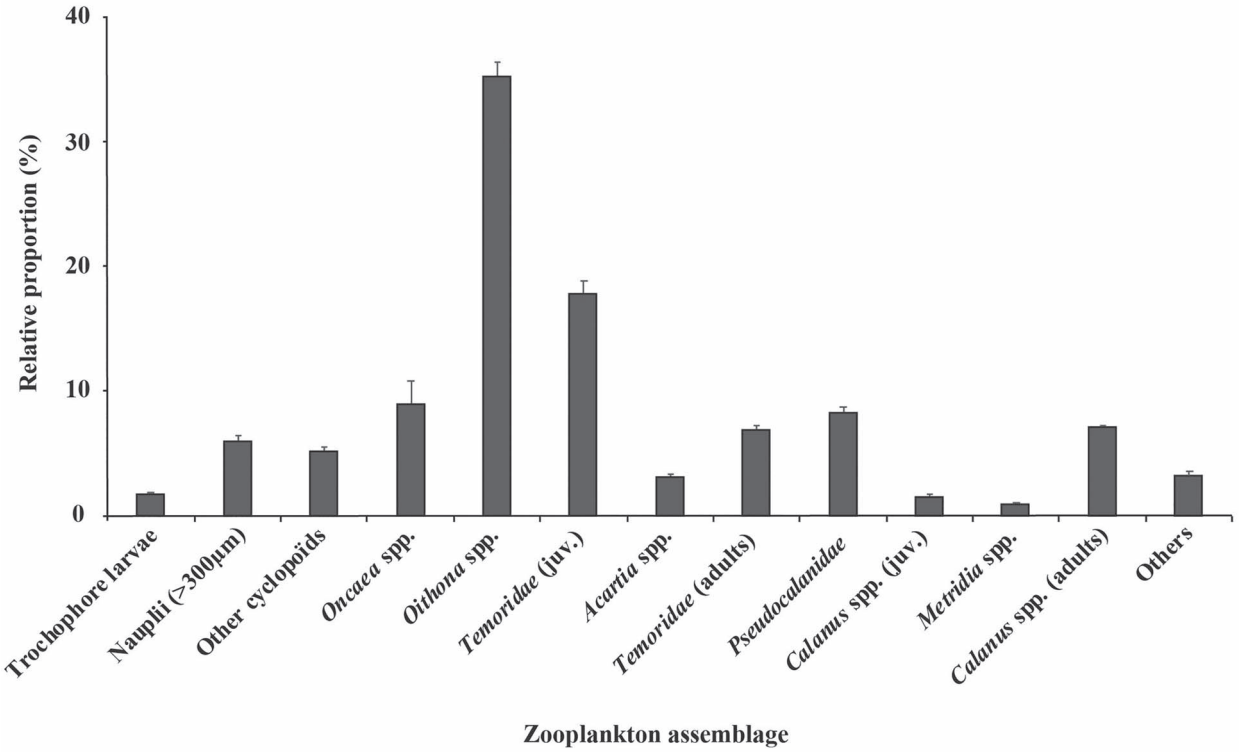

Fig. 3. Zooplankton prey composition (black bars; $n = 13$) and the respective carbon contents (empty dot) used during zooplankton experiments. Only zooplankton which contributed more than 1% of total abundance or total carbon content has been included. Mean ± SE.

in the Godthåbsfjord. Ingestion rates found at low phytoplankton concentration for *M. norvegica* (i.e. 0.017 $\mu gC.mgC^{-1}.h^{-1}$ for 135 $\mu gC.L^{-1}$ of prey) were similar to results from McClatchie (1985), after carbon conversion (0.014 $\mu gC.mgC^{-1}.h^{-1}$), and Agersted and Nielsen (2016) when exposed to a pure culture of *T. weissflogii* (0.0092 $\mu gC.mgC^{-1}.h^{-1}$). However, ingestion rate of *M. norvegica* found at high phytoplankton concentrations (>500 $\mu gC.L^{-1}$) were 5–10 times lower than in the feeding experiments by McClatchie (1985) and Agersted and Nielsen (2016), respectively. This suggests a negative effect of the high phytoplankton concentrations in our experiments, which might have several causes (e.g. phytoplankton size and composition, experimental setup).

Phytoplankton species composition might affect feeding efficiency and ingestion rates. Lower ingestion rates of *M. norvegica* as compared to those reported may be due to the utilization of a natural phytoplankton assemblage composed of different taxa, which might not be the preferred prey of *M. norvegica*. However, 75% of the phytoplankton feeding assemblage was composed of diatoms, including *Thalassiosira* spp., which is a well-known food item. Size distribution of the phytoplankton might also have an effect on ingestion rates. In the present study, the phytoplankton assemblage ranged from 2 to 200 µm (Fig. 3), and the distance between adjacent setae on the feeding appendages of *M. norvegica* is 25 µm (Berkes, 1973). Therefore, *M. norvegica* can likely efficiently exploit phytoplankton cells from 20 to 140 µm (Artiges *et al.*, 1978), and it was found to ingest also cells of 10 µm in the Gulf of St. Lawrence (Sameoto, 1980). This implies that the offered phytoplankton assemblage was accessible to *M. norvegica* feeding; however, the composition and size distribution (Fig. 3) might have had a combined and inhibitory effect when concentrations were high, though we are not able to prove or disentangle these effects. Several of the phytoplankton species might have been suboptimal, not available for efficient feeding or have affected the feeding behavior, leading to an overestimation of the actually available phytoplankton concentration. Therefore, these feeding rates should be regarded as conservative estimates.

