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Metabolic rates and spontaneous swimming activity of two krill species (Euphausiacea) under different temperature regimes in the St. Lawrence Estuary, Canada

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(ṀO2 g–1 wet mass)

Oxygen consumption (ṀO2)

ABSTRACT

Two dominant krill species *Meganyctiphanes norvegica* (Sars, 1857) and *Thysanoessa raschii* (Sars, 1864) coexist in the subarctic waters of lower St. Lawrence Estuary, Canada. Both species perform diel vertical migrations representing often large displacements of ~100–150 m through several temperature regimes. We studied the impact of temperature, a fundamental factor controlling the metabolism of ectothermic species, on the metabolic rate and swimming activity of the two species. Annular respirometers were used to quantify simultaneously oxygen consumption ($\dot{M}O_2$ g^{-1} wet mass) and the spontaneous swimming activity of individual krill over a period of 24 h at six temperatures, by intermittent-flow respirometry. Both species significantly increased their low routine and maximal metabolic rates from 0 °C to 15 °C, suggesting high thermal plasticity. The spontaneous swimming activity of *M. norvegica* was reduced to almost zero at 0 °C, whereas *T. raschii* swam 1.0 cm s^{-1} at this temperature. Based on swimming performance, *M. norvegica* might avoid the cold intermediate layer (CIL, < 1 °C) in the estuary, which coincides with actual daytime distribution below the CIL in the warmer deep-water layer. Despite the rare occurrence of 15 °C in the estuary, both species still showed high metabolic and swimming performance at that temperature. High and differential thermal plasticity of both krill species might have important ecological consequences for their distribution patterns in their natural environment, as energy requirements differ in the two species.

Key Words: *Meganyctiphanes norvegica*, respiration, subarctic waters, thermal plasticity, swimming speed, *Thysanoessa raschii*

THIRD INTERNATIONAL SYMPOSIUM ON KRILL

INTRODUCTION

Temperature is one of the most important factors controlling metabolism in ectothermic species. Low temperatures usually limit metabolic processes, whereas increasing temperature accelerates the velocity of enzymatic reactions, thus directly increasing energy demand (Fry, 1971; Prosser, 1973; Somero, 1978). A change in environmental temperature can affect growth performance, survival, and recruitment of ectotherms and consequently induces changes in their geographical distribution (Pörtner *et al.*, 2006; Pörtner & Knust, 2007). The influence of temperature on energy requirements has been studied mostly in fishes (e.g., Fry & Hart, 1948; Duthie, 1982; Clark *et al.*, 2011), whereas much less is known on small holoplanktonic crustaceans such as krill (e.g. Saborowski *et al.*, 2000, 2002; Huenerlage et al., 2015, 2016). Energy requirements have been commonly estimated using aerobic metabolic rates (via oxygen uptake), due to the difficulty to measure heat production in water (Steffensen, 1989; Nelson, 2016). Such knowledge on krill is crucial to better understand consequences of ocean warming (global mean surface temperature increase of 3–5 °C predicted for 2100; IPCC, 2014) on functional traits and ultimately on the productivity of these key species.

Determine propose of strobe light for krill net

There are about 86 krill species recorded around the world, but most studies have focused on the Antarctic krill *Euphausia superba* Dana, 1850 (e.g., Clarke & Morris, 1983; Meyer *et al.*, 2010; Tarling & Thorpe, 2014), which occupies a pivotal ecologic and economic role in the Southern Ocean (Mauchline, 1980; Meyer *et al.*, 2010; Tarling, 2010). Other krill species abound in the North Atlantic, in particular two dominant species *Meganyctiphanes norvegica* (Sars, 1857) and *Thysanoessa raschii* (Sars, 1864) (Mauchline, 1980; Tarling, 2010). Both species are found over a wide geographic distribution range. *Meganyctiphanes norvegica* is found in the temperate and boreal zones of the North Atlantic, including the Mediterranean Sea (Mauchline, 1980; Tarling, 2010). *Thysanoessa raschii* is mostly distributed in neritic waters, extending from the Arctic to its southern range limit in the Gulf of Maine (Mauchline, 1980; Everson, 2000; Tarling, 2010). The biogeographic distributions of the two species overlap in several regions of the North Atlantic, including the subarctic region of the Estuary and Gulf of St. Lawrence (Canada). Both species coexist, thrive, and occur in dense concentrations in this highly dynamic environment, which is partly ice covered in winter. This is particularly true in the lower St. Lawrence Estuary, which is characterized by high spatial and temporal variability of temperature conditions (Simard & Lavoie, 1999; McQuinn *et al.*, 2015). A cold intermediate layer (CIL) forms during winter and a three-layer system is created during spring persisting until late autumn. This system includes a warming surface layer (summer mean temperature of 11 °C), a CIL (–1.9 to < 1 °C) and a bottom layer (~5 °C) (Gilbert & Pettigrew, 1997; Galbraith, 2006; Galbraith *et al.*, 2013, 2016). Krill species in the St. Laurence Estuary, performing diel vertical migration (DVM), not only experience seasonal but also daily temperature variations.

Like most zooplankton species, these two species of krill perform DVM representing often large active displacements of ~100–150 m through several temperature regimes within a short period of time (Simard *et al.*, 1986; Buchholz *et al.*, 1995; Onsrud & Kaartvedt, 1998). Observations on vertical daytime distribution showed distinct thermal habitats of both predominant species in the St. Lawrence Estuary (Plourde *et al.*, 2014). During daytime, individuals of *M. norvegica* aggregate in the deep layer (< 100 m) at temperatures higher than 1.3 °C, whereas swarms of *T. raschii* mostly occur in association with the CIL (< 1 °C at ~50–100 m) (Sourisseau *et al.*, 2008; Plourde *et al.*, 2014; McQuinn *et al.*, 2015). They both ascend into the surface layer at night to feed and then share the same thermal habitat. Spontaneous swimming activity, corresponding to voluntarily movements, is essential to maintain the position of these species in the water column and to change their location during DVM (Kils, 1981; Kaartvedt *et al.*, 2002; Abrahamsen *et al.*, 2010). As these species have to swim almost continuously, they had to develop energetic strategies to optimize their energy expenditure (Arnold, 1988). Spontaneous swimming speed could therefore change according to temperature encountered in the natural environment. Given potential ecophysiological differences in temperature tolerance of *M. norvegica* and *T. raschii*, energy requirements and spontaneous swimming speed of both species might differ.

