Tolerant but facing increased competition: Arctic zooplankton versus Atlantic invaders in a warming ocean

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The Arctic Ocean is rapidly changing. Air temperature is rising two to four times faster in the Arctic than the global average, with dramatic consequences for the ecosystems. Polar zooplankton species have to cope with those increasing temperatures, whilst simultaneously facing increasing competition by boreal-Atlantic sister species advected into the Arctic Ocean via a stronger Atlantic inflow. To assess the sensitivity of Arctic and Atlantic zooplankton to rising temperatures, respiration rates of dominant Arctic species (*Calanus hyperboreus*, *Calanus glacialis*, *Paraeuchaeta glacialis*, *Themisto libellula*) and their co-occurring Atlantic congeners (*Calanus finmarchicus*, *Paraeuchaeta norvegica*, *Themisto abyssorum*) were measured at ambient temperatures and simulated conditions of ocean warming from 0 to 10°C during three expeditions with RV *Polarstern* to the Arctic Fram Strait. Arctic zooplankton showed only slowly increasing respiration rates with increasing temperatures, also indicated by low Q_{10} ratios. In contrast, boreal-Atlantic representatives responded to higher temperatures by a rapid and steeper increase in their respiration rates (higher Q_{10}), suggesting higher metabolic activity. These results imply that Arctic species are physiologically more tolerant to ocean warming than expected but might be outcompeted by their Atlantic congeners beyond a certain temperature threshold in areas of strong distribution overlap. Thus, the 'Atlantification' of the Arctic zooplankton community seems to be driven rather by ecological interactions than by physiological limitations. Changes in zooplankton community composition and biodiversity will have major consequences for trophodynamics and energy flux in Arctic ecosystems, since polar species tend to be larger than their southern counterparts and have a higher lipid content, providing more energy-rich food for higher trophic levels.

KEYWORDS

Calanus, respiration, aerobic metabolism, cold adaptation, climate change, Fram Strait, Atlantification, Borealization

1 Introduction

The Arctic Ocean and adjacent ice-covered seas are the regions that are most rapidly affected by global warming. Air surface temperature is rising two to four times faster in the Arctic than the global average (Bekryaev et al., 2010; Masson-Delmotte et al., 2013; Meredith et al., 2019), and the sea surface and Atlantic Water core temperatures in the Arctic Ocean have been increasing for the last decades (Polyakov et al., 2012; Polyakov et al., 2013; Hartmann et al., 2013; Meredith et al., 2019).

The increasing northward inflow of warm and saline Atlantic waters is referred to as 'Atlantification' or 'Borealization' of the Arctic (Polyakov et al., 2017). Associated with Atlantic water masses are boreal-Atlantic species, which are rapidly expanding their ranges poleward (Beaugrand et al., 2009). For instance, copepods (Beaugrand et al., 2002; Weydmann et al., 2014), gelatinous zooplankton (Mańko et al., 2020) and fishes (Fossheim et al., 2015; Vihtakari et al., 2018) are shifting northward in their biogeographic distribution. This is emphasized by first evidence of reproductive success of boreal zooplankton species, such as the amphipod *Themisto compressa* and the euphausiid *Thysanoessa raschii* near the Svalbard archipelago in Fram Strait and in Kongsfjorden, Svalbard, respectively (Buchholz et al., 2012; Kraft et al., 2013). Thus, the Atlantic-influenced regions of the Arctic Ocean are increasingly invaded and successfully colonized by boreal-Atlantic species, resulting in the Atlantification of the Arctic fauna.

In Fram Strait, the only deep-water connection of the Arctic with the Atlantic Ocean, three species of *Calanus* co-occur, with two 'true polar-Arctic' species, *Calanus hyperboreus* and *C. glacialis*, and one expatriate from the boreal-Atlantic, *C. finmarchicus* (Wassmann et al., 2015). Copepods of the genus *Calanus* are a key component in the Arctic marine food web, as they usually dominate in terms of biomass and represent a crucial link between primary production and higher trophic levels (Mumm et al., 1998; Auel and Hagen, 2002; Kosobokova and Hirche, 2009). The three species share similarities considering morphology and life-history traits; however, they differ particularly considering size, life-cycle duration and phenology (Møller and Nielsen, 2020; Daase et al., 2021). Both Arctic species are characterized by larger size, higher lipid content and life-cycles exceeding one year (Daase et al., 2021). Reproductive strategies of polar *Calanus* species are highly adapted to the harsh and strongly seasonal Arctic conditions. *C. hyperboreus* is a capital breeder, i.e. using stored lipid resources for reproduction (Daase et al., 2021). Hence, *C. hyperboreus* can reproduce independent of immediate food supply and is able to initiate reproduction prior to the onset of the ice algal bloom. By the time the spring bloom is commencing, nauplii of *C. hyperboreus* have reached their feeding stage (from naupliar stage 3 onward) and are able to

utilize the early ice algal bloom for growth and development (Jung-Madsen et al., 2013; Daase et al., 2021). *C. glacialis* is also well adapted due to a high flexibility in its reproductive strategy, being able to fuel reproduction both by lipid reserves and by utilizing the early ice algal bloom (Hirche and Kattner, 1993; Wold et al., 2011). *C. finmarchicus*, in contrast, is smaller in size, hence possesses comparably smaller lipid reserves, has a one-year life-cycle and is an income breeder, i.e. reproduction is dependent on direct food intake (Daase et al., 2021).

Shifting from a community dominated by large and lipid-rich copepods with multi-year life cycles to one with smaller, less lipid-rich and shorter-lived species could have consequences for the entire Arctic food web. For instance, the Arctic planktivorous little auk (*Alle alle*) and juvenile polar cod (*Boreogadus saida*) are strongly dependent on the larger Arctic *Calanus* species and, in the case of little auks, even extend their foraging trips to find their preferred prey (Karnovsky et al., 2010; Kwaśniewski et al., 2010; Bouchard and Fortier, 2020). It is, thus, crucial to better understand the processes driving transitions in community composition.

As a consequence of species-specific temperature tolerance limits and temperature-dependent effects on performance, organisms occupy distinct thermal niches, which are an important factor in defining their biogeographical distribution (Schulte et al., 2011). Polar marine ectotherms are considered to have a comparably narrow optimum at low temperatures and a limited ability to cope with rising environmental temperatures (Peck, 2002). This stenothermy is particularly pronounced in Antarctic ectotherms (Pörtner et al., 2007; Peck et al., 2010; Sandersfeld et al., 2015), but has also been reported for Arctic invertebrates and fishes (Franklin et al., 2013; Huenerlage and Buchholz, 2015).

The concept of oxygen- and capacity-limited thermal tolerance (OCLTT) explains temperature effects on the aerobic scope as a main driver in influencing energy availability for performance, and thus eventually the biogeographic distribution of species (Pörtner et al., 2017). The aerobic scope is determined by the difference between the standard and maximum metabolic rate and represents excess capacity of aerobic energy available for achieving fitness and supporting biological functions. Beyond a threshold temperature (pejus temperature), a mismatch between oxygen supply capacity and oxygen demand occurs, reducing the aerobic scope, and thus limiting available energy for essential biological processes such as foraging, growth and reproduction. While temperatures beyond the pejus temperature do not necessarily influence the survival of a species yet, they reduce its performance, and hence its competitive fitness (Pörtner, 2001; Verberk et al., 2016).

