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RESEARCH ARTICLE

Northern shrimp from multiple origins show similar sensitivity to global change drivers, but different cellular energetic capacity

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ABSTRACT

Species with a wide distribution can experience significant regional variation in environmental conditions, to which they can acclimatize or adapt. Consequently, the geographic origin of an organism can influence its responses to environmental changes, and therefore its sensitivity to combined global change drivers. This study aimed at determining the physiological responses of the northern shrimp, *Pandalus borealis*, at different levels of biological organization and from four different geographic origins, exposed to elevated temperature and low pH to define its sensitivity to future ocean warming and acidification. Shrimp sampled within the northwest Atlantic were exposed for 30 days to combinations of three temperature (2, 6 or 10°C) and two pH levels (7.75 or 7.40). Survival, metabolic rates, whole-organism aerobic performance and cellular energetic capacity were assessed at the end of the exposure. Our results show that shrimp survival was negatively affected by temperature above 6°C and low pH, regardless of their origin. Additionally, shrimp from different origins show overall similar whole-organism performances: aerobic scope increasing with increasing temperature and decreasing with decreasing pH. Finally, the stability of aerobic metabolism appears to be related to cellular adjustments specific to shrimp origin. Our results show that the level of intraspecific variation differs among levels of biological organization: different cellular capacities lead to similar individual performances. Thus, the sensitivity of the northern shrimp to ocean warming and acidification is overall comparable among origins. Nonetheless, shrimp vulnerability to predicted global change scenarios for 2100 could differ among origins owing to different regional environmental conditions.

KEY WORDS: Ocean warming, Ocean acidification, Comparative physiology, Aerobic performance, *Pandalus borealis*, Conservation

INTRODUCTION

Latitudinal gradients of environmental parameters promote large-scale physiological variation among species, with populations from species with a wide distribution likely experiencing a broad range of various regional and local environmental conditions (Addo-Bediako et al., 2000; Lardies et al., 2014; Orr et al., 2005). This may lead to acclimatization or adaptation of organisms to prevalent environmental conditions, but macrophysiological studies addressing this topic at the population level are scarce (Chown et al., 2004; Gaston et al., 2009; Koeller et al., 2009). Local adaptation can be advantageous as it limits the costs linked to plasticity by aligning average performances of organisms to the environmental optimum, ultimately maximizing their fitness (Kawecki and Ebert, 2004). However, local adaptation can sometimes be disadvantageous as organisms can reach the limits of their plastic capacity, and thus be more sensitive to future rapid environmental changes (Calosi et al., 2016). Indeed, although inter-individual variation promotes allostasis to environmental changes, resistance to extinction risk and even range expansions in newly colonized environments (Forsman and Wennersten, 2016), low intraspecific phenotypic variation suggests a low ability for further adaptation based on the selection of existing phenotypes (Calosi et al., 2016, 2013; Sunday et al., 2014). Moreover, long-term acclimatization and adaptation can influence population responses to changes in global environmental conditions, such as increasing temperature and increasing P_{CO_2}/decreasing pH (Bozinovic et al., 2011; Darnell and Darnell, 2018; Gaston et al., 2009; Hollarsmith et al., 2020; Lardies et al., 2014; Sorte et al., 2011). The variation in the physiological responses of populations to temperature changes is of particular interest within the context of ongoing ocean warming (OW) (IPCC, 2022). Acclimatization and adaptation have also been shown to shape the responses of multiple populations to future ocean acidification (OA) (Calosi et al., 2017; Pespeni et al., 2013; Thor et al., 2018; Vargas et al., 2017). We have a relatively solid understanding of the physiological variation among populations to OW and OA in isolation. However, very few studies have investigated the potential influence of acclimatization and adaptation on the physiological response of populations to these combined drivers, which will co-occur as a result of global ocean change (e.g. Leung et al., 2021; Rivest et al., 2017). Consequently, it is paramount to address the various responses among populations of a same species to combined OW and OA, which are ultimately responsible for defining the overall sensitivity of a species, particularly for those species declining under global changes. As shown in the common periwinkle, *Littorina littorea* (Calosi et al., 2017), populations closer to the edges of their species' distribution range are often more sensitive to global changes compared with central populations (Kolzenburg, 2022). This can be due to the limited adaptive ability of marginal populations as a consequence of their lower genetic diversity, or to their lower population density, which is itself linked to living under less favourable environmental conditions (Kolzenburg, 2022).