The aims of this study were to evaluate how temperature affects aerobic metabolic rates and spontaneous swimming speeds of these two krill species and compare the energetic performances of *M. norvegica* and *T. raschii*. Oxygen consumption ($\dot{M}O_2$) and spontaneous swimming activity were quantified simultaneously for the two species at six temperatures (0 °C to 15 °C), using individual annular glass respirometers.

MATERIALS AND METHODS

Krill sampling and rearing

Krill were collected in the lower St. Lawrence Estuary, Eastern Canada (~ 48°60'N, 68°80'W) between July and September 2015. Krill was detected using a multifrequency echosounder (Simrad combi D 38/200; Horten, Norway) and captured using a ring net equipped with a strobe light to prevent krill from escaping (JackNet, 1 m diameter ring net, 333 µm mesh; Filmar, Québec, QC, Canada) (Sameoto *et al.*, 1993). Each net was hauled obliquely from the bottom to the surface to increase the probability of catching both species (McQuinn *et al.*, 2013, 2015). Following capture, krill was immediately transferred to 3.5 l bottles filled with filtered seawater from the estuary at a salinity of ~28 and transported in coolers to the Maurice-Lamontagne Institute (Fisheries & Oceans Canada, Mont-Joli, QC, Canada) within 6 hours.

Meganyctiphanes norvegica and *T. raschii* were separated rapidly (1.5 h) from the rest of the zooplankton. Both species were randomly divided into two groups in 360 l tanks, one at 3 °C and the other at 6 °C. Theses temperatures reflected conditions encountered in different depth layers in the estuary. To obtain our six experimental temperatures in a short period of time (3 d) we brought krill from 3 °C to 0 °C and from 6 °C to 9 °C, 12 °C and 15 °C by increments of 3 °C per day. We kept at least 15 individuals of each species per final temperature. Krill were kept under dark conditions to mimic their natural environment. Salinity was stable over the exposure and the experimental periods at 27.6 ± 0.2 (pumped from the estuary). Krill were considered ready for respirometry experiments starting at day 4 post-capture, when all individuals were exposed to experimental temperature for at least 24 h. To minimize possible negative effects of captivity and to avoid inducing bias in respirometry experiments, both species were kept in the tanks at each experimental temperature for a maximum of four weeks after capture. Krill were fed with microalgae (Instant Algae®, N-Rich™ High PRO; Campbell, CA, USA) and frozen copepods (collected along with krill in the estuary) three times a week. Krill were fasted 24 h prior to respirometry experiments to ensure a post-absorptive state (Chabot *et al.*, 2016a; Nelson & Chabot, 2017).

post-absorptive state | metabolic comparison

Measurement of oxygen consumption ($\dot{M}O_2$)

Oxygen consumption ($\dot{M}O_2$) of individual krill was measured by intermittent-flow respirometry (Steffensen, 1989; Svendsen *et al.*, 2016b). Two models of annular glass respirometers were used for the experiments (based on Torres *et al.*, 1982). The respirometers were adjusted to the size of each species: length 10 and 8 cm; width 7 cm; tube's internal diameter 1.35 and 1.15 cm for *M. norvegica* and *T. raschii*, respectively. Each respirometer was equipped with a recirculation loop to ensure water mixing within the respirometer. This loop was connected to a peristaltic pump (model KPP-S10DCC0; Kamoer®, Shanghai, China) with silicone tubing (Kamoer®; ID: 3 mm, OD: 5 mm). Internal volumes of respirometers, including the recirculation loop, were 44.92 and 30.71 ml for *M. norvegica* and *T. raschii*, respectively. The annular design allowed krill to swim spontaneously while keeping the water volume at a minimum to increase the precision of the determination of oxygen consumption (Svendsen *et al.*, 2016a).

How did we ensure the DO oxygen of our supply water

Dissolved oxygen (DO) was measured at all temperatures, except at 0 °C, every second by a fiber optic sensor (DP-PSt3; PreSens, Regensburg, Germany) connected to an oxymeter OXY-4 mini (PreSens). A submersible pump (DC30A-1230; VOVYO Technology, ShenZhen, China), connected by PVC clear tubing (Excelon RNT®, Lima, OH, USA), was used to flush the respirometers. This pump was connected to a DAQ4 automated control system and a computer running AutoResp software v.2.0.1 (Loligo® Systems, Tjele, Denmark; Fig. 1). A different respirometry system was used at 0 °C. It was independent from the system described above because of difficulties to reach such cold conditions. OXROB3 fiber optic sensors and FireStingO_2 oxymeter were used (Pyro Science GmbH, Aachen, Germany). The flush pump was controlled using a timer (5010–67; VWR® Controller/timer, Toronto, ON, Canada) and DO was logged with the Pyro Oxygen Logger software v.3.126 (Pyro Science, Aachen,