To assess the sensitivity of polar-Arctic versus boreal-Atlantic zooplankton to rising temperatures, we conducted respiration measurements as a proxy for metabolic activity at five temperatures ranging from 0 to 10°C with the three co-existing *Calanus* species in Arctic Fram Strait. In addition, pairs of polar versus boreal-Atlantic congeners of other zooplankton taxa, the predatory copepods

Paraeuchaeta glacialis and *P. norvegica* and the hyperiid amphipods *Themisto libellula* and *T. abyssorum*, were included in the study. Specifically, we hypothesize that (1) polar species show a stenothermic response, i.e. rapidly increasing metabolic rates at lower temperatures (high Q_{10} value), followed by a narrow optimum and a sharp drop, including increased mortality at higher temperatures; (2) mass-specific respiration rates are generally higher in the smaller boreal-Atlantic species compared to their larger polar congeners; (3) the mechanism behind the Atlantification of the Arctic fauna is mainly driven by physiological limits of Arctic zooplankton to increasing temperatures.

2 Materials and methods

2.1 Sampling

Sampling was conducted at the end of summer during three cruises with RV *Polarstern* to Arctic Fram Strait in July-September 2016, 2017, and 2019 (PS100, PS107 and PS121, respectively, Figure 1).

2.1.1 *In situ* conditions

In situ temperatures were obtained with a CTD (Conductivity Temperature Depth) profiling system prior to each sampling of zooplankton. *In situ* temperatures did not vary distinctly between years, but rather between regions in Fram Strait. The western part of Fram Strait is under strong influence of the East Greenland Current (EGC), exporting cold and fresh Polar Surface Water out of the Arctic Ocean. Temperature
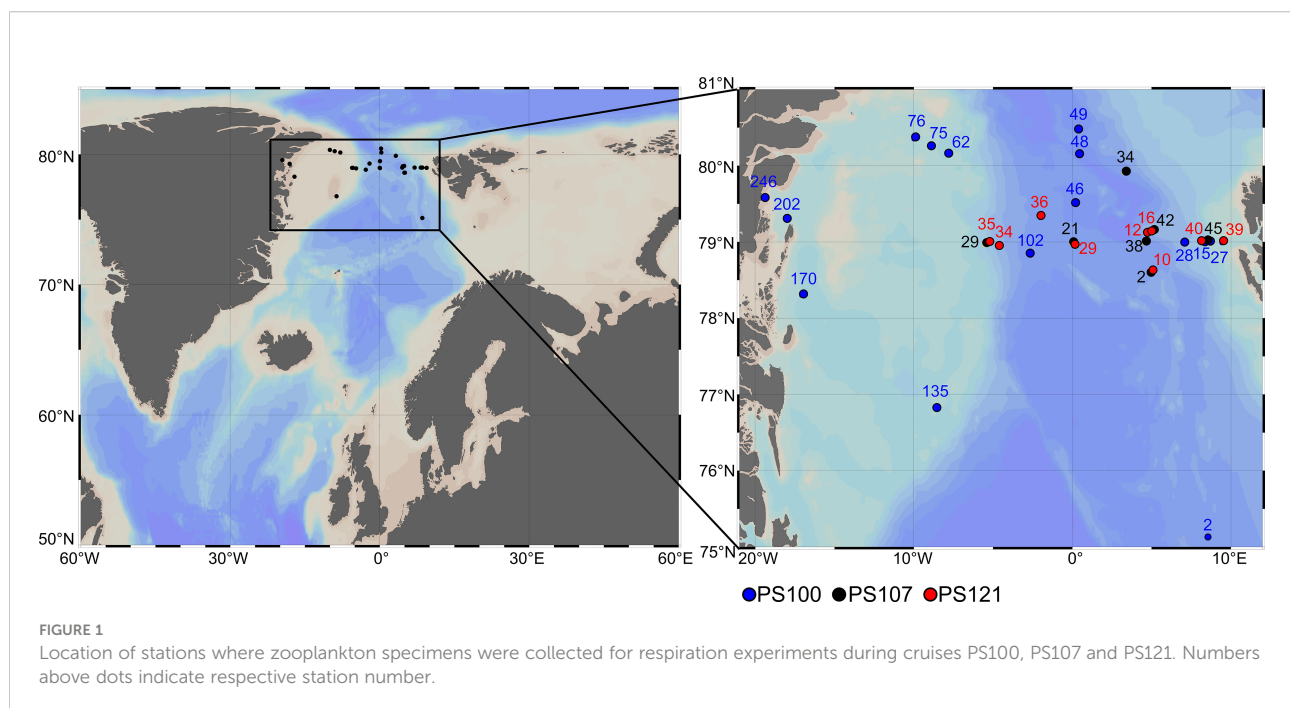
profiles of the stations during the three cruises were characterized by temperatures below 0°C in epipelagic layers (Supplement Material S1). Between 200 to 300 m, temperatures increased up to a maximum of 3°C and then decreased again to around 0°C in 1000 m.

In the eastern part of Fram Strait, the West Spitsbergen Current (WSC) flows northward and transports rather warm, saline Atlantic water into the Arctic Ocean. Profiles during the three cruises showed high temperatures of 5 to 9°C in surface waters. With increasing depth temperatures steadily decreased to ≤0°C below 600 m.

The zone in between the two currents, here referred to as central Fram Strait, is characterized by a highly dynamic and turbulent hydrographic regime (Kawasaki and Hasumi, 2016; von Appen et al., 2018). While partly under influence of the EGC, branches of the WSC turn westward to 'recirculate' and subduct below the Polar Surface Water (Hattermann et al., 2016). The variability of the central Fram Strait was reflected in the temperature profiles during the three expeditions. Four stations showed similar profiles as the ones under influence of the EGC (PS100 Stns 48, 49 and PS121 Stns 29, 36), three showed a mix of both characteristics (PS100 Stns 46, 102 and PS107 Stn 21) and one was influenced by the WSC (PS107 Stn 34; Supplement Material S1).

2.1.2 Zooplankton sampling

Zooplankton sampling was conducted using either a multiple opening and closing net equipped with five nets for stratified vertical hauls (Hydrobios Multinet Midi, mouth opening 0.25 m^2, mesh size 150 μm, hauling speed 0.5 m s^{-1})

FIGURE 1
Location of stations where zooplankton specimens were collected for respiration experiments during cruises PS100, PS107 and PS121. Numbers above dots indicate respective station number.

or a bongo net (mesh size: 200 to 500 μm, towing speed 1-2 kn) with filtering cod-ends, respectively. Vertical hauls with the Multinet usually sampled the entire water column from the seafloor or a maximum sampling depth of 1,500 m to the surface (Kanzow, 2017; Schewe, 2018; Metfies, 2020). Specimens used for respiration measurements were sorted immediately after the hauls in a temperature-controlled lab container (2 to 4°C). Only apparently healthy and active individuals were selected and kept at 0°C. 0°C were chosen, as it was within the *in situ* temperature range for all species.