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Many species are already declining owing to the negative effects of global change drivers. For example, as a consequence of the increase in seawater temperature, the Israeli population of the purple sea urchin (*Paracentrotus lividus*) collapsed in the early 2000s (Yeruham et al., 2015), and the blue mussel (*Mytilus edulis*) recruitment has been declining every year in the northwest Atlantic over the last two decades (Petraitis and Dudgeon, 2020). Also, in the northwest Atlantic in the past 15 years, the abundance of the northern shrimp (*Pandalus borealis*) has fluctuated or remained stable in the northern fishing areas (DFO, 2021a), but drastically declined in the southern regions (e.g. Gulf of Maine, Estuary and Gulf of St Lawrence, Newfoundland and Labrador; DFO, 2021a, 2022a; Hunter et al., 2021). These declines may also be related to increasing predator pressure and changes in phenology, but are most likely linked to direct environmental changes, including OW (Richards and Hunter, 2021). For instance, for the last few decades, both surface and bottom waters have warmed in the Gulf of Maine, negatively impacting recruitment and settlement of shrimp (Richards and Hunter, 2021). This appears to have led to the shrimp stock collapse in the Gulf of Maine that raised the urgent need of a fishery moratorium, established in 2013 (Whitmore et al., 2013).

Considering the unprecedented decline of shrimp stocks, its broad circumpolar distribution and the contrasting regional environmental conditions it experiences, *P. borealis* is an ideal candidate species for examining the relevance of using intraspecific variation in the response to global change drivers to define a species' sensitivity. Being a cold-water species, the thermal window of preference of *P. borealis* spans from 0 to 5°C (Shumway et al., 1985) and OW has been shown to negatively impact both larvae and adults (Arnberg et al., 2013; Brillon et al., 2005; Chabot and Ouellet, 2005; Chemel et al., 2020; Daoud et al., 2010, 2007; Dupont-Prinet et al., 2013; Ouellet and Chabot, 2005). Shrimp larvae have also been shown to be sensitive to OA, whereas adults seem to better tolerate it (Arnberg et al., 2013; Bechmann et al., 2011; Chemel et al., 2020; Hammer and Pedersen, 2013). Nonetheless, the sensitivity of both larvae and adults to OW and OA may vary along the species distribution range under the influence of the potential local acclimatization or adaptation to different regional environmental conditions throughout the North Atlantic (Koeller et al., 2009; Ouellet et al., 2017). Indeed, along the east coast of Canada and outside the St Lawrence system, shrimp are most abundant in deep waters characterized by ~0–3°C and ~7.8–8 pH units, whereas in the Estuary and Gulf of St Lawrence, shrimp are most abundant at depths at which temperatures are higher and pH levels are lower (~4–7°C, ~7.6 pH units) (Bourdages et al., 2022; Cyr et al., 2022; DFO, 2021b, 2022b,c). In this context, our study aimed at determining the level of intraspecific variation in physiological responses of female shrimp, the life stage targeted by the fishery, exposed to future OW and OA conditions at multiple levels of biological organization and from different geographic origins, to understand the potential contribution of acclimatization and local adaptation in defining the species' sensitivity. For each geographic origin, survival, whole-organism aerobic performance and cellular energetic capacity were estimated. Based on our current understanding of larval potential adaptation in the Estuary and Gulf of St Lawrence and adult sensitivity to ocean global change drivers, we hypothesize that shrimp from different geographic origins will show different levels of sensitivity at the whole-organism and cellular levels when exposed to isolated and combined OW and OA conditions.