Furthermore, we cannot completely exclude that differences found between studies may be related to different experimental setups. Large volumes should be used in experiments with pelagic animals, as smaller volumes are known to induce a decrease of ingestion rates (Båmstedt *et al.*, 2000). Our experimental volume was a trade-off between largest volume possible, space and handling logistics, resembling more the setup by McClatchie (1985)

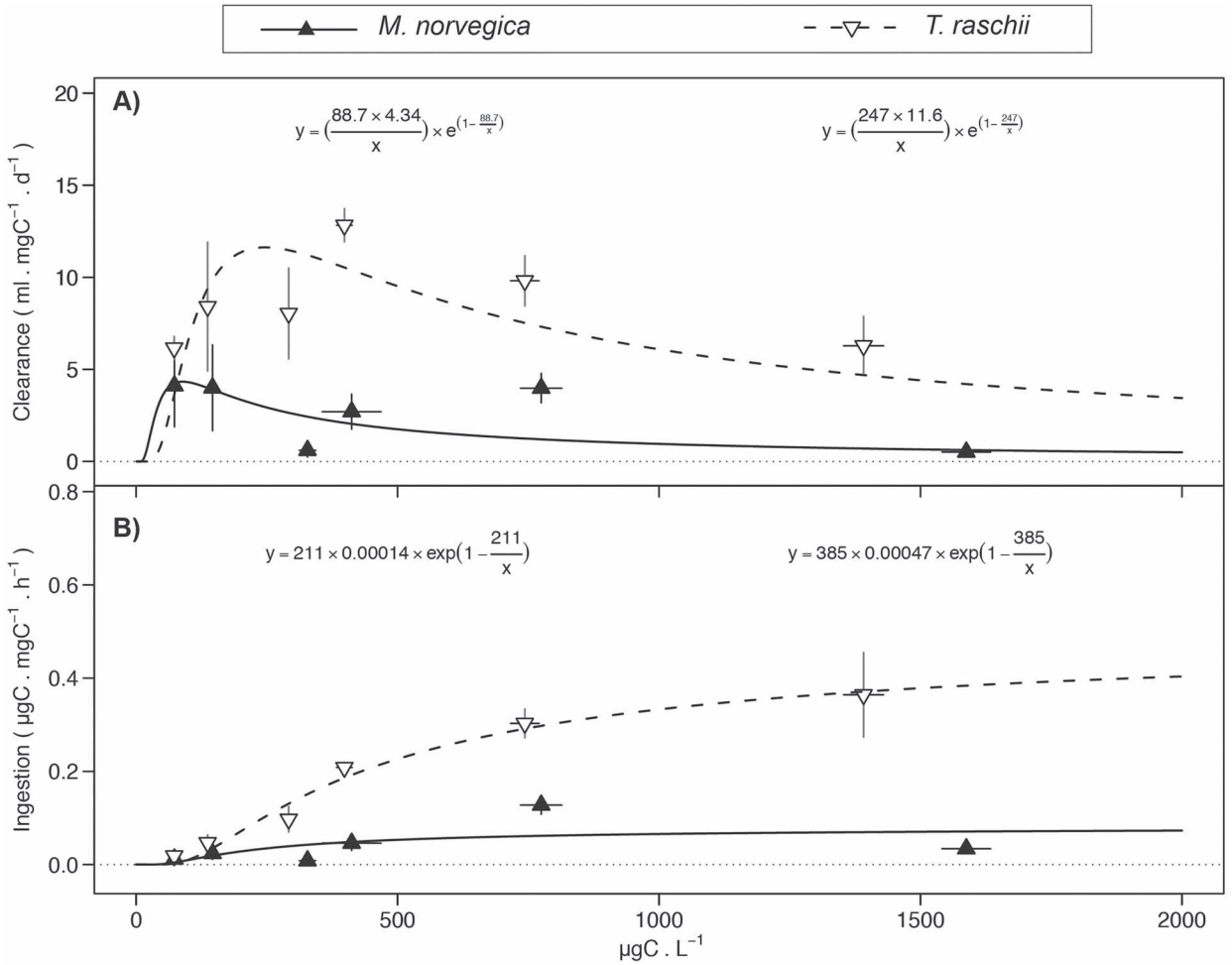

Fig. 4. Clearance rate (A; ml. mgC^{-1}.d^{-1}) and ingestion rates (B; µgC.mgC^{-1}.h^{-1}) of *M. norvegica* (black triangles, solid line; $n = 18$) and *T. raschii* (empty inverted triangles, dashed line; $n = 18$) as a function of phytoplankton concentration (µgC.L^{-1}) at 6°C in the dark. Mean ± SE ($n = 3$) for each concentration.

than that of Agerstedt and Nielsen (2016). In addition, a potential bottle effect for the larger species *M. norvegica* could not be excluded and might lead to a decrease of the ingestion rates.

Despite sharing similar threshold concentrations to trigger a feeding response, both krill species exhibited two contrasted saturation levels on phytoplankton (Fig. 4). *T. raschii* showed a maximum phytoplankton ingestion rate of one order of magnitude higher than *M. norvegica*, indicating that *T. raschii* might exploit the highest density patches of phytoplankton before reaching saturation (e.g. highest prey concentration at K_m; Fig. 4). These results are in accordance with previous studies, showing that *T. raschii* was more herbivorous than *M. norvegica* (e.g. Falk-Petersen *et al.*, 2000; Agersted *et al.*, 2014; Cabrol *et al.*, 2019a). The comparison of phytoplankton concentrations at K_m with *in situ* phytoplankton concentrations found in the Estuary and Gulf of St. Lawrence (EGSL; e.g. Blais *et al.*, 2018; Cabrol *et al.*, 2019b) suggests that *T. raschii* could not reach feeding saturation in the field, except in high-density phytoplankton patches. However, generalization from experiments to field conditions should be made with caution, as the results from experiments might change according to the experimental setup (see review of Gorokhova and Hansson, 1999). Nevertheless, krill are not just passive particles but interact with their biotic and abiotic environments (e.g. Tarling and Thorpe, 2014; Weissburg *et al.*, 2019). Krill, including *T. raschii*, is able to detect phytoplankton concentration gradients or odor and adapt their swimming behavior (e.g. speed, path orientation, time spent sinking) to remain near phytoplankton layers (Price, 1989). In agreement, the large range of phytoplankton ingestion rates found in the experiments demonstrate that *T. raschii* might feed on a large range of food concentration, allowing to adapt to heterogeneous preyscapes. For example, high food con-