2.2 Respiration measurements

Respiration rates of zooplankton organisms were measured on board at different temperatures (0, 4, 6, 8 and 10°C) non-invasively by optode respirometry using a 10-Channel Fiber Optic Oxygen Meter (OXY-10, PreSens, Precision Sensing GmbH, Regensburg, Germany). Each individual was only measured once at one of the experimental temperatures and they were selected randomly for the respective temperatures. Prior to the measurements, specimens were transferred from 0°C to the incubator, brought slowly to their respective experimental temperature and acclimated for at least 24 hours.

For the experiments, individuals were carefully transferred into gas-tight glass bottles containing 13 ml of 0.2 μm GF/F filtered and oxygenated seawater. The number of individuals per bottle depended on size, ontogenetic stage and metabolic activity with a maximum of six specimens per bottle (for *Calanus finmarchicus* copepodite stage C5). Experiments were run in a temperature-controlled incubator in the dark (refrigerator with external precision thermostat) for generally 8 to 24 hours with continuous measurements every 15 seconds. If oxygen levels fell below a critical level (below 60% air saturation), experiments were terminated earlier (usually in case of larger animals such as the amphipods *Themisto* spp.). In each experimental run, two channels of the multi-channel optode respirometer were used for animal-free controls to compensate for potential microbial oxygen consumption or production.

After the experiments, the taxonomic identification of species and developmental stages was confirmed under a dissecting microscope (Leica MS5) and amphipods were measured for body length. *Calanus glacialis* and *C. finmarchicus* are two sister species that are morphologically difficult to distinguish. Differentiation based on prosome length is a commonly used method to discriminate between the two congeners (Daase et al., 2018). However, due to an overlap of size distributions in regions of co-occurrence (Gabrielsen et al., 2012; Choquet et al., 2018) and depth-dependent size distributions (Kaiser et al., 2021), this can lead to individuals being misidentified, usually with a bias towards an underestimation of *C. glacialis* (Choquet et al., 2018; Daase et al., 2018). Nevertheless, *C. glacialis* reaches distinctly larger sizes

than *C. finmarchicus*. Therefore, to avoid the overlapping size ranges, only larger individuals of the same stage were used for experiments with *C. glacialis* and smaller individuals for *C. finmarchicus*.

All individuals were deep-frozen at -80°C for subsequent dry mass (DM) determination after lyophilization for 48 hours, in the home laboratory at the University of Bremen, Germany. Deep-frozen at -80°C for subsequent dry mass (DM) determination after lyophilization for 48 hours, in the home laboratory at the University of Bremen, Germany. Individuals were then weighed using a microbalance (Sartorius MC215).

The first two hours of each measurement (or 20 min when measurements had to be terminated early due to oxygen depletion) were excluded from further analysis to avoid potential bias by handling stress or temperature adjustments at the start of the experiments. Animal-free controls were treated equally. The mean decline in dissolved oxygen concentration in the animal-free controls was subtracted from the respective measurements with animals of the same experimental run.

To compare respiration between different species, mass-specific respiration rates (MSRR) were calculated. Statistical analyses were performed using GraphPad Prism (version 8.0.2). Differences between MSRR during the three years (2016, 2017 and 2019) were tested for significance using Welch-ANOVA, as homogeneity of variance was not always met and sample size was highly variable, followed by the Games-Howell's *post hoc* multiple comparison test. Both analyses were chosen, as they do not assume equal variances and sample sizes. No significant differences were detected in MSRR of the seven species between the three years at each temperature; thus, the experimental results from the different years were pooled for each species and stage.

MSRR were standardized for all species to exclude the factor body mass on respiration. For the standardization, $\log_{10}$ transformed MSRR of all species at 0°C were plotted against $\log_{10}$ transformed dry masses to obtain the scaling coefficient b (-0.25) from the linear slope of the regression line. Standardized MSRR were calculated as follows:

$$R_{stand} = \frac{R_{MSRR}}{DM^{-025}} * stDM^{(-0.25)}$$

where R_{MSRR} is the mass-specific respiration rate, DM is the respective dry mass, stDM is the genus- and stage-specific mean dry mass (2 mg for *Calanus* females, 1.2 mg for *Calanus* C5, 5.6 mg for *Paraeuchaeta* females, 1.8 mg for *Paraeuchaeta* C5, 7 mg for *Themisto*). Genus- and stage-specific DMs were obtained by averaging dry masses of all sampled individuals of the respective genus and stage.

Intraspecific temperature-dependent differences in MSRR were tested for significance using Welch-ANOVA, followed by Games-Howell's *post hoc* multiple comparison test. Differences in slopes of linear regression performed on $\log_{10}$ transformed MSRR were tested for significance between species of the same

genus to identify significant differences in the species-specific increase of MSRR.

Finally, species- and stage-specific Q_{10} values were calculated based on exponential regression of all MSRR data at the different temperatures. With the obtained exponential function, calculated MSRR rates for 10°C were divided by rates at 0°C, providing the Q_{10} values, i.e. the factorial increase associated with a 10°C rise in temperature. To exclude that *Calanus* females and C5s from greater depths had an impact on MSRR, Q_{10} values of specimens from the surface layers (0 – 100 m) were compared to Q_{10} values including individuals from deeper layers. Q_{10} values did not distinctly change, whether deeper-dwelling individuals were included in the analysis or not. We therefore assume that these specimens did not yet enter diapause and included all *Calanus* individuals in the analyses.

3 Results

In total, 517 measurements of seven different polar (*Calanus hyperboreus, Calanus glacialis, Paraeuchaeta glacialis, Themisto libellula*) and boreal-Atlantic (*Calanus finmarchicus, Paraeuchaeta norvegica, Themisto abyssorum*) zooplankton species were conducted at 0, 4, 6, 8 and 10°C (Table 1 and Figure 2).

3.1 Temperature-dependence of respiration

In general, mass-specific respiration rates (MSRR) increased with temperature for all species and stages (Table 1 and Figure 2). Adult females of polar *Calanus hyperboreus* and *C. glacialis* showed a slow, but steady increase in MSRR (Figure 2A and Table 1). Respiration rates in these organisms doubled from 0 to 8°C, which represents a significant increase for *C. hyperboreus* (p<0.001) and *C. glacialis* females (p< 0.001; Games-Howell's multiple comparison test). The increase from 0 to 6°C was also significant in *C. glacialis* (p= 0.05). A summary of all statistical analyses can be found in the Supplement Material S2.

In *C. hyperboreus* C5, MSRR remained rather stable between 0 and 6°C (mean values around 12 nmol O_2 h^{-1} mg^{-1} DM for all three temperatures), but at 8 and 10°C an increase was noticeable to 20 and 27 nmol O_2 h^{-1} mg^{-1} DM, respectively (0 and 8°C: p< 0.001). In *C. glacialis* C5 no distinct increase in MSRR was observed between 0 and 8°C (p> 0.999; Figure 2A and Table 1).