MATERIALS AND METHODS
Specimen collection, transport and maintenance
Female shrimp (*Pandalus borealis* Krøyer 1838) were collected between 2018 and 2019 from four different geographic origins within the northwest Atlantic: St Lawrence Estuary (SLE, 48°35′N, 68°35′W; May 2018), Eastern Scotian Shelf (ESS, 45°23′N, 61°04′W; February 2019), Esquiman Channel (EC, 50°44′N, 57°29′W; July 2019) and Northeast Newfoundland Coast (NNC, 50°18′N, 54°16′W; November 2019) (Fig. 1). Specimens from SLE were fished with a rigid-frame trawl, those from EC and NNC were collected by fishers with commercial shrimp trawls, whilst specimens from ESS were collected by fishing traps. After collection, shrimp were held in 750-liter tanks filled with cold (2–3°C), well-oxygenated seawater and transported to the Maurice-Lamontagne Institute (MLI), Fisheries and Oceans Canada (Mont-Joli, QC, Canada). Here, shrimp were kept for approximately 8 weeks in rectangular rearing tanks (1700 liters) before the beginning of each experiment to reduce some of the potential physiological variability linked to differences in collection times, while maintaining long-term acclimatization or adaptation signals. Experiments were performed during August 2018 for shrimp from SLE and April, September and December 2019 for shrimp from ESS, EC and NCC, respectively. Maintenance of shrimp from all geographic origins was similar to that detailed for shrimp from the SLE in Chemel et al. (2020). Average conditions during this period were 4.5°C, pH 7.9 (total scale, pH_T), 100% O_2 saturation relative to air and salinity 32. Shrimp were fed *at libitum* three times a week with capelin (*Mallotus villosus*) and shrimp (*Pandalus* spp.), and uneaten food was removed after 24 h to ensure high water quality levels.

Experimental design, setup and system monitoring
To determine the effects of isolated and combined seawater temperature and pH on the survival and physiology of shrimp, we employed an orthogonal experimental design. Three levels of seawater temperature were chosen: (1) 2°C, a favourable temperature for this species (Shumway et al., 1985), (2) 6°C, the recent (1990–2021) temperature of shrimp habitat in the Gulf of St Lawrence (5–7°C; Bourdages et al., 2022), also corresponding to a +4°C increase scenario predicted globally for the end of the century (RCP 8.5 scenario; IPCC, 2014) for other origins, such as ESS and NNC; and (3) 10°C, representing predicted conditions at the end of the century for shrimp of the Gulf of St Lawrence (Lavoie et al., 2020). Two levels of pH were selected: (1) pH 7.75, based on the current conditions of the deep waters of the Estuary and Gulf of St Lawrence (Mucci et al., 2018, 2011) and a −0.3/–0.4 pH unit decrease scenario predicted to occur in the northwest Atlantic by the year 2100 (RCP 8.5 scenario; IPCC, 2014), and (2) pH 7.40, representing predicted conditions at the end of the century in the Estuary and Gulf of St Lawrence bottom waters (RCP 8.5 scenario; IPCC, 2014).

Treatments were identified as: low temperature and current pH (2C: 2°C, pH 7.75), low temperature and low pH (2A: 2°C, pH 7.40), intermediate temperature and current pH (6C: 6°C, pH 7.75), intermediate temperature and low pH (6A: 6°C, pH 7.40), elevated temperature and current pH (10C: 10°C, pH 7.75), and elevated temperature and low pH (10A: 10°C, pH 7.40), for a total of six treatments with two replicate tanks per treatment.