centrations in microlayers might allow to quickly fulfill the metabolic needs of *T. raschii*. In contrast, *M. norvegica* exhibited lower ingestion rates and prey concentration at K_m than *T. raschii*, indicating that this species was not be able to exploit similarly high phytoplankton density patches. Phytoplankton concentration found at K_m was slightly higher than the average concentration of phytoplankton found in the EGSL, suggesting that most of the time *M. norvegica* might not reach saturation.

As both species showed *in situ* trophic overlaps (Berkes, 1976; Agersted and Nielsen, 2016; Cabrol *et al*., 2019a), differences in ingestion rates between both krill species might be of importance in supporting the stable coexistence occurring in some North Atlantic regions (e.g. Plourde *et al*., 2014). Differences in ingestion efficiency might permit exploitation of similar resources when present at different concentrations in the space. Since *T. raschii* might feed on a larger range of phytoplankton concentration than *M. norvegica*, this difference might result in a potential spatial segregation of both species when feeding at different concentrations. Consequently, this could limit the potential competition for shared resources in addition to other processes already observed in the EGSL (see Plourde *et al*., 2014 and Cabrol *et al*., 2019a, b).

Ingestion rates on zooplankton

Using the natural zooplankton assemblage, dominated by intermediate-sized taxa (Fig. 3), *M. norvegica* and *T. raschii* showed some differences in their feeding strategies. The presence of phytoplankton did affect the type of feeding response of *M. norvegica* switching from Holling type II in absence of phytoplankton to a Holling type III feeding function when phytoplankton was present. At lowest zooplankton concentrations, ingestion was higher when phytoplankton was present; however, this tendency changed at higher zooplankton concentrations so that ingestion was lower when phytoplankton was present. Thus, the threshold concentration to trigger an efficient feeding response of *M. norvegica* was lower in presence of phytoplankton. This resulted in the lower K_m in the treatment with phytoplankton, demonstrating that *M. norvegica* reached the saturation of its ingestion rate at lower zooplankton prey density than in absence of phytoplankton. This result was unexpected, since *M. norvegica* did not ingest large amounts of phytoplankton during the phytoplankton experiment. Rapid saturation of zooplankton ingestion observed in presence of phytoplankton (Fig. 5A) might be related to the high phytoplankton density used during zooplankton experiment. Background phytoplankton concentrations during the zooplankton experiment were high and clearly above the half-saturation constant on phytoplankton ingestion rate of *M. norvegica* in the phytoplankton-only feeding experiments. Hence, a decrease in ingestion rates might potentially be due to an increase of searching or handling time of appropriate prey, when obscured by a high number of particles leading to a decrease of the feeding efficiency. This has already been observed in high-turbidity environments when the number of inorganic particles became too high for other krill species (e.g. Fuentes *et al*., 2016) or other macrozooplankton species (e.g. mysids; Carrasco *et al*., 2007). In contrast, *T. raschii* fed opportunistically on zooplankton expressed by a Holling type II response in both treatments. As the encounter probability increased with increasing prey concentration, *T. raschii* was apparently limited by the handling, ingestion and the digestive time (Kiørboe *et al*., 2018). However, phytoplankton did not influence the ingestion rate as well as the selectivity on mesozooplankton of *T. raschii* (Figs 4b and 5).

Observed prey selectivity response during the zooplankton feeding experiments with and without phytoplankton in the background showed high variability for both krill species. This is not surprising, as krill is able to feed on a broad size range of prey (e.g. Mauchline, 1980; Agersted and Nielsen, 2016), and thus the diet will largely vary among individuals, depending on random encounter events between prey and predator. This will result in a high variability between replicates. Nevertheless, the results highlight that both species fed on all mesozooplankton prey but with different degrees of selectivity, indicating very responsive and adaptable feeding strategies to the available prey type. According to the optimal foraging theory (*sensus* MacArthur and Pianka, 1966), the individuals should maximize the energy gain by feeding on the easiest prey to catch or the most nutritious, resulting in reality in a combination of both. Accordingly, both krill species may show high selectivity for lipid-rich copepods, as *Calanus* spp., or abundant species like *Temoridae*. However, several species were not selected independently of their availability, such as *Oithona* spp. (the most abundant species, Fig. 3). Such feeding behavior might be explained by a lack of detection or the escape capacities of the prey. Interestingly, we found that phytoplankton affected the selectivity; especially *M. norvegica* selected less species in presence of phytoplankton (Fig. 6A and C). In comparison, *M. norvegica* tended to select several copepods (e.g. *Temoridae*, *Oncaea* spp., *Pseudocalanidae* juv., *Calanus* sp.), whereas *T. raschii* selected only *Pseudocalanidae* strongly in treatments without phytoplankton. These selectivity patterns were less pronounced in feeding treatments with phytoplankton present. Nevertheless, these results confirm *in situ* results of estimated diet composition of *M. norvegica* and *T. raschii* found in the SLE using fatty acids and stable isotopes as trophic markers (Cabrol *et al*., 2019a, b).