Adult females of *C. finmarchicus* showed similar MSRR at 0°C as their Arctic congeners (Figure 2A and Table 1). However, in contrast to the slow and steady increase of Arctic *Calanus* species, MSRR of boreal-Atlantic *C. finmarchicus* females showed a much more rapid and steeper increase, with a more than threefold increase in mean MSRR from 0 to 6°C (i.e. 24 to 90 nmol O_2 h^{-1} mg^{-1} DM, Table 1 and Figure 2A). At 8°C the distinct rise in MSRR of *C. finmarchicus* females flattened into a plateau. MSRR of *C. finmarchicus* females were significantly different between 0 and 4°C (p= 0.04), 0 and 6°C (p< 0.001) and 4 and 6°C (p= 0.02). The slope of the regression line of $\log_{10}$ transformed MSRR with increasing temperature of *C. finmarchicus* females was significantly higher than the slope of females of *C. hyperboreus* (p= 0.0089) and *C. glacialis* (p= 0.0117).

Copepodite stages C5 of *C. finmarchicus* also showed a significant increase in MSRR from 0 to 8°C, with mean values increasing from 15 to 44 nmol O_2 h^{-1} mg^{-1} DM, respectively (0 and 8°C: p= 0.02, 4 and 10°C: p= 0.01). The increase leveled off at 10°C (Figure 2A). The slope of the linear regression of MSRR with increasing temperature was significantly higher in *C. finmarchicus* C5 compared to *C. hyperboreus* C5 (p= 0.0004) and *C. glacialis* C5 (p= 0.0027).

Adult females of the predatory copepod species *Paraeuchaeta glacialis* and *P. norvegica* showed similar trends among each other with little change in MSRR between 0 and 4°C and an increase at 8°C (Table 1 and Figure 2B). At all temperatures, mean MSRR of the Arctic *P. glacialis* females were higher than those of their Atlantic congener *P. norvegica* (Table 1). Respiration of *P. glacialis* C5 changed only slightly with increasing temperature, with essentially no difference in mean MSRR from 0 to 10°C (20 and 21 nmol O_2 h^{-1} mg^{-1} DM, respectively). While mean MSRR of *P. norvegica* C5 was similar to *P. glacialis* C5 at 0°C, a distinct increase of mean values could be observed for *P. norvegica* C5 at temperatures above 4°C (Table 1 and Figure 2B).

In the amphipods *Themisto libellula* and *T. abyssorum* mean MSRR increased only slightly with temperature for both species. Mean standardized MSRR of the Arctic *T. libellula* were higher than those of the boreal-Atlantic *T. abyssorum* at all temperatures (Table 1 and Figure 2C).

3.2 Q_{10} values

Q_{10} values were generally higher for boreal-Atlantic congeners than for polar-Arctic species (Figure 3). These differences in Q_{10} coefficients were most pronounced in *Calanus* species. Polar-Arctic *C. hyperboreus* and *C. glacialis* had Q_{10} values between 1.3 and 2.7. In contrast, the boreal-Atlantic *C. finmarchicus* had much higher Q_{10} values of 4.2 in C5s and 5.9 in adult females.

Similar, but less pronounced differences in Q_{10} values between polar-Arctic and boreal-Atlantic sister species were determined for *Paraeuchaeta* spp. and *Themisto* spp., with higher values for the Atlantic species (*P. norvegica* C5: 2.3, females: 1.8; *T. abyssorum*: 2.5) compared to the Arctic congeners (*P. glacialis* C5: 1.0, females: 1.7; *T. libellula*: 1.7; Figure 3).

TABLE 1 Individual, mass-specific and standardized mass-specific respiration rates of polar-Arctic and boreal-Atlantic (grey highlighted) zooplankton species measured at different ambient temperatures (Exp. temp.) during three expeditions PS100 (2016), PS107 (2017) and PS121 (2019) with RV *Polarstern* to Arctic Fram Strait in summer (July-September).