The regulation and monitoring of temperature and pH in the experimental setup was described in Chemel et al. (2020). Briefly, a 1/16 DIN Micromega autotune PID Temperature controller (Omega Engineering Inc., Norwalk, CT, USA) regulated the automatic
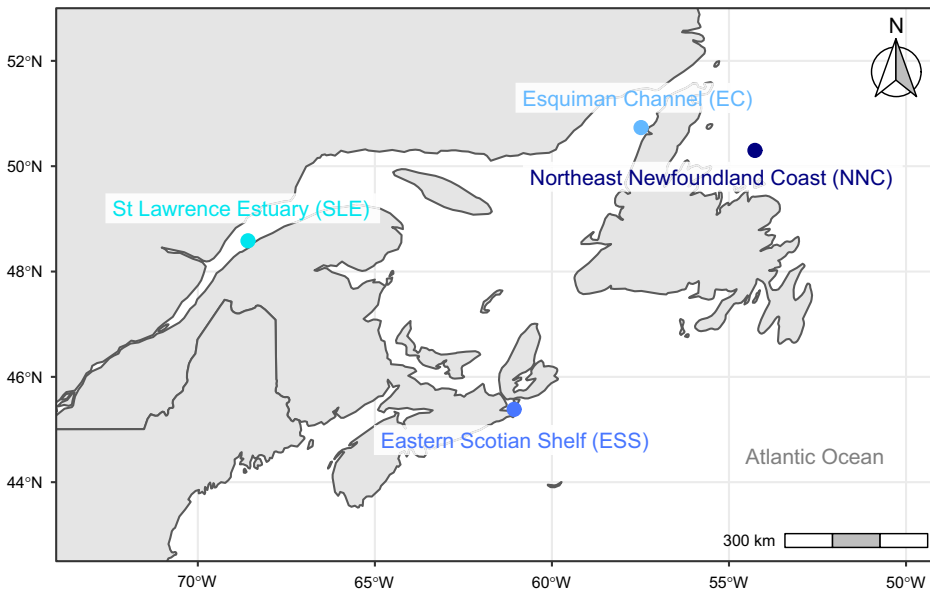
Fig. 1. Map representing the collection sites of female northern shrimp (*Pandalus borealis*) in the northwest Atlantic. The four geographic origins are the St Lawrence Estuary (SLE, azure), Esquiman Channel (EC, light blue), Eastern Scotian Shelf (ESS, blue) and Northeast Newfoundland Coast (NNC, dark blue).

mixing of cold and hot water to provide each tank with seawater at the set temperature, whereas an Aquastar (IKS ComputerSysteme GmbH, Karlsbad, Germany) controlled the injection of pure gaseous CO_2 into each tank's gas exchange column to maintain pH levels. Environmental parameters were monitored daily with handheld multimeters in each tank throughout the duration of each experiment. Carbonate chemistry parameters were calculated weekly, based on pH and alkalinity measurements, using the R package seacarb (http://CRAN.R-project.org/package=seacarb). Mean±s.d. physico-chemical parameters for the duration of the 30-day experiment are summarized in Table S1.

Experimental protocol

At the beginning of each experiment, approximately 60 non-ovigerous females were randomly assigned to one of the 12 tanks composing the experimental setup. The experimental tanks were gradually adjusted over 4 days until treatment values were reached, and shrimp were exposed for a total of 30 days. The number of live shrimp was recorded daily to determine survival rate. Over the exposure period, shrimp were fed the same way as during their maintenance period, and they were fasted at day 23 to avoid energy demands related to food ingestion (specific dynamic action, SDA) during the following metabolic rate determination. The duration of the fasting period was judged sufficient because even at 2°C, when digestion is the slowest, oxygen uptake was elevated owing to a combination of oxygen debt payment following chasing, handling stress and possible SDA for less than 24 h after introducing shrimp into the respirometers. On day 28 of exposure, five individuals per tank (10 per treatment) were haphazardly selected for metabolic rate determination. They were transferred to an 'exhaustion tank', where they were first chased to exhaustion and then exposed for 1 min to air to further increase their oxygen debt (method modified from Roche et al., 2013). They were then rapidly and carefully transferred into individual respirometers for the metabolic rate determination by measuring oxygen uptake ($\dot{M}_{O_2}$, in mg O_2 h^{-1} g^{-1}) via intermittent-flow respirometry (Steffensen, 1989; Svendsen et al., 2016) (see the following section and Supplementary Materials and Methods for details). At day 30, shrimp were removed from their respirometers, gently blotted with tissue paper and weighed on a digital scale (Mf-300, A&D Company, Tokyo, Japan; ±0.001 g) to determine wet mass (WM). Shrimp were then rapidly dissected on ice and the

abdomen muscle was sectioned into three equal parts (approximately 1 g each) and flash-frozen in Eppendorf tubes in liquid nitrogen to instantly interrupt all biochemical reactions. Samples were then stored at −80°C pending analyses.