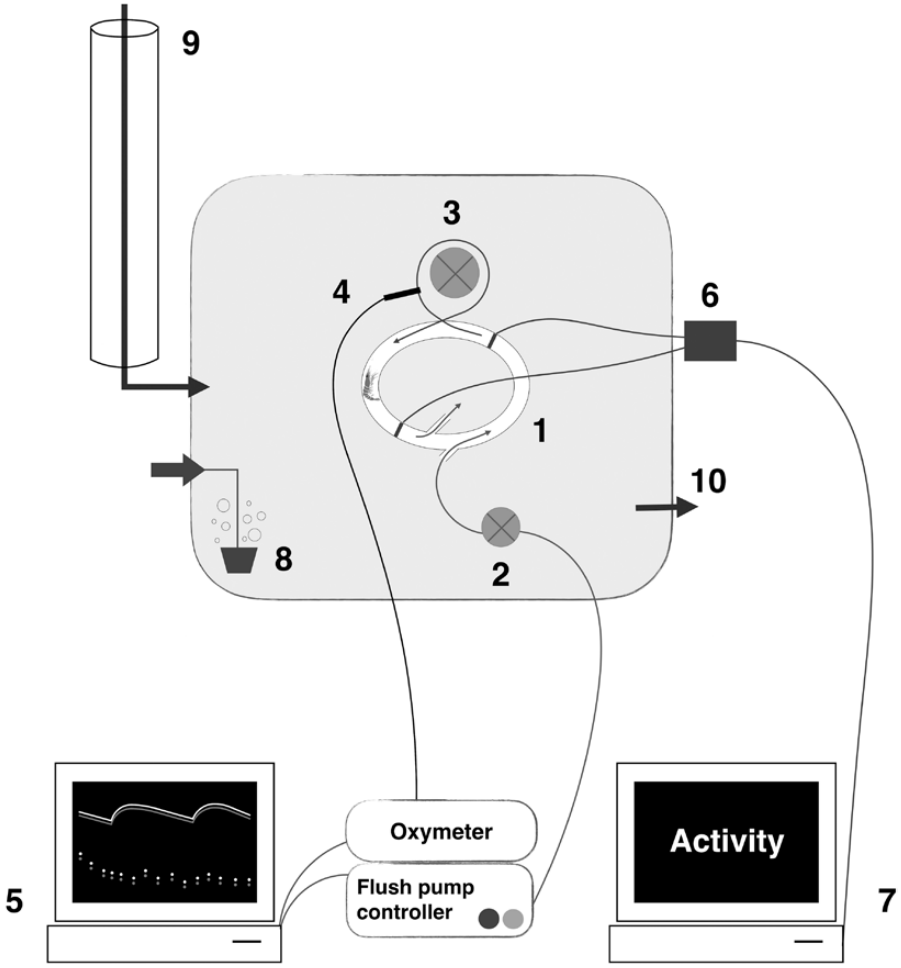

Figure 1. Experimental set-up to measure oxygen consumption and spontaneous swimming activity of krill: annular respirometer (1); submersible pump flush (2); submersible recirculation pump (peristaltic) (3); fibre optic sensor (4); computer with software Autoresp or Pyro (5); detection of activity (6); computer with SerialLogger software (7); airstones (8); mixing column, flow of water into the basin (9); drain of basin (10).

Germany; Fig. 1). All pumps were connected to a power supply (GPS-3030DD, GW Instek, New Taipei, Taiwan; ~7.2 V DC).

Measurement of spontaneous swimming activity

Krill was placed inside the annular respirometers facing the recirculation flow that was kept at the minimum required to insure sufficient mixing while having a negligible impact on spontaneous swimming activity (i.e. flow was not sufficient to transport krill when it stopped swimming). The detection of spontaneous swimming activity was done with infrared-emitting diodes (890–940 nm, LED IR333/L10; Everlight Electronics, Miao-Li, Taiwan) and phototransistor detectors (OP801WSL; OPTEK Technology, Medina, OH, USA) placed on each side of the glass tube. The wavelength was chosen to avoid disturbing the krill during the respirometry experiments (Frank & Widder, 1999). The detection system was connected to the software SerialLogger v.1.2.0.0 (DFO–MPO 2015©, Québec, QC, Canada; Fig. 1).

Respirometry: experimental design

$\dot{M}O_2$ and spontaneous swimming activity were measured for 126 individuals (71 *M. norvegica*, 55 *T. raschii*). Each krill was used only once at a single temperature. Three respirometry systems ran from July to October 2015. Two were identical and consisted of four respirometers (two of each model) placed in an open 360 l temperature-controlled water bath. They were used for all temperatures except at 0 °C for which we used a 37 l closed system containing a single respirometer of each model. All tanks were filled using sand filtered (0.8–1.2 µm) seawater. The different temperatures were tested in random order, except for 0 °C, which was operated continuously since a single respirometer was available each session for each species. Oxygen consumption was measured during 24 h for each individual. Measurement cycles lasted 25 min at all temperatures for both species. Respirometers were flushed with normoxic water for 5 min and were closed for 20 min. Krill of each species were randomly selected for each experiment from the rearing tank at the experimental temperature. Total sample size varied from 6 to 19 for each species by temperature combination (Table 1). The length and wet and dry mass from individuals of a given species (Table 1) did not differ significantly among the six temperatures (ANOVAs: $F_{5,65} < 2.08$, $P > 0.08$; $F_{5,49} < 1.82$, $P > 0.13$ for *M. norvegica* and *T. raschii*, respectively).

Oxygen probes were calibrated with fresh water saturated with sodium sulfite and sodium borate (for 0%) prior to each experiment, and with seawater saturated in air (for 100%) at the experimental temperature (Rosewarne *et al.*, 2016). The tanks and respirometers were cleaned using iodine solution (~10 ml l^{-1}) to minimize bacterial respiration, and rinsed prior to each experimental set. Background respiration was measured at the beginning and at the end of each experimental set, during 30 to 60 min (without krill). Respirometers were kept in the dark to avoid disturbing the animals. At the end

Table with Treatment Trial Wet Weight Vial Number? telson

Number mismatch?

Background respiration measured with blanks

Table 1. Sample size (*N*), total length (L_t), wet mass (W_w), and dry mass (W_d) of two species of krill at six different temperatures. Mean values and 95% confidence interval are presented.

		0 °C	3 °C	6 °C	9 °C	12 °C	15 °C
Meganyctiphanes norvegica	*N*	6	17	19	11	10	8
	L_t (mm)	25.993 ± 3.785	31.248 ± 2.311	29.390 ± 2.195	32.859 ± 3.699	30.136 ± 3.282	28.734 ± 4.420
	W_w (g)	0.136 ± 0.052	0.241 ± 0.062	0.209 ± 0.051	0.305 ± 0.089	0.228 ± 0.079	0.219 ± 0.105
	W_d (g)	0.025 ± 0.006	0.051 ± 0.015	0.041 ± 0.010	0.058 ± 0.015	0.045 ± 0.017	0.043 ± 0.021
Thysanoessa raschii	*N*	8	8	11	10	10	8
	L_t (mm)	22.160 ± 1.508	21.724 ± 1.620	22.748 ± 1.640	22.734 ± 0.947	21.083 ± 1.112	20.774 ± 1.703
	W_w (g)	0.074 ± 0.018	0.072 ± 0.010	0.081 ± 0.018	0.073 ± 0.012	0.065 ± 0.010	0.061 ± 0.014
	W_d (g)	0.016 ± 0.007	0.016 ± 0.005	0.015 ± 0.004	0.014 ± 0.003	0.012 ± 0.003	0.013 ± 0.005

of each experiment, the krill were sacrificed. Krill were blotted dry by rolling them on paper towels for a few seconds to obtain wet mass and were subsequently dried at 60 °C for 48 h to determine their dry mass (± 0.0001 g, model AG245, Mettler Toledo, Giessen, Germany; Torres *et al.*, 1982). The total length of krill (from the rostrum to the end of the telson) was measured using µScope Essentials v.3.6 (PixeLINK®; Ottawa, ON, Canada).