Species	Stage	Exp. temp. [°C]	Exp. run time [h]	Mort. [%]	*In situ* temp. min/max [°C]	Depth range [m]	Replicates (No. ind.)	Dry mass [mg]	Ind. respiration [nmol O_2 h^{-1} $ind.^{-1}$]	Mass-specific respiration [nmol O_2 h^{-1} mg^{-1} DM]	Stand. mass-specific respiration [nmol O_2 h^{-1} $ind.^{-1}$]
C. hyperboreus	f	0	13.7 ± 5.1	0	-1.8 / 3.5	0-1000	43 (43)	3.92 ± 1.44	46.6 ± 26.4	12.4 ± 7.5	14.3 ± 8.1
		4	16.3 ± 2.3	0	-1.7 / 4.3	0-1500	22 (23)	3.98 ± 1.38	55.4 ± 29.2	13.3 ± 6.4	15.9 ± 7.6
		6	11.9 ± 6.1	0	-1.4 / 9.3	0-50	6 (6)	4.28 ± 1.68	89.6 ± 49.5	20.1 ± 7.8	24.3 ± 10.0
		8	10.9 ± 4.1	0	-1.4 / 2.7	0-1500	22 (22)	4.42 ± 0.90	98.4 ± 26.8	23.2 ± 7.9	25.2 ± 7.8
		10	5.8	0	-1.6 / -1.3	0-50	3 (3)	3.35 ± 0.26	104.1 ± 18.9	30.9 ± 4.0	31.8 ± 4.5
		12	5	100	-1.7 / -1.5	0-50	2 (2)	5.28 ± 0.16	–	–	–
	C5	0	16.2 ± 5.9	0	-1.7 / 3.5	0-350	47 (52)	2.16 ± 0.89	24.6 ± 10.4	12.1 ± 4.6	13.6 ± 4.8
		4	16.0 ± 2.0	0	-1.7 / 2.8	0-1500	14 (14)	2.50 ± 1.00	33.4 ± 24.0	12.4 ± 6.3	14.9 ± 8.5
		6	25.5	0	–	1000-1500	6 (6)	1.80 ± 0.49	20.4 ± 5.0	11.4 ± 0.8	12.5 ± 1.0
		8	13.0 ± 2.6	0	-1.2 / 2.7	0-1500	16 (16)	2.19 ± 0.87	42.5 ± 16.1	20.4 ± 5.3	23.1 ± 5.7
		10	5.8	0	-1.7 / -1.2	0-50	4 (4)	2.52 ± 1.06	63.7 ± 13.9	27.4 ± 5.1	31.7 ± 3.4
		12	5	100	-1.7 / -1	0-50	5 (10)	1.97 ± 0.45	–	–	–
C. glacialis	f	0	16.6 ± 4.8	0	-1.8 / 3.5	0-320	25 (26)	1.50 ± 0.61	20.3 ± 7.7	14.9 ± 7.3	13.4 ± 6.01
		4	17.0 ± 3.9	0	-1.7 / 2.8	0-200	7 (11)	1.26 ± 0.10	27.5 ± 8.4	21.1 ± 5.3	18.9 ± 5.0
		6	18.3 ± 5.4	50	-1.4 / 1.9	0-50	4 (4)	1.37 ± 0.19	36.0 ± 6.4	26.4 ± 3.4	24.0 ± 3.1
		8	12.2 ± 5.1	8	-1.7 / 2.8	0-200	18 (26)	1.34 ± 0.25	40.8 ± 14.2	29.4 ± 8.8	24.1 ± 7.1
	C5	0	16.5 ± 6.1	0	-1.7 / 3.5	0-300	21 (26)	0.73 ± 0.34	13.5 ± 3.5	23.8 ± 12.5	19.3 ± 8.0
		8	9.8 ± 1.7	4	-1.6 / 2.8	0-200	5 (18)	1.13 ± 0.15	30.5 ± 2.4	26.4 ± 2.0	26.1 ± 1.3
		12	5	100	-1.6 / -1	0-50	1 (3)	1.13	–	–	–
C. finmarchicus	f	0	17.5 ± 1.8	5	0 / 6.7	50-100	7 (18)	0.44 ± 0.13	10.5 ± 2.7	24.4 ± 8.5	16.5 ± 5.10
		4	18.3 ± 0.5	0	1.4 / 5.8	0-100	6 (18)	0.38 ± 0.05	16.6 ± 2.6	44.7 ± 7.1	29.3 ± 4.4
		6	12.3 ± 2.3	0	4.6 / 9.3	0-500	14 (22)	0.26 ± 0.08	18.8 ± 5.3	89.7 ± 35.4	50.2 ± 15.9
		8	9.7 ± 0.4	0	4.6 / 7.9	0-500	5 (19)	0.32 ± 0.06	25.7 ± 9.2	75.6 ± 23.6	43.7 ± 13.7
	C5	0	20.9 ± 1.9	0	0 / 6.7	100-770	6 (9)	0.52 ± 0.06	7.5 ± 4.4	14.7 ± 8.2	11.9 ± 6.7
		4	15.5 ± 2.7	2	1.4 / 6.2	0-100	12 (42)	0.42 ± 0.11	7.4 ± 1.7	20.8 ± 7.7	15.2 ± 4.8
		6	8.5 ± 4.3	5	1.5 / 7.5	0-100	7 (21)	0.56 ± 0.13	11.8 ± 3.2	23.7 ± 8.4	18.7 ± 4.8
		8	11.0 ± 2.0	0	1.5 / 7.9	0-50	12 (39)	0.55 ± 0.18	21.8 ± 8.6	44.0 ± 18.8	34.8 ± 13.1
		10	6.8	0	3.4 / 4.2	100-200	3 (14)	0.38 ± 0.04	12.6 ± 1.7	33.3 ± 1.7	24.9 ± 1.7
P. glacialis	f	0	6.9 ± 4.4	8	-1.8 / 3.4	0-400	26 (26)	6.96 ± 1.62	87.8 ± 27.8	13.0 ± 4.1	13.5 ± 3.9
		4	16.0 ± 5.7	0	-1.7 / 1.4	0-1000	4 (4)	5.03 ± 0.63	62.3 ± 9.0	12.8 ± 3.1	11.7 ± 2.7
		8	11.8 ± 1.5	29	-1.5 / 2.8	0-500	5 (5)	4.51 ± 0.79	90.2 ± 22.3	20.0 ± 4.4	18.9 ± 4.2

(Continued)

TABLE 1 Continued

Species	Stage	Exp. temp. [°C]	Exp. run time [h]	Mort. [%]	*In situ* temp. min/max [°C]	Depth range [m]	Replicates (No. ind.)	Dry mass [mg]	Ind. respiration [nmol O$_2$ h^{-1} ind.$^{-1}$]	Mass-specific respiration [nmol O$_2$ h^{-1} mg^{-1} DM]	Stand. mass-specific respiration [nmol O$_2$ h^{-1} ind.$^{-1}$]
	C5	0	11.9 ± 5.3	14	-1.8 / 5.3	0-400	18 (19)	1.95 ± 0.74	36.1 ± 14.6	20.2 ± 9.5	19.9 ± 8.6
		4	19.6 ± 3.0	0	-1.7 / -1.5	0-50	4 (4)	1.76 ± 0.45	24.3 ± 7.0	14.6 ± 4.4	14.2 ± 3.7
		8	11.6 ± 1.4	0	-1.2 / 2.8	0-500	6 (6)	2.38 ± 1.00	43.4 ± 12.1	19.6 ± 4.9	20.3 ± 3.4
		10	6.8	50	-1.6 / -1.0	0-50	2 (2)	1.59, 1.68	38.4, 29.4	24.2, 17.5	23.4, 17.2
P. norvegica	f	0	14.7 ± 6.9	0	-0.6 / 8.8	100-770	13 (13)	4.53 ± 1.17	40.0 ± 10.9	9.5 ± 3.3	8.8 ± 2.8
		4	6.8 ± 1.7	0	-0.4 / 2.9	200-1000	5 (5)	5.30 ± 0.53	36.6 ± 7.8	7.1 ± 2.0	6.9 ± 1.8
		8	11.0 ± 2.4	0	0.6 / 3.1	200-850	4 (4)	5.20 ± 0.92	89.2 ± 23.0	17.4 ± 4.6	16.9 ± 4.3
	C5	0	21.3 ± 1.7	0	-1.5 / 9.4	0-320	6 (6)	1.93 ± 1.03	28.2 ± 5.7	20.6 ± 12.5	18.7 ± 9.4
		6	17.4	0	3.2 / 4.4	50-200	4 (4)	1.12 ± 0.39	35.2 ± 10.6	32.1 ± 6.8	28.1 ± 5.7
		8	9.5 ± 3.3	17	1.3 / 4.7	50-500	5 (5)	1.52 ± 0.54	48.8 ± 20.8	35.2 ± 17.0	32.7 ± 15.1
T. libellula		0	7.6 ± 1.9	36	-1.5 / 8.8	0-600	9 (9)	8.51 ± 8.89	162.4 ± 86.5	28.4 ± 13.5	25.5 ± 10.7
		4	2.7 ± 0.5	0	0.9 / 8.8	0-500	9 (9)	15.85 ± 9.37	437.5 ± 184.1	32.5 ± 11.0	36.9 ± 9.4
		6	5.7 ± 2.0	0	0.9 / 2.9	200-500	3 (3)	10.94 ± 4.83	285.5 ± 106.1	26.8 ± 3.2	29.2 ± 3.8
		8	4.3 ± 2.0	0	0.4 / 5.4	0-500	6 (6)	9.65 ± 7.40	309.2 ± 205.8	37.8 ± 12.1	36.9 ± 11.7
T. abyssorum		0	13.1 ± 8.0	9	-1.6 / 3.4	0-1500	26 (32)	4.24 ± 5.15	69.3 ± 76.3	20.4 ± 14.2	14.3 ± 8.0
		4	8.9 ± 3.5	0	-0.4 / 0.9	500-1000	8 (12)	2.91 ± 3.10	77.8 ± 70.9	23.1 ± 5.6	17.5 ± 4.1
		6	16.2	0	1.5 / 7.5	0-500	6 (6)	0.87 ± 0.17	32.6 ± 13.4	36.8 ± 14.1	21.9 ± 8.4
		8	6.3 ± 4.1	0	-1.2 / 2.7	0-1000	11 (13)	7.21 ± 6.85	220.4 ± 201.9	28.2 ± 7.1	26.2 ± 7.2