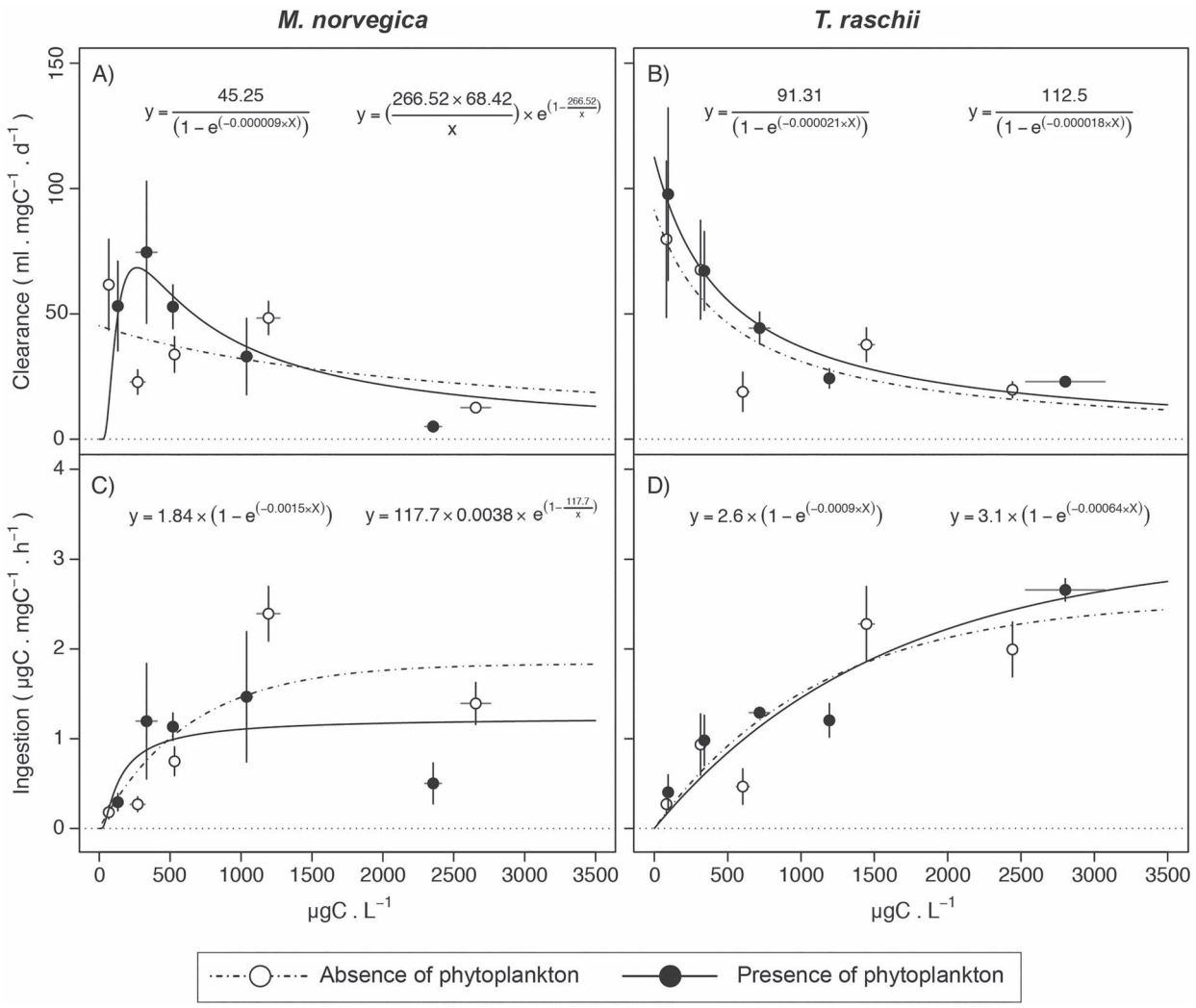

Fig. 5. Clearance rate (**A**, **B**; ml. $mgC^{-1}.d^{-1}$) and ingestion rates (**C**, **D**; µgC.$mgC^{-1}.h^{-1}$) of *M. norvegica* (**A**, **C**) and *T. raschii* (**B**, **D**) as a function of mesozooplankton concentration (µgC.L^{-1}) in absence of phytoplankton (empty dots, dashed line; $n = 14$ for *M. norvegica* and $n = 15$ for *T. raschii*) and in presence of phytoplankton in background (~10.8 µgClh *a*.L^{-1}; black dots, solid line; $n = 15$ for both species) at 6°C in the dark. Mean ± SE for each concentration.

Daily rations

In our experiment, maximum DRs were similar to values available from literature of < 2% for *M. norvegica* feeding on phytoplankton (McClatchie, 1985; Agersted and Nielsen, 2016) and of 0–33% feeding on zooplankton (McClatchie, 1985; Båmstedt and Karlson, 1998; Agersted and Nielsen, 2016). DRs in *T. raschii* were 0.5–1.5% when feeding on phytoplankton (Teglhus *et al*., 2015; Agersted *et al*., 2011; Agersted and Nielsen, 2016). The values were also comparable with DRs of other krill species, such as 1.0–1.5% in *E. superba* (Meyer *et al*., 2010), although the maximum ingestion rate could be up to 20% (Schmidt and Atkinson, 2016). From an energetic point of view, the DRs of energy intake should be higher than the net cost of respiration to allow energy accumulation available for other processes such as growth or reproduction (Van-Noordwijk and De Jong, 1986). Energy needs to fuel routine metabolism amounts to at least 0.87 ± 0.11% in *M. norvegica* and 0.91 ± 0.17% in *T. raschii*, based on the oxygen consumption for the routine metabolism at 6°C from individuals sampled in the SLE (Ollier *et al*., 2018). These percentages assume an oxycaloric coefficient of 11.72 $kJ.g^{-1}O_2$ (Kleiber, 1965 after unit conversion) and an average energy content of 5.2 ± 0.45 $kJ.j^{-1}.g^{-1}$ww for *M. norvegica* and 4.31 ± 0.58 $kJ.j^{-1}.g^{-1}$ww for *T. raschii* in the EGSL (Guilpin et al. 2019). These calculations are first-order estimates and will vary with numerous factors (e.g. temperature, current state of the animal). However, the estimate of energy needed by *M. norvegica*