Estimation of routine metabolic rate, maximal metabolic rate and aerobic scope

$\dot{M}O_2$ of each individual krill was estimated from the linear decline of dissolved oxygen (DO) during 20 min, each time the respirometer was closed over a period of 24 h (see above; Supplementary material Fig. S1). Each value of $\dot{M}O_2$ was calculated using the equation of Steffensen (1989):

$$\dot{M}O_2 = \frac{Vr.\ \beta wO_2 \cdot \Delta PwO_2}{\Delta t \cdot bw} \quad (1)$$

where $\dot{M}O_2$ is oxygen consumption expressed per unit of wet mass (µg O_2 h^{-1} g wet^{-1}); Vr = water volume inside the respirometer (l, total volume of respirometer minus volume of the krill); βwO_2 = solubility of oxygen in water according to García & Gordon (1992) per unit of pressure (µg O_2 l^{-1} kPa^{-1}); ΔPwO_2 = drop of partial pressure of oxygen in the water (kPa); Δt = duration (h); and bw = the body mass of the animal (g).

The minimum acceptable R^2 value was fixed at 0.80; however, most of the slopes had R^2 value higher than 0.95. Only a small proportion (< 10%) of slopes were eliminated. Each slope was corrected for background respiration presuming a linear increase during the experiments (Daoud *et al.*, 2007; Chabot *et al.*, 2016a; Rosewarne *et al.*, 2016).

Two metabolic rates were estimated from the available $\dot{M}O_2$ measurements for each individual krill. Routine metabolic rate (RMR) corresponds to a low level of energy expenditure by the animal, including a non-quantified activity cost (Brett, 1962; Dall, 1986). RMR is slightly higher than standard metabolic rate (SMR) observed in a resting and fasting animal (Fry & Hart, 1948; Chabot *et al.*, 2016b). Maximal metabolic rate (MMR) corresponds to the greatest rate of energy expenditure that the animal may spend either for activity or in response to stress (Brett, 1964; Fry, 1971). The difference between maximum and minimum energy demand of animals is an estimate of the energy available for other purposes, which is called the aerobic scope (AS) (Fry, 1947, 1971).

We first planned to use the relationship between $\dot{M}O_2$ and spontaneous swimming activity to estimate individual SMR by extrapolation to zero activity (e.g., Brett, 1964; Zimmermann & Kunzmann, 2001). Only 46% of regressions obtained had a significantly positive slope, probably due to the narrows range of spontaneous swimming speeds. We therefore decided to calculate a low RMR based on the distribution of $\dot{M}O_2$ values, according to the quantile method recommended by Chabot *et al.* (2016b). Most of the time, a decrease of $\dot{M}O_2$ values was observed during the first 3 h after the introduction of krill inside the respirometer, indicating that a habituation period to the respirometer environment was necessary for the krill. The data of these first 3 h were excluded from the low RMR calculations. The individual MMR was determined as the maximum $\dot{M}O_2$ observed for each krill. MMR was often obtained during the first 3 h of a set, but in some individuals, it occurred much later. The aerobic scope (AS) was estimated for each individual as MMR minus RMR. After calculations of individual RMR, MMR and AS, an average was calculated by temperature and species combination.

Estimation of spontaneous swimming speed and net cost of locomotion

Data of spontaneous swimming activity were verified for each krill with LogAnalyser2 software v.1.0.1.0 (DFO-MPO 2015©). The spontaneous swimming activity was calculated during 24 h of the experiment for the same 20 min periods when $\dot{M}O_2$ measurements were taken. The number of laps the krill swam during each measurement period was transformed into distance. We obtained spontaneous swimming speed (cm s^{-1}), combining distance and duration. Maximum and mean speeds at each temperature were calculated. The net cost of locomotion was calculated only for each krill with a significantly positive slope (46%) between $\dot{M}O_2$ and spontaneous swimming speed using this equation:

$$\text{Net cost} = \frac{\dot{M}O_2 - \text{RMR}}{\text{speed}} \quad (2)$$

where Net cost is the net cost of locomotion after removing the cost of maintenance metabolism, estimated by RMR (µg O_2 cm^{-1} g wet^{-1}); $\dot{M}O_2$: µg O_2 h^{-1} g wet^{-1}; RMR: µg O_2 h^{-1} g wet^{-1}; and speed: the spontaneous swimming speed of krill (cm s^{-1}). The pattern of net cost of locomotion in relation to spontaneous swimming speed was similar for the majority of individuals from both species at each temperature, except for *M. norvegica* at 0 °C which barely swam. In general, individual net costs of locomotion were higher at low spontaneous swimming speeds between 0 to 0.3 cm s^{-1} and stabilized beyond 0.3 cm s^{-1} (visually determined). The average net cost of locomotion was calculated using the speed exceeding 0.3 cm s^{-1} for each individual krill.

Statistical analyses

Two-factor ANCOVAs were used to test the effects of species (*M. norvegica* and *T. raschii*), temperature (0, 3, 6, 9, 12, 15 °C) and

accounting for krill wet mass as a covariate on all dependent variables (RMR, MMR, AS, mean maximum speed, mean speed, and net cost of locomotion). ANOVAs were used when the effect of mass was not significant. The metabolic variables were log-transformed to obtain homoscedasticity and to linearize their relationship with wet mass. The data for spontaneous swimming speeds and net cost of locomotion, however, did not need transformation prior to statistical analysis. The net cost of locomotion for *M. norvegica* at 0 °C was not calculated because these animals did not swim, thus statistical tests on the net cost of locomotion were only carried out for experiments in the temperature range of 3 °C to 15 °C for both species.

The R software (R Core Team, 2016) was used for all statistical analyses. Homoscedasticity of data at different temperatures and normality of residuals were verified using Levene's test (package car; Fox & Weisberg, 2011) and the Shapiro-Wilk normality test, respectively. Homoscedasticity was always respected, while residuals were not always normally distributed, but ANOVAs are robust against departure from normality when variances are equal (visually determined using observed *versus* expected residuals; Quinn & Keough, 2002). When significant differences were found, post hoc multiple comparisons procedures (Tukey's all-pair comparisons, package multcomp) were carried out.

RESULTS

Temperature effect on metabolic rates (SMR, MMR, AS) of M. norvegica *and* T. raschii

The third-order interaction (species × temperature × mass) were never significant for RMR, MMR, and AS (for all variables $F_{5,102} < 1.56$, $P > 0.18$). The analysis was repeated with second-order interactions (species × temperature, species × mass, temperature × mass), which were also not significant (for all variables $F_{5,107} < 2.04$, $P > 0.08$). The covariate (mass) was not significant (for all variables $F_{5,113} < 2.32$, $P > 0.13$), thus the model was simplified to a two-way ANOVA. The effect of temperature on RMR, MMR, and AS were similar for both species, interactions terms between temperature and species were not significant (for all variables $F_{5,114} < 2.04$, $P > 0.08$) and will not be mentioned further.