Data are given as mean values ± standard deviation. f, adult female; C5, copepodite stage C5; DM, dry mass; Exp. temp., Experimental temperature; Mort., Mortality.
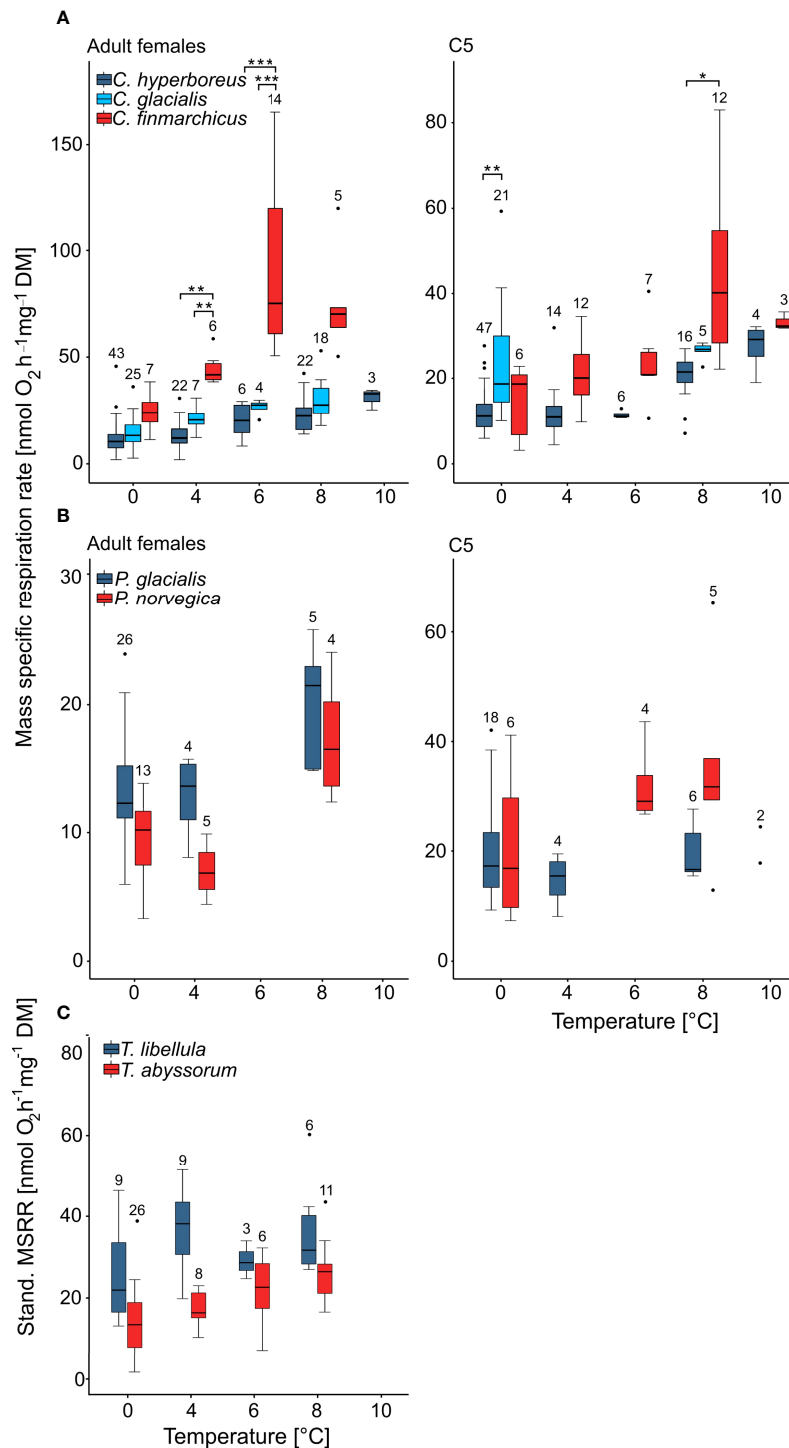
FIGURE 2
Mass-specific **(A, B)** and standardized mass-specific **(C)** respiration rates (Stand. MSRR) of polar-Arctic (blue) versus boreal-Atlantic (red) zooplankton species from Fram Strait. Stand. MSRR were used for *Themisto* species, as they had highly variable dry masses. Box represents the interquartile range (lower edge: 25th percentile, the upper edge: 75th percentile, central line: median, whiskers extend to minimum and maximum values within 1.5 times the interquartile range). Dots represent potential outliers that are above or below 1.5 times the interquartile range, respectively. Asterisks show significant differences in standardized respiration rates between species at the respective temperature (*p≤ 0.05, **p≤ 0.01, ***p≤ 0.001). Values above the boxplots show number of measurements. **(A)** *Calanus* spp., **(B)** *Paraeuchaeta* spp., **(C)** *Themisto* spp.
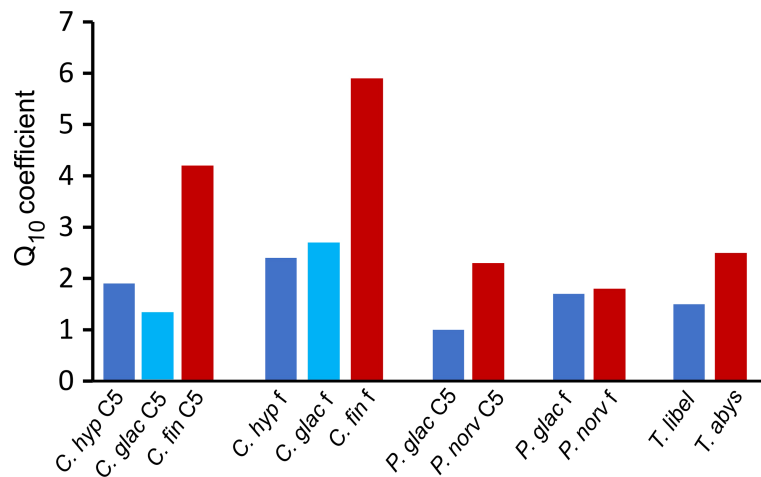
3.3 Mortality

Mortality of the species was generally low (Table 1). In *Calanus* species, survival of Arctic *C. hyperboreus* C5s and females was exceptionally high, with 100% at temperatures from 0 to 10°C (Table 1). Survival of the Arctic congener *C. glacialis* was 100% at lower temperatures (0 to 4°C). At 6°C mortality of females rose to 50% (mind the low number of replicates). At 8°C mortality was below 10% in females and C5s, respectively. During one experimental run at simulated ambient temperatures of 12°C with *C. hyperboreus* (females, C5) and *C. glacialis* (C5) mortality of both Arctic species was 100%. In contrast, boreal-Atlantic *C. finmarchicus* females and C5 experienced a low mortality (≤5%) at all temperatures. At temperatures ≥4°C (females) and ≥8°C (C5) survival was 100%.