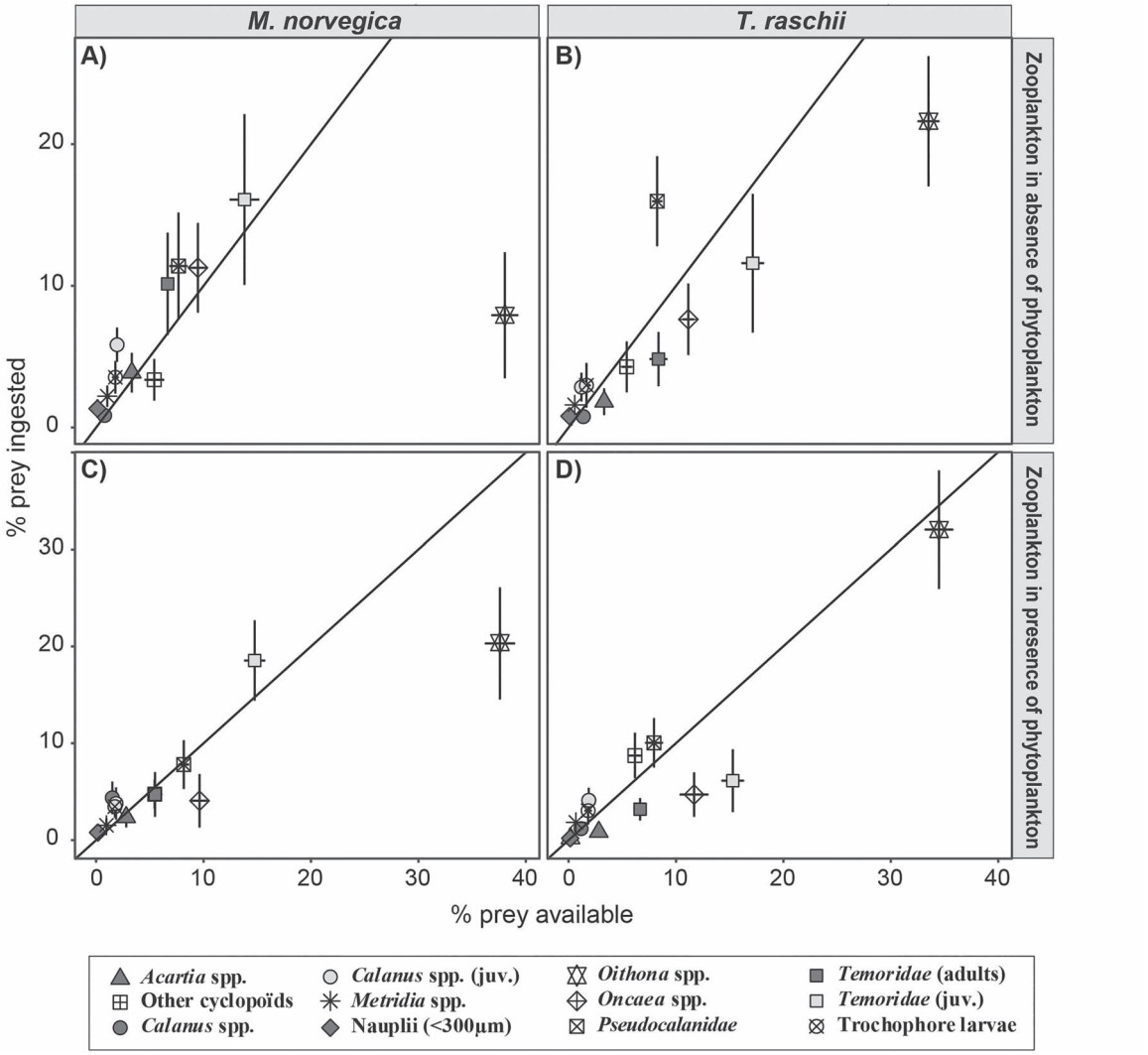

Fig. 6. Relative contribution of mesozooplankton prey (% ind. Ingested) to the diet of *M. norvegica* (**A**, **C**) and *T. raschii* (**B**, **D**) in absence (**A**, **B**) and in presence (**C**, **D**) of phytoplankton in background (mean ± SD; $n = 15$) against their relative contribution (% prey available). Straight dashed line corresponds to 1:1 ratio, and dots above this line indicate positive selection. Only zooplankton which contributed more than 1% of total abundance or total carbon content has been included.