Meganyctiphanes norvegica and *T. raschii* increased their mean RMR with temperature ($F_{5,114} = 25.88$, $P < 0.0001$). Mean RMR was three times higher at 15 °C than at 0 °C (Fig. 2A). The two species had similar average RMR ($F_{1,114} = 1.48$; $P = 0.22$; Fig. 2B). With increasing temperatures from 0 °C to 15 °C, the mean MMR of

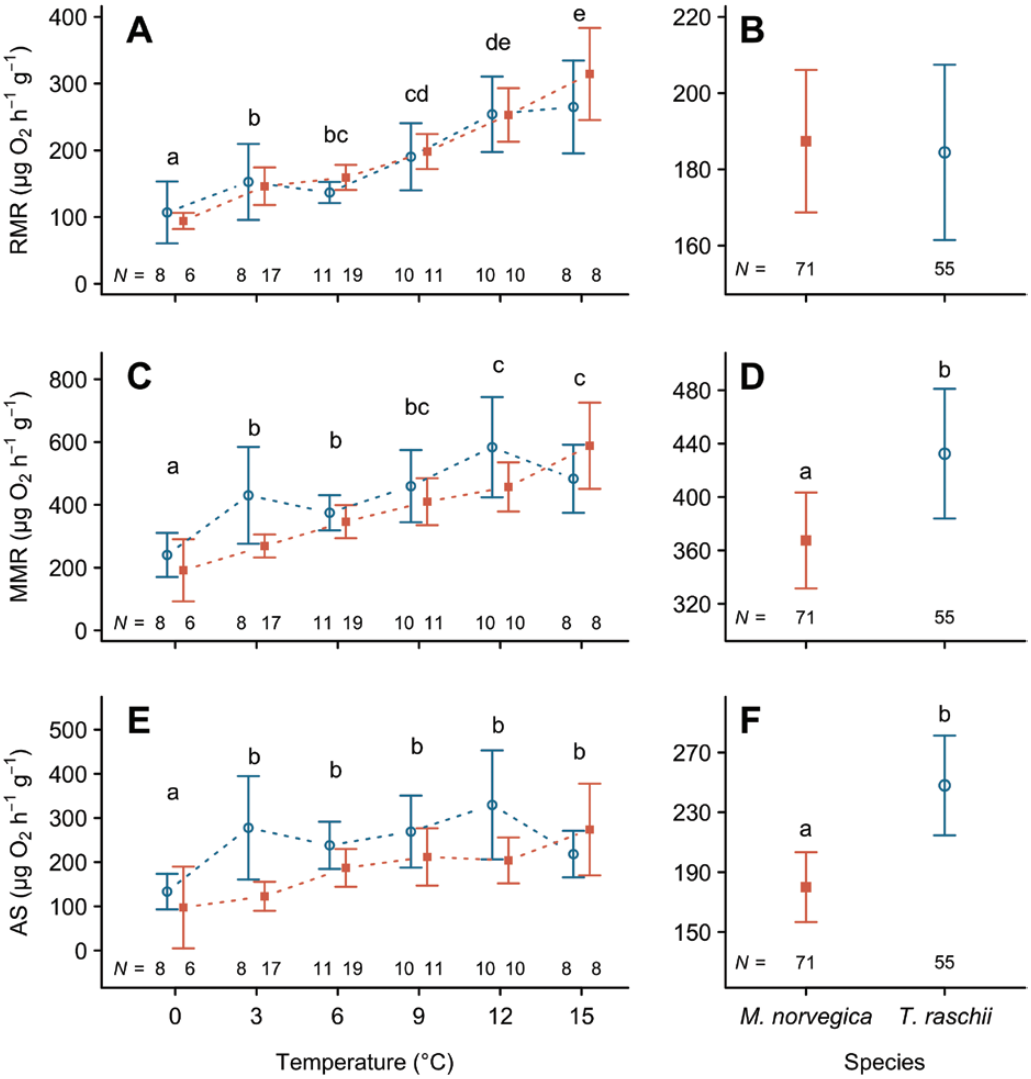

Figure 2. Mean routine metabolic rate (RMR), mean maximal metabolic rate (MMR) and mean aerobic scope (AS) in relation to water temperature (**A, C, E**) in *Meganyctiphanes norvegica* and *Thysanoessa raschii* (data of all temperatures combined) (**B, D, F**). Metabolic rates are expressed as oxygen consumption ($\dot{M}O_2$, µg O_2 h^{-1} g wet^{-1}). Error bars represent the 95% confidence interval. The post-hoc test (Tukey's all-pair comparisons) was done on data combining both species of krill. Means of each metabolic rate with different letters indicate significant differences; *N*, number of individuals.

both species increased more gradually than observed for the mean RMR ($F_{5,114}$ = 18.32, P < 0.0001; Fig. 2C). In contrast to the mean RMR, *M. norvegica* showed a lower mean MMR than *T. raschii* ($F_{1,114}$ = 5.76, P < 0.05; Fig. 2D). The mean AS of both krill species at 0 °C was around half the AS measured at all warmer temperatures ($F_{5,114}$ = 7.04, P < 0.0001; Fig. 2E). Mean AS was lower in *M. norvegica* than in *T. raschii* ($F_{1,114}$ = 15.48, P < 0.001; Fig. 2F).

Temperature effect on spontaneous swimming speed and net cost of locomotion of M. norvegica *and* T. raschii

The third-order interaction (species × temperature × mass) was never significant for the mean maximum speed, mean speed and the net cost of locomotion (for speed variables $F_{5,102}$ < 1.76, P > 0.13 and for the net cost of locomotion variable $F_{4,27}$ < 0.88, P > 0.49). The following second-order interactions (species × temperature, species × mass, temperature × mass) were not significant (for speed variables $F_{5,107}$ < 1.81, P > 0.12 and for the net cost of locomotion variable $F_{4,31}$ < 0.50, P > 0.74). Only the interaction terms species × mass for the mean maximum and the mean speed were significant (for both variables $F_{5,107}$ > 4.21, P < 0.05). The mean maximum and the mean speed were analyzed separately for each species. Only the covariate (mass) for *M. norvegica* was significant (for speed variables $F_{1,64}$ > 11.04, P < 0.01) and speed was corrected for the effect of mass (package lsmeans; Russell, 2016), even though certain values became negative once this correction was applied.