In Arctic *Paraeuchaeta glacialis* the mortality of females and C5s was low (<15%) at temperatures below 8 and 10°C, respectively. At 8°C mortality increased to 29% in females and at 10°C to 50% in C5s (mind low number of replicates). In boreal-Atlantic *P. norvegica* survival rates were high. Mortality was only observed at 8°C in C5s (17%).

In both *Themisto* species mortalities were only observed at 0°C with 36% for *T. libellula* and 9% for *T. abyssorum* (Table 1).

4 Discussion

Between 1982 and 2017 the summer-mixed layer of the seasonally ice-free regions of the Arctic basin has warmed on average by 0.5°C per decade (Meredith et al., 2019), i.e. by more than 1.5°C in total. This warming trend is observable throughout various areas of the Arctic Ocean, e.g. in the warming of the Atlantic Water inflow (Beszczynska-Möller et al., 2012), in the northern Barents Sea (Lind et al., 2018) and even in the Deep Water of the Greenland Sea and Eurasian Basin (von Appen et al., 2015). With steadily increasing temperatures, it is expected that the Arctic community composition will shift towards an Atlantic regime (Chust et al., 2014; Fossheim et al., 2015). As polar zooplankton species are generally bigger and accumulate larger lipid stores (Kattner and Hagen, 2009), a shift in species composition towards smaller, less lipid-rich Atlantic congeners negatively affects food quality for higher trophic levels, with consequences for food-web structure and energy flux in the entire Arctic ecosystem (Møller and Nielsen, 2020). In the current study we discuss species-specific temperature tolerances and performance ranges of Arctic and co-occurring boreal-Atlantic zooplankton species to elucidate mechanisms causing the ongoing regime shifts.

4.1 Evidence against Arctic stenothermy

During our experiments, all Arctic species generally survived up to rather high temperatures of 10°C. Polar zooplankton species showed a slow increase in their metabolic rates, also emphasized by low Q_{10} values, which is contradicting the expected pattern for typical stenotherm species, i.e. a rapid increase of respiration, followed by a narrow optimum and a sharp decline (high Q_{10}, Pörtner et al., 2017). Hence, our first hypothesis of polar stenothermy in these Arctic species has to be rejected. At one experimental run conducted at 12°C, the mortality of *Calanus glacialis* and *C. hyperboreus* was high,

suggesting that this temperature is close to their lethal limit. Similar or even higher (15°C) critical temperatures were reported for both Arctic *Calanus* species by Hirche (1987) for short-term non-feeding experiments with individuals from the Greenland Sea and Hildebrandt et al. (2014) for long-time feeding experiments with specimens from Fram Strait.

The hypothesis of polar stenothermy, i.e. the inability of polar species to cope with a broader temperature range in polar species, was mainly based on experiments with invertebrates and fishes from the Southern Ocean (Pörtner et al., 2007; Peck et al., 2010; Sandersfeld et al., 2015). In contrast to the Antarctic, the Arctic Ocean cold-water ecosystem is comparably young and much less isolated (Buchholz et al., 2012); thus, Arctic species may be subjected to a much higher variability of temperatures than their southern counterparts (Pörtner et al., 2007). During the present study, *in situ* water temperatures ranged from -1.8 up to 9.3°C for Arctic zooplankton species (Table 1), with higher abundances usually between -1.8 and 3.5°C. Distributional ranges of Arctic *Calanus* species extend from Norwegian fjords and the Gulf of Maine, USA, to the high Arctic. Hence, they cover a wide ambient temperature range from -2 to 8°C (Hirche and Niehoff, 1996; Niehoff and Hirche, 2005), suggesting robustness and adaptive mechanisms to cope with such variable temperatures.

4.2 Mass-specific respiration

Contradictory to our second hypothesis, larger Arctic *Paraeuchaeta glacialis* and *Themisto libellula* had higher MSRR at each temperature compared to their smaller Atlantic congeners *P. norvegica* and *T. abyssorum*, respectively (except *Paraeuchaeta* C5 at 8°C). For larger specimens, the experimental setup may not have been optimal, possibly due to increased stress in the relatively small incubation bottles. Closed-system incubations of larger specimens may also result in rapid depletion of dissolved oxygen concentrations with additional stress. To exclude that stressed large individuals were responsible for higher MSRR, we checked for species-specific correlation between dry mass and MSRR. For *T. libellula*, expected trends were observed, i.e. smaller individuals having higher MSRR than larger ones. Further, smaller-sized *T. libellula* with comparable dry mass to *T. abyssorum* generally had higher MSRR. Measured rates of *T. libellula* were within the reported range (Auel and Werner, 2003; Darnis et al., 2017). It is, thus, unlikely that the higher rates were due to handling stress and/or oxygen deficits.

Although further proof is necessary, our results suggest a metabolic adaptation to the cold environment in those polar-Arctic zooplankton species. This is indicated by oxygen consumption, and thus metabolic activity, being generally higher in species of Arctic *Themisto* and *Paraeuchaeta* compared to their Atlantic congeners (see Sandersfeld et al., 2017 for higher metabolic rates in Antarctic fish). The concept of

metabolic cold adaptation postulates that polar ectotherms have elevated metabolic rates compared to temperate species, as metabolic costs are higher at low temperatures. It is, however, one of the more controversially discussed hypotheses in polar ecophysiology (Peck and Conway, 2000).

4.3 Performance of Arctic versus Atlantic zooplankton

Aerobic respiration reflects an organism's current demand of energy (Clarke, 2003). At 0°C, Arctic and Atlantic *Calanus* species showed the same ranges of mass-specific respiration rates (MSRR) in the present study, suggesting similar requirements. However, with increasing temperatures, the rise in MSRR differed significantly between Arctic and Atlantic *Calanus* species. While the MSRR of Arctic *C. glacialis* and *C. hyperboreus* showed only a slow increase (Q_{10} between 1.3 and 2.7), the MSRR of boreal-Atlantic *C. finmarchicus* increased much more rapidly (Q_{10} 4.2 and 5.9).

A steep increase in respiration rates could be either stress-related or due to higher metabolic activity (e.g. growth, reproduction, digestion). *C. finmarchicus* is usually found in highest abundances in temperatures from 0 to 10°C (Bonnet et al., 2005; Strand et al., 2020), but occurrences in waters <0°C and ≥15°C have also been documented (Hirche, 1990; Turner et al., 1993; Bonnet et al., 2005). *In situ* temperatures for *C. finmarchicus* (0 to 9°C) during the present study were within the range of experimental temperatures. Absence of thermal stress is further supported by low mortality rates at high temperatures in the present and similar studies (Hirche et al., 1997). Physiological performances of *C. finmarchicus* at higher temperatures show that this boreal-Atlantic species is thriving with increasing temperatures. For instance, growth, egg production and feeding rates steadily increase with increasing temperatures (measurements from -1.5 to 15°C; Hirche et al., 1997; Campbell et al., 2001; Pasternak et al., 2013; Smolina et al., 2015), emphasizing a higher energy demand due to higher performance rates.