(0.87 ± 0.11%) was significantly lower than 4.56% as previously suggested by McClatchie (1985), whereas the calculated value for *T. raschii* was similar to values of 0.5–1.2% recently found by Teglhus *et al.* (2015) and Agersted *et al.* (2011). According to Agersted and Nielsen (2016), energy requirements of 4.56% for *M. norvegica* found by McClatchie (1985) might be overestimated, which is also in line with our calculations. Hence, *M. norvegica* did not satisfy its physiological needs during the phytoplankton experiment, despite high phytoplankton concentrations, while it easily met its physiological needs ingesting mesozooplankton, even at low concentrations (225 µcC.L^{-1} equivalent ~34 ind.L^{-1}, including small species and early developmental stages). Therefore, *M. norvegica* would be obliged to feed on both phytoplankton and zooplankton or zooplankton alone to efficiently accumulate energy reserves, which is in agreement with *in situ* results found in the SLE (e.g. Cabrol *et al.*, 2019a; Benkort *et al.*, 2019). Moreover, feeding on a single adult *Calanus* specimen (~200 µgC.ind^{-1}) would allow *M. norvegica* to meet its daily respiration cost at 6°C.

We found that the phytoplankton assemblage as unique food source could cover daily energetic requirements of *T. raschii*, when available at high concentrations (up to 1200 µgC.L^{-1} equivalent to 28 µgChl *a*.L^{-1}). However, it is important to note that, in our experiment, like for *M. norvegica*, almost 10% of all available phytoplankton was likely too small (<5 µm) for consumption by *T. raschii*, leading to a potential overestimation of the actual prey concentration available, although such size class also

occur in nature. In addition, as already observed for *M. norvegica*, *T. raschii* could switch from a phytoplankton to a zooplankton diet to quickly meet its energetic requirements, as already suggested by Cabrol *et al*. (2019a) in the SLE and by Falk-Petersen *et al*. (2000) in high latitude fjords.

CONCLUSION

In this study, we analyzed the functional feeding response of the ingestion rates on natural phytoplankton and zooplankton assemblages with increasing concentrations. We illustrated that phytoplankton affected the ingestion rate on zooplankton of *M. norvegica*, but not of *T. raschii*. The occurrence of phytoplankton influences more the quantity than the type of ingested mesozooplankton, providing new insights into functional feeding ecology of these two ecologically relevant species in the Northern Atlantic. These findings demonstrate the importance of including prey diversity when modeling dynamics of northern krill stocks. These data should contribute to improve parameterization of individual-based models of separate krill stock dynamics and ecosystem-based food web models, even though quantitative studies are still needed to assess the amount of phytoplankton or zooplankton standing stock, required to support krill populations. Extending these results in view of the ecology of krill and their role in ecosystem functioning, our study also suggests that omnivory and the large feeding plasticity observed in both krill species might enable them to efficiently exploit dominant or profitable preys even if these are often distributed heterogeneously in time and space.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

ACKNOWLEDGEMENTS

We thank our captain P. Joly for his help in the field and laboratory. Special thanks are extended to all participants to laboratory experiments, especially L. St-Amand for her help during lab preparation and analyses and J.-Y. for the couture for phytoplankton identification. We also thank Dr C. Hammer and two anonymous reviewers for revising the English language and improving the manuscript. J.C. was granted a two-year PhD scholarship from the Fond de Recherche Québec Nature et Technologie (FRQNT).

FUNDING

This research was financially supported by the strategic partnership grant (STPGP-447363) from the Natural Sciences and Engineering Research Council of Canada (NSERC) awarded to G.W., S.P., R.T., C.N. and M.S. This is a contribution to the program of Québec-Océan (Groupe interinstitutionnel de recherche en océanographie du Québec).

REFERENCES

Agersted, M. D. and Nielsen, T. G. (2016) Functional biology of sympatric krill species. *J. Plankton Res.*, **38**, 575–588. doi: 10.1093/plankt/fbw017.

Agersted, M. D., Bode, A. and Nielsen, T. G. (2014) Trophic position of coexisting krill species: a stable isotope approach. *Mar. Ecol. Prog. Ser.*, **156**, 139–151.

Agersted, M. D. and Nielsen, T. G. (2014) Krill diversity and population structure along the sub-Arctic Godthåbsfjord, SW Greenland. *J. Plankton Res.*, **36**, 800–815.

Agersted, M. D., Nielsen, T. G., Munk, P., Vismann, B. and Arendt, K. E. (2011) The functional biology and trophic role of krill (*Thysanoessa raschii*) in a Greenlandic fjord. *Mar. Biol.*, **158**, 1387–1402.

Artiges, J., Pagano, M. and Thiriot, A. (1978) Morphologie fonctionnelle des appendices nutritionnels de *Meganycriphanes norvegica* (M. Sars, 1856) et *Euphausia krohnii* (brand, 1851). *Arch. Zool. Exp. Gen.*, **119**, 95–106.

Atkinson, A. and Snÿder, R. (1997) Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. *Mar. Ecol. Prog. Ser.*, **160**, 63–76.

Båmstedt, U., Gifford, D. J., Irigoien, X., Atkinson, A. and Roman, M. (2000) Feeding. In Harris, R. P., Wiebe, P. H., Lenz, J., Skjoldal, H. R. and Huntley, M. (eds.), *ICES Zooplankton methodology manual*, Academic, San Diego.

Båmstedt, U. and Karlson, K. (1998) Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. *Mar. Ecol. Prog. Ser.*, **172**, 149–168.

Blais, M., Devine, L., Lehoux, C., Galbraith, P. S., Michaud, S., Plourde, S. and Scarratt, M. (2018) Chemical and biological oceanographic conditions in the estuary and gulf of St. Lawrence during 2016. *DFO Can. Sci. Advis. Sec. Res. Doc.*, **2018/037**, Iv + 57 pp.