Spontaneous swimming activity in *M. norvegica* was significantly lower at 0 °C than at the other temperatures (ANCOVA: $F_{5,64}$ = 5.15, P < 0.001). Swimming speed was negligible at 0 °C and was constant around 1.0 cm s^{-1} at all warmer temperatures (Fig. 3A). The mean maximum speed of *T. raschii* was not affected by temperature and was kept constant around 1.0 cm s^{-1} (ANOVA: $F_{5,49}$ = 1.18, P = 0.33; Fig. 3B). Furthermore, the mean maximum speed of both species stayed above 0.80 cm s^{-1}, even at 15 °C (Fig. 3). Similar results were obtained when testing the mean speed instead of the mean maximum speed for both species separately. There was no spontaneous swimming activity at 0 °C in *M. norvegica* and mean speed was kept constant at 0.37 ± 0.07 cm s^{-1} from 3 °C to 15 °C, whereas the mean speed was constant 0.34 ± 0.07 cm s^{-1} for the entire temperature range in *T. raschii*.

The mean net cost of locomotion, estimated after removing the cost of low RMR, approached zero (0.0295 ± 0.0073 µg O_2 cm^{-1} g wet^{-1}) for both species. Furthermore, the mean net cost of locomotion was similar among the entire range of tested temperatures ($F_{4,37}$ = 0.12, P = 0.97; Fig. 4A). No differences were observed between *M. norvegica* and *T. raschii* ($F_{1,37}$ = 0.21, P = 0.65; Fig. 4B).

DISCUSSION

Measurement of RMR and MMR

This study provided among the lowest RMR estimates currently known for *M. norvegica* and *T. raschii*. It is easy to overestimate the RMR and almost impossible to measure a real SMR in animals that swim almost continuously. We therefore compared our individuals RMR estimates for both species (from calculations recommended by Chabot *et al.* 2016b) to individual SMR estimates calculated by extrapolation to zero activity between $\dot{M}O_2$ and

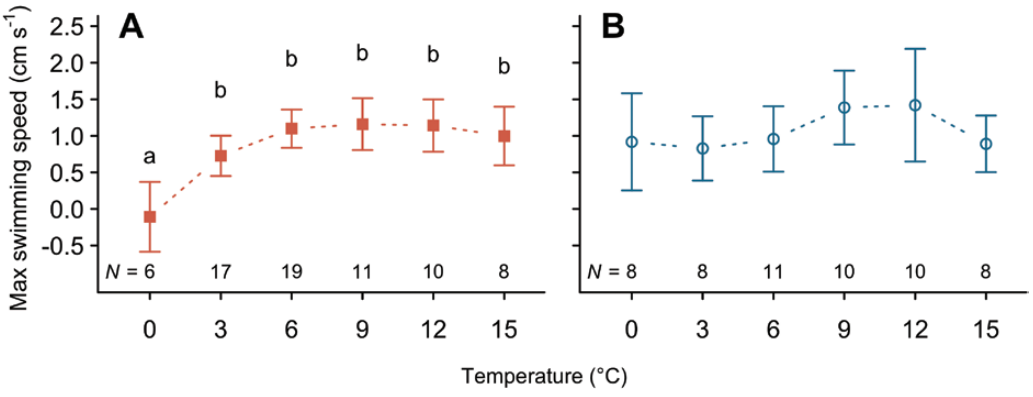

Figure 3. Mean maximum swimming speed in relation to water temperature of *Meganyctiphanes norvegica* (**A**) and *Thysanoessa raschii* (**B**). Errors bars represent the 95% confidence interval. Means with different letters indicate significant differences (post-hoc test, Tukey's all-pair comparisons); *N*, number of individuals.

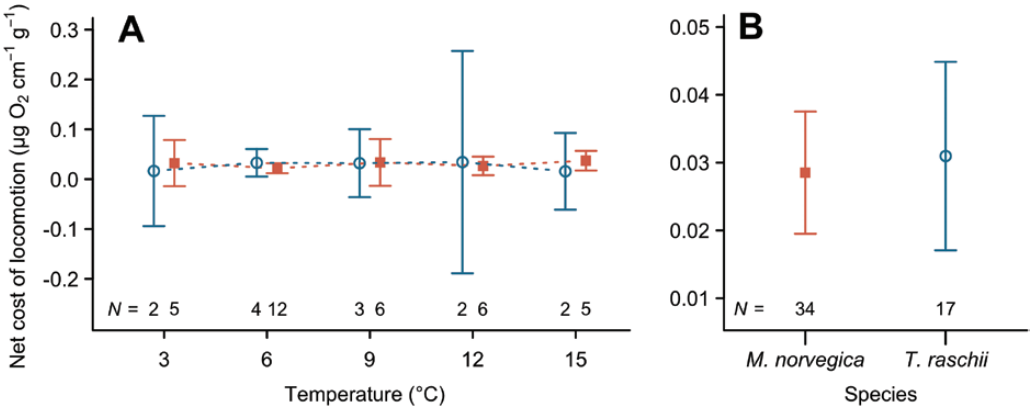

Figure 4. Mean net cost of locomotion in relation to water temperature (**A**) in *Meganyctiphanes norvegica* and *Thysanoessa raschii* (data of all temperatures combined) (**B**). Net cost of locomotion is expressed on a wet mass basis. Error bars represent the 95% confidence interval; *N*, number of individuals.

spontaneous swimming speed (only for individuals with significant positive slopes from our data; see section on methods). There was only a small (4%) difference between these metabolic rates for *M. norvegica* (i.e., RMR slightly higher than SMR) and no difference for *T. raschii*, probably due to lesser N for this species (paired comparison t-test: $t = 2.14$, $P = 0.04$, $N = 39$ and $t = -1.31$, $P = 0.21$, $N = 19$, respectively). The method of Chabot *et al.* (2016b) normally used for measurements from static respirometers (i.e., small respirometers that restrict activity level) was therefore sufficient to provide low and reliable RMR estimates, regardless of the activity level.