Adaptation to higher temperatures is further supported by gene regulation, as *C. finmarchicus* down-regulates proteins that are associated with thermal stress response at 5 and 10°C (Smolina et al., 2015), which indicates the absence of stress within this temperature range. In contrast to these performance experiments, specimens were not fed in the present study. Therefore, a stress-related increase in metabolic activity due to starvation cannot be completely ruled out. However, starvation generally did not last longer than a couple of days, suggesting that internal reserves could have been utilized to maintain a high metabolism. Especially C5 individuals had large lipid reserves due to the imminent diapause (mean lipid content >40% DM). To exclude that elevated metabolic rates in *C. finmarchicus* were stress-related at higher temperatures during starving conditions, additional studies are needed.

The weak response in MSRR of Arctic *Calanus* species suggests that they do not experience a distinct increase in their energy demand, neither for metabolic processes nor for a thermal stress response. Apparently, they cannot benefit from higher temperatures with an increase in their performance. The increase in respiration rates in *C. glacialis* and *C. hyperboreus* could solely be due to a passive response (Havird et al., 2020) and, thus, indicates a reduced sensitivity of metabolic processes to temperature. Indeed, our results are supported by a study on the genetic activity of fed *C. glacialis*, which showed no response in up- or down-regulation of protein expression with increasing temperatures from 0 to 10°C during short- and long-term experiments (Smolina et al., 2015).

Our results and the findings by Smolina et al. (2015) on genetic regulation in *C. glacialis* emphasize the absence of a thermal stress response in Arctic *Calanus*. For species inhabiting cold environments, several studies suggest that they accumulate heat shock proteins at a constant level to compensate for the damage associated with protein folding at low temperatures (Buckley et al., 2004; Place et al., 2004; Place and Hofmann, 2005; Huenerlage et al., 2016). This adaptation to cold temperatures results in a loss of thermal sensitivity of genes that encode such thermal stress proteins due to constantly high gene expression (Buckley et al., 2004).

Although respiration rates and genetic activity are not affected by rising temperatures in Arctic *Calanus* species, their physiological performances are reduced at higher temperatures. This has been shown for decreasing assimilation efficiency (experiments with *C. glacialis* up to 10°C; Grote et al., 2015), declining egg production rates (above 5°C for *C. glacialis*; Pasternak et al., 2013) and depression of gonad maturation (at 10°C for *C. hyperboreus*; Hildebrandt et al., 2014). The performance losses observed in Arctic *Calanus* species can be explained by a reduction of available energy associated with a decline in aerobic scope, as the pejus temperature is approached.

Hence, with increasing temperatures, Arctic zooplankton species may already reach their pejus temperature, while boreal-Atlantic congeners might still have sufficient energy available for their performance and fitness. High basal metabolic rates, as observed for boreal-Atlantic species in the current study, allow for a greater absolute aerobic scope, and thus a more active lifestyle (Clarke, 2003). Temperatures around 5 to 6°C apparently mark a threshold at which *C. finmarchicus* may outcompete its Arctic congeners (Henriksen et al., 2012; Kjellerup et al., 2012; Jung-Madsen and Nielsen, 2015). This is in line with our results of a much higher increase in metabolic activity at 4 to 6°C in *C. finmarchicus* than in the Arctic *Calanus* species. Thus, the Atlantification of Arctic zooplankton communities might be driven rather by ecological interactions, biological fitness and reproductive potential at higher ambient temperatures than by absolute physiological temperature limits, stenothermy and lower resilience against rising temperatures.

In conclusion, our third hypothesis, stating that the main driving force of the Atlantification would be physiological limits of Arctic species owing to increasing temperatures, has to be rejected. Additional experiments are necessary to exclude that those higher metabolic rates of Atlantic species were a stress response and long-term monitoring of community dynamics in regions of co-occurrence are essential to observe the consequences of different metabolic adaptations.

In the current study, we discussed direct physiological responses of Arctic versus boreal-Atlantic zooplankton species to rising temperatures, suggesting a higher competitive ability of Atlantic species with increasing temperatures due to higher metabolic activity. Yet, the Arctic Ocean is a harsh environment, which requires efficient adaptation. For instance, Arctic *Calanus*, especially *C. hyperboreus*, are able to start reproducing early in the year before sea-ice break-up, prior to the onset of a phytoplankton bloom, relying on internal energy reserves (Daase et al., 2021). Arctic *Calanus* species therefore have a competitive advantage over boreal *C. finmarchicus* in regions with strongly pulsed primary production regimes (Hatlebakk et al., 2022a, Hatlebakk et al., 2022b).

However, due to climate change, environmental conditions in the Arctic Ocean are shifting more and more to boreal regimes. The earlier sea-ice retreat and associated earlier phytoplankton production may result in increasing habitat suitability for boreal species and may further facilitate the successful establishment of boreal-Atlantic zooplankton populations in the Arctic Ocean (Freer et al., 2021). Indeed, Tarling et al. (2022) found first evidence of locally recruiting *C. finmarchicus* in Fram Strait, indicating that the system is becoming more suitable for boreal species.

At the same time, recent studies show that the shrinking of sea-ice cover results in a northward shift in the core distribution of *C. hyperboreus* and *C. glacialis* (Ershova et al., 2021) and in a mismatch between ice algae production and *Calanus* recruitment (Dezutter et al., 2019), adding to the factors that possibly decrease the competitive ability of Arctic zooplankton species.

A future Arctic ecosystem comprising boreal zooplankton communities with higher Q_{10} values may result in a system of higher metabolic activity, and thus a shift to a regime with higher turnover rates (Renaud et al., 2018). Individual size and lipid content of zooplankton species may generally become smaller and life cycles shorter, however, due to the faster growth and higher reproduction rates of boreal species, the future Arctic may be more efficient (Renaud et al., 2018). Yet, in a future Arctic scenario, highly prey-selective predators, such as little auks or young polar cods, will have to adapt to smaller and less energy-rich prey, or they will perish.

The present study demonstrates that, besides physiological effects, knowledge about complex ecological interactions is essential for a better understanding of global change implications on marine communities and ecosystems. These interactions should be included in models to develop realistic

and reliable predictive capacities. This is especially important in the Arctic, where the Atlantification of the Arctic fauna is accompanied by the strong alternation of the environment. The loss of sea-ice and associated ice algal primary production results in drastic changes in habitat suitability, plankton phenology and overall productivity, affecting the entire Arctic marine ecosystem.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

HA and PK conducted the fieldwork. PK analyzed the samples and conducted the data analyses. PK drafted the manuscript. PK, WH, MB-D, and HA significantly contributed to improving the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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