Benkort, D., Plourde, S., Winkler, G., Cabrol, J., Ollier, A., Cope, L. E. and Maps, F. (2019) Individual-based modelling explains the contrasted seasonality in size, growth and reproduction of the sympatric Arctic (*Thysanoessa raschii*) and Nordic krill (*Meganyctiphanes norvegica*) in the St. Lawrence estuary, eastern Canada. *Limnol. Oceanogr.*, **64**, 217–237.

Berkes, F. (1973) *Production and comparative ecology of euphausiids in the Gulf of St. Lawrence*. PhD Thesis, McGill University, Montreal, Canada.

Berkes, F. (1976) Ecology of euphausiids in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.*, **33**, 1894–1905.

Beyer, F. (1992) *Meganyctiphanes norvegica* (Sars) (Euphausiacea) a voracious predator on Calanus, other copepods and ctenophores, in Oslofjorden, southern Norway. *Sarsia*, **77**, 189–206.

Cabrol, J., Trombetta, T., Amaudrut, S., Aulanier, F., Sage, R., Tremblay, R., Nozais, C., Starr *et al.* (2019a) Trophic niche partitioning of dominant North-Atlantic krill species, *Meganyctiphanes norvegica*, *Thysanoessa inermis* and *T. raschii*. *Limnol. Oceanogr.*, **64**, 165–181.

Cabrol, J., Nadalini, J.-B., Galbraith, P. S., Tremblay, R., Nozais, C., Starr, M., Plourde, S. and Winkler, G. (2019b) Seasonal and large-scale spatial variability of the energy reserves and the feeding selectivity of *Meganyctiphanes norvegica* and *Thysanoessa inermis* in a subarctic environment. *Prog. Oceanogr.*, **179**, 102203.

Cabrol, J., Tremblay, R. and Winkler, G. (2015) Physiological condition and differential feeding behaviour in the cryptic species complex *Eurytemora affinis* in the St. Lawrence estuary. *J. Plankton Res.*, **37**, 372–387.

Carrasco, N. K., Perissinotto, R. and Miranda, N. A. (2007) Effects of silt loading on the feeding and mortality of the mysid *Mesopodopsis*

africana in the St. Lucia estuary, South Africa. *J. Exp. Mar. Biol. Ecol.*, **352**, 152–164.

Einarsson, H. (1945) *Euphausiacea* I. northern Atlantic species. *Dana Rep.*, **27**, 1–184.

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A. and Sargent, J. R. (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can. J. Fish. Aquat. Sc.*, **57**, 178–191.

Frost, B. W. (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.*, **17**, 805–815.

Frost, B. W. (1975) A threshold feeding behavior in *Calanus pacificus*. *Limnol. Oceanogr.*, **20**, 263–266.

Fuentes, V., Alurralde, G., Meyer, B., Aguirre, G. E., Canepa, A., Wölfl, A. C., Christian, H., Williams, G. N. *et al.* (2016) Glacial melting: an overlooked threat to Antarctic krill. *Sci. Rep.*, **6**, 27234.

Galbraith, P. S., Chassé, J., Gilbert, D., Larouche, P., Brickman, D., Pettigrew, B., Devine, L. and Lafleur, C. (2017) Physical oceanographic conditions in the Gulf of St. Lawrence in 2016, DFO can. *Sci. Adv. Sec.*, (pp. v+−91).

Gorokhova, E. and Hansson, S. (1999) An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. *Can. J. Fish. Aquat. Sci.*, **56**, 2203–2210.

Grothendieck, G. (2013) *nls2: Non-Linear Regression with Brute Force*. R package. version 0.2. https://CRAN.R-project.org/package=nls2.

Granéli, E., Granéli, W., Rabbani, M. M., Daugbjerg, N., Fransz, G., Roudy, J. C. and Alder, V. A. (1993) The influence of copepod and krill grazing on the species composition of phytoplankton communities from the scotia Weddell Sea. *Polar Biol.*, **13**, 201–213.

Guilpin, M., Lesage, V., McQuinn, I., Goldbogen, J. A., Potvin, J., Jeanniard-du-Dot, T., Doniol-Valcroze, T., Michaud, R., Moisan, M., and Winkler, G. (2019). Foraging energetics and prey density requirements of western North Atlantic blue whales in the Estuary and Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.*, **625**, 205–223.

Hirche, H. J. and Mumm, N. (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep-Sea Res. Part A*, **39**, 485–505.

Holling, C. S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.*, **31**, 293–320.

Juul-Pedersen, T., Nielsen, T. G., Michel, C., Møller, E. F., Tiselius, P., Thor, P., Olesen, M., Selander, E. *et al.* (2006) Sedimentation following the spring bloom in Disko Bay, West Greenland, with special emphasis on the role of copepods. *Mar. Ecol. Prog. Ser.*, **314**, 239–255.

Kiørboe, T. (2008) *A Mechanistic Approach to Plankton Ecology*. Princeton University Press, New Jersey.

Kiørboe, T., Saiz, E. and Viitasalo, M. (1996) Prey switching behaviour in the planktonic copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.*, **143**, 65–75.

Kiørboe, T., Saiz, E., Tiselius, P. and Andersen, K. H. (2018) Adaptive feeding behavior and functional responses in zooplankton. *Limnol. Oceanogr.*, **63**, 308–321.

Kleiber, M. (1965) Feeding behavior in *Meganyctiphanes norvegica* (M. Sars) (Crustacea, Euphausiacea). *J. Exp. Mar. Biol. Ecol.*, **86**, 271–284.

Lam, R. K. and Frost, B. W. (1976) Model of copepod filtering response to changes in size and concentration of food. *Limnol. Oceanogr.*, **21**, 490–500.