The estimation of MMR based on spontaneous swimming activity measurements in *M. norvegica* and *T. raschii* seems not to be an appropriate method. We expected spontaneous swimming activity to be sufficient to estimate MMR, because it can result in higher $\dot{M}O_2$ than chasing, as shown in crustaceans (e.g., Dupont-Prinet *et al.*, 2013a, b). The maximum spontaneous swimming speeds we obtained, however, were modest (~1 cm s^{-1}) in comparison to *in situ* data (Supplementary material Table S3), suggesting that MMR was likely underestimated. This was confirmed by calculating the factorial aerobic scope of each species of krill (FAS; i.e., MMR divided by RMR). FAS facilitates the comparison of aerobic scope among species with very different RMRs. FAS of the two species of krill investigated in this study were very low (~2), compared with values typically obtained in fishes (e.g., Lucas & Priede, 1992; Schurmann & Steffensen, 1997; Fitzgibbon *et al.*, 2007), shrimps (e.g., Dupont-Prinet *et al.*, 2013a), and crabs (e.g., Booth & McMahon, 1992) (FAS > 3; Supplementary material Fig. S2). FAS is usually even higher in highly active species such as *Euphausia superba*, showing a FAS of ~6 (Swadling *et al.*, 2005). MMR and AS were thus likely underestimated so that no inference about the complete thermal niche can be made from the relationship, or lack of, between AS and temperature.

Effect of temperature

The metabolic rate increases as a result of increasing temperature within the thermal tolerance range of a species (Fry & Hart, 1948; Bullock, 1955), as it has been already shown in many fishes (Fry & Hart, 1948; Graham, 1949; Clark *et al.*, 2011) and shrimps (Dall, 1986; Daoud *et al.*, 2007). Such an increase was therefore expected for *M. norvegica* and *T. raschii* and was observed in this study. Both species were able to adjust their oxygen consumption ($\dot{M}O_2$) to meet their increasing metabolic rate up to the highest temperature conditions. Neither of the two species was constrained by the temperature (15 °C) tested, even though they are rarely exposed to such high temperatures in the lower St. Lawrence Estuary. Mean summer surface temperature is 11 °C with rare peaks of 15 °C in late summer (Galbraith *et al.*, 2013). This performance is likely due to their thermal plasticity. As our experiments lasted only 24h, we cannot infer about the long-term effects of exposure to temperatures of 15 °C or higher.

The changes in RMR with temperature followed the patterns observed in other studies (Fig. 5). Saborowski *et al.* (2002) showed that the metabolic rate of *M. norvegica* varied according to temperature conditions in the water column, which were closely related to geographical locations and seasonal conditions. Data on *M. norvegica* in the lower St. Lawrence Estuary were remarkably well correlated to data obtained on populations of the same species from the Clyde Sea, Scotland (summer and winter; Saborowski *et al.*, 2002), the Ligurian Sea in the Mediterranean (summer; Saborowski *et al.*, 2002), and the Kongsfjord, Norway (spring and autumn; Huenerlage & Buchholz, 2015). The lack of methodological standardization in measuring oxygen uptake in small crustaceans calls nonetheless for caution when making comparisons with the literature. Studies varied in the duration of the experiment, duration of exposure to temperature, and in the type and volume of respirometers. All these factors might influence the precision of the determination of oxygen uptake and the ability of the animals to swim. The ability to measure changes in dissolved oxygen in small respirometers has increased considerably during the last 40 years. All these arguments may also explain the high oxygen uptake measured for *M. norvegica* and *T. raschii* from the Gulf of St. Lawrence by Sameoto (1976) compared to the present study. Data on metabolic rates of *T. raschii* are scarce. The RMR of *T. raschii* captured in the estuary, however, was similar to the one of *T. raschii* from Kongsfjord, where the upper pejus temperature (where AS begins to declines fast) was defined as ~12 °C (Huenerlage & Buchholz, 2015). RMR of *T. raschii* from the present study seemed to reach a plateau close to 12 °C, in agreement with Huenerlage & Buchholz (2015) (Fig. 5).

Our study is the first to also provide spontaneous swimming speeds for *M. norvegica* and *T. raschii* facing different temperature regimes. Only a few studies have documented the relationship

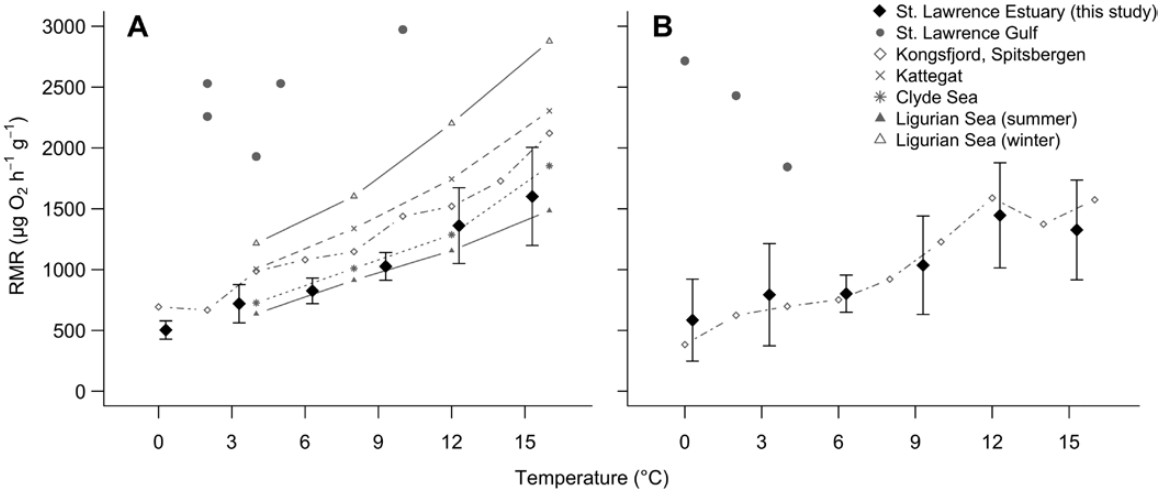

Figure 5. Mean routine metabolic rate (RMR, µg O_2 h^{-1} g dry^{-1}) in relation to water temperature for *Meganyctiphanes norvegica* (**A**) and *Thysanoessa raschii* (**B**) in comparison to others studies. Black diamonds represent mean RMR of each species from the lower St. Lawrence Estuary (this study). Error bars represent the 95% confidence interval. Grey symbols represent RMR of the two species in different locations: Gulf of St. Lawrence (spring, summer and winter; rates calculated for 10 mg animals; Sameoto, 1976); Kongsfjord, Spitsbergen (spring and autumn; Huenerlage & Buchholz, 2015); Kattegat (summer and winter; Saborowski *et al.*, 2000); Clyde sea (summer and winter; Saborowski *et al.*, 2002); Ligurian sea (summer and winter; Saborowski *et al.*, 2002). Values from Huenerlage & Buchholz (2015) were converted applying a fresh to dry weight conversion factor of 22%, estimated from our data.

between swimming speed and temperature in krill (e.g., Torres & Childress, 1983), and none exists for the two species we studied. Swimming speed can provide supplementary information about performance of the species. Mean maximum spontaneous swimming speed of *M. norvegica* was reduced to almost zero at 0 °C. Low temperatures have already been shown to severely reduce swimming speed in fishes due to the effects on biochemical and physiological processes involved in muscle contraction (Wardle, 1980). Our results suggest that this low temperature (0 °C) is below the lower critical temperature of *M. norvegica*. In contrast, the mean maximum spontaneous swimming speed of *T. raschii* was not influenced by temperature, indicating that the lower critical temperature was not reached in our study.