Lavoie, D., Chassé, J., Simard, Y., Lambert, N., Galbraith, P., Roy, N. and Brickman, D. (2017) Large-scale atmospheric and oceanic control on krill transport into the St. Lawrence estuary evidenced with 3D numerical modelling. *Atmosphere-Ocean*, **54** , 299–325.

Madsen, C. V. and Riisgård, H. U. (2010) Ingestion-rate method for measurement of clearance rates of the ctenophore *Mnemiopsis leidyi*. *Aqua. Invasions*, **5**, 357–361.

Maps, F., Plourde, S., Lavoie, D., McQuinn, I. and Chassé, J. (2014) Modelling the influence of daytime distribution on the transport of two sympatric krill species (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in the Gulf of St. Lawrence, eastern Canada. *ICES J. of Mar. Sci.*, **72**, 282–292.

Mauchline, J. (1980) The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**, 1–681.

Mauchline, J. and Fisher, L. R. (1969) The biology of Euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.

MacArthur, R. H. and Pianka, E. R. (1966) On optimal use of a patchy environment. *Am. Nat.*, **100**, 603–609.

McClatchie, S. (1985) Feeding behavior in *Meganyctiphanes norvegica* (M. Sars) (Crustacea, Euphausiacea). *J. Exp. Mar. Biol. Ecol.*, **86**, 271–284.

McClatchie, S. (1986) Time-series feeding rates of the Euphausiid *Thysanoessa raschii* in a temporally patchy food environment. *Limnol. Oceanogr.*, **31**, 469–477.

McClatchie, S. (1988) Functional response of the Euphausiid *Thysanoessa raschii* grazing on small diatoms and toxic dinoflagellates. *J. Mar. Res.*, **46**, 631–646.

McQuinn, I. H., Plourde, S., St. Pierre, J.-F. and Dion, M. (2015) Spatial and temporal variations in the abundance, distribution and aggregation of krill (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in the lower estuary and gulf of St. Lawrence. *Prog. Oceanogr.*, **131**, 159–176.

Meyer, B., Auerswald, L., Siegel, V., Spahic, S., Pape, C., Fach, B. A., Teschke, M., Lopata, A. L. *et al.* (2010) Seasonal variation in body composition, metabolic activity, feeding and growth of adult krill *Euphausia superba* in the Lazarev Sea. *Mar. Ecol. Prog. Ser.*, **398**, 1–18.

Noyon, M., Gasparini, S. and Mayzaud, P. (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). *Polar biol.*, **32**, 1559–1570.

Ohman, M. D. (1984) Omnivory by *Euphausia superba*: the role of copepod prey. *Mar. Ecol. Prog. Ser.*, **19**, 125–131.

Ollier, A., Chabot, D., Audet, C. and Winkler, G. (2018) Metabolic rates and spontaneous swimming activity of two krill species (Euphausiacea) under different temperature regimes in the St. Lawrence estuary, Canada. *J. Crustac. Biol.*, **38**, 697–706.

Parsons, T. R., Maita, Y. and Lalli, C. M. (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford.

Pilditch, C. A. and McClatchie, S. (1994) Quantitative analysis of carnivory in the krill *Nyctiphanes australis*, with an examination of the effect of non-preferred phytoplankton alternative prey. *Mar. Ecol. Prog. Ser.*, **107**, 41–54.

Plourde, S., McQuinn, I. H., Maps, F., St-Pierre, J., Lavoie, D. and Joly, P. (2014) Daytime depth and thermal habitat of two sympatric krill species in response to surface salinity variability in the Gulf of St. Lawrence, eastern Canada. *ICES J. Mar. Sci.*, **71**, 272–281.

Price, H. J. (1989) Swimming behavior of krill in response to algal patches: a mesocosm study. *Limnol. Oceanogr.*, **34**, 649–659.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/.

Sameoto, D. D. (1980) Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (Crustacea Euphausiacea). *J. Plankton Res.*, **2**, 129–143.

Satapoomin, S. (1999) Carbon content of some common tropical Andaman Sea copepods. *J. Plankton Res.*, **21**, 2117–2123.

Savenkoff, C., Comtois, S. and Chabot, D. (2013) Trophic interactions in the St. Lawrence estuary (Canada): must the blue whale compete for krill? *Estuar. Coast. Shelf Sci.*, **129**, 136–151.

Schmidt, K. and Atkinson, A. (2016) Feeding and food processing in Antarctic krill (*Euphausia superba* Dana). In Siegel, S. (ed.), *Biology and Ecology of Antarctic Krill*. Springer, Cham.

Schultz, M. and Kiørboe, T. (2009) Active prey selection in two pelagic copepods feeding on potentially toxic and non-toxic dinoflagellates. *J. Plankton Res.*, **31**, 553–561.

Tarling, G. A. and Thorpe, S. E. (2014) Instantaneous movement of krill swarms in the Antarctic circumpolar current. *Limnol. Oceanogr.*, **59**, 872–886.

Teglhus, F. W., Agersted, M. D., Arendt, K. E. and Nielsen, T. G. (2015) Gut evacuation rate and grazing impact of the krill *Thysanoessa raschii* and *T. inermis*. *Mar. Biol.*, **162**, 169–180.

Tönnesson, K., Nielsen, T. G. and Tiselius, P. (2006) Feeding and production of the carnivorous copepod *Pareuchaeta norvegica* in the Skagerrak. *Mar. Ecol. Prog. Ser.*, **314**, 213–225.

Van Noordwijk, A. J. and De Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.*, **128**, 137–142.

Weissburg, M. J., Yen, J. and Fields, D. M. (2019) Phytoplankton odor modifies the response of *Euphausia superba* to flow. *Polar Biol.*, **42**, 509–516.