Comparison between species

As for MMR and AS, we expected a lower RMR for *M. norvegica* than for *T. raschii* due to differences in size intrinsic to the species. In most animals, larger organisms consume less oxygen (per unit body mass) than smaller ones because of an allometric exponent typically < 1 (e.g., endothermic species and fishes; Schmidt-Nielsen, 1984; Steffensen *et al.*, 1994; White *et al.*, 2006; Lefevre *et al.*, 2017). For crustaceans and specifically euphausiids, this allometric exponent tends to be ~1 (Paranjape, 1967; Harding, 1977; Van Ngan *et al.*, 1997). Larger euphausiids do not consume less oxygen per unit body mass than smaller ones, which likely explains why there was no difference between the two species even though *M. norvegica* is larger than *T. raschii*.

The net cost of locomotion was remarkably similar in both species, even though *M. norvegica* is around twice as long as *T. raschii* (mean of body length: 40 mm and 24 mm, respectively). The low spontaneous swimming speeds observed were not very costly in terms of energy (only ~0.03 µg O_2 cm^{-1} g^{-1}), which makes sense in species that swim quasi-continuously. These results are in agreement with Kils (1981) on *E. superba* showing that swimming activity between 0 and 13 cm s^{-1} (or ~2.4 body length s^{-1}) did not affect the "standard metabolism." *Meganyctiphanes norvegica* and *T. raschii* are also able to swim faster (Supplementary material Table S3), and these should involve greater energetic costs (i.e., increased cost of ventilation, circulation, and muscle activity).

Ecological consequences

Physiological data from the present study suggest potentially overlapping distributions of *M. norvegica* and *T. raschii* in the temperature range of 3–15 °C and avoidance of colder waters by *M. norvegica*. Distinct vertical daytime distribution patterns of *M. norvegica* and *T. raschii* are actually found in the lower St. Lawrence Estuary, with very restricted overlap. *Meganyctiphanes norvegica* is mostly found below the cold intermediate layer (CIL) at temperatures between 1.3 °C and 4.2 °C, whereas individuals of *T. raschii* aggregate in or close to the CIL between –0.7 °C and 3.5 °C (Plourde *et al.*, 2014; McQuinn *et al.*, 2015). The deeper distribution of *M. norvegica* than *T. raschii* could be a response to the debilitating effect of long exposure to temperatures around 0 °C on its swimming ability. Both species perform diel vertical migrations (DVM) ascending to the surface layers during night time (Simard *et al.*, 1986; Buchholz *et al.*, 1995; Sourisseau *et al.*, 2008). *Meganyctiphanes norvegica* has to swim through the CIL (< 1 °C) to reach the surface layer each night, and again return to its daytime depth in the morning, even though, according to our results, the low temperatures of the CIL are close to its lower critical temperature. *Meganyctiphanes norvegica* would nevertheless only need approximately 30 min with an estimated swimming speed of 3 cm s^{-1} (I. McQuinn, personal communication; Tarling, 2010) to cross the CIL (~50 m; Galbraith *et al.*, 2016). This is much shorter than the time *M. norvegica* spent at 0 °C in our experiments (i.e., 24 h duration of exposure period at this temperature and experimental time in the respirometer). Field data (Simard *et al.*, 1986; Sourisseau *et al.*, 2008) suggest that swimming performance of *M. norvegica* is not dangerously reduced during short exposure to very low temperatures (~0 °C). Such temperate-boreal species must therefore stay in deeper and warmer waters, despite the increasing cost of the longer migration distance.

Both species showed tolerance to a wide temperature range and still showed high performances of spontaneous swimming activity at the highest temperature tested (15 °C), even if 15 °C is rarely encountered in the surface layer of the estuary (Galbraith *et al.*, 2013). This finding suggests the occurrence of high thermal plasticity in both species and might suggest that the higher critical temperature is above 15 °C. High mortality was observed in *M. norvegica* from the Kattegat when exposed to 15 °C (Buchholz *et al.*, 1995), suggesting that individuals in this population reached their upper thermal tolerance limit and would not migrate into the surface layer at 14–15 °C. These differences in temperature tolerance can probably be attributed to differences among distinct genetic populations of *M. norvegica* (Patarnello *et al.*, 2010). The arcto-boreal *T. raschii* rarely encounters 15 °C in the estuary, although in other nearby regions, such as the Gulf of Maine, they are regularly exposed to summer surface temperatures reaching 15 °C (Mauchline, 1980; Everson, 2000; Richaud *et al.*, 2016). The capacity to cope with temperatures of 15 °C could be inherent to the species as part of their thermal plasticity.

In the context of warming oceans, Long *et al.* (2015) predicted an increase of temperature at all depths by 0.6–1.2 °C in the Estuary and Gulf of St. Lawrence between 2040 and 2069. *Meganyctiphanes norvegica* and *T. raschii* might therefore encounter more frequently waters of 15 °C or warmer in the surface layer, which could change their migration behavior. The increase of temperature in deeper layers, which would then result in a thinner CIL, may imply changes of their vertical distribution. The increase of global mean temperature (IPCC, 2014) might also change the geographic distribution of both species. In this context, the future distribution of *M. norvegica* might extend and/or move to higher latitudes, whereas the distribution of *T. raschii* would be more restricted to the north. This boreal-Arctic species could not remain at latitudes as low as in *M. norvegica*. All these changes would impact the higher trophic levels, in particular krill-dependent predators such as the blue whale (Atlantic population already critically endangered; Sears & Calambokidis, 2002), and consequently might contribute to global changes of the entire ecosystem.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Figure. Example of a measurement cycle of oxygen depletion by *Meganyctiphanes norvegica* in an annular respirometer.

S2 Figure. Factorial aerobic scope (MMR/RMR = FAS) in relation to temperature for *Meganyctiphanes norvegica* and *Thysanoessa raschii* compared to data from several studies.

S3 Table. Swimming speeds of *Meganyctiphanes norvegica*, *Thysanoessa raschii*, and *Euphausia superba*, obtained from doppler current profilers (ADCP) or experimental data.

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