Metabolic traits

To determine shrimp whole-organism responses to isolated and combined seawater temperature and pH, standard and maximum metabolic rate (SMR and MMR, respectively) were estimated individually from oxygen uptake measurements and used to calculate aerobic scope (AS=MMR–SMR) (Chabot et al., 2016a, b; Fry, 1971, 1947; Norin and Clark, 2016). We report the detailed description of respirometry method and setup and the determination of metabolic traits in Supplementary Materials and Methods and Table S2, as suggested by Killen et al. (2021).

Cellular energetic capacity

To determine the effect of isolated and combined seawater temperature and pH on the cellular energetic capacity of shrimp, we measured the activity of enzymes involved in the aerobic and anaerobic pathways of the abdominal tissue and calculated their ratio. Specifically, we measured citrate synthase (CS), cytochrome C oxidase (COX) and lactate dehydrogenase (LDH) enzyme activity as proxy for mitochondrial density (Moyes et al., 1997; Rabøl et al., 2006), for aerobic metabolic capacity (Marie et al., 2006) and for anaerobic metabolic capacity (Farhana and Lappin, 2021), respectively. We then calculated the ratios of CS to LDH activities, COX to LDH activities as expressions of metabolic phenotype, and CS to COX activities as expression of mitochondrial morphology. Details of the protocol for sample preparation can be found in Supplementary Materials and Methods.

Statistical analyses

Mixed-effect models (lmerTest package, Kuznetsova et al., 2017; and lme4 package, Bates et al., 2015) were used to test the effects of isolated and combined seawater temperature and pH, and geographic origin (fixed factors) on shrimp survival, metabolic traits and cellular energetic capacity, with replicate tank as a random variable. Survival rates were arcsin-square-root-transformed as required (Sokal and Rohlf, 1995). Mass-specific metabolic traits and WM were $\log_{10}$ transformed to meet the assumption of linearity.

Log_{10} WM was used as a covariate for analyses of mass-specific metabolic traits. Log_{10} WM had a significant effect on log_{10} SMR, log_{10} MMR and log_{10} AS. Considering that the random term 'tank' was never found to be significant, it was removed from the analyses. Thus, ANCOVAs were performed on log_{10} SMR, log_{10} MMR and log_{10} AS, and ANOVAs were performed on enzyme activities and their ratios (lmTest package, https://cran.R-project.org/web/packages/lmtest/lmtest). Tukey HSD tests (Hothorn et al., 2008) were used to conduct *post hoc* analyses when significant effects were found for main factors in absence of interactions. Alternatively, general linear hypotheses tests (multcomp package, Bretz et al., 2016) were used to conduct *post hoc* analyses on selected comparisons when significant interactions were evidenced in order to increase the power of the analysis and focus on comparisons relevant for our study. Specifically, we compared: (1) means at different temperatures for the same origin and means of different origins at the same temperature when the interaction between temperature and origin was found to be significant; (2) means at different temperatures for the same pH and means at the two pH levels at the same temperature when the interaction between temperature and pH was found to be significant; and (3) means of different origins at the same pH and means at the two pH levels for the same origin when the interaction between origin and pH was found to be significant. *P*-values were adjusted for multiple comparisons using the Holm method. Normality of residuals was verified using the Shapiro–Wilk test, whereas homoscedasticity was verified using the Brown–Forsythe test. Most data met the assumptions of normality and homoscedasticity without transformation or following log_{10} transformation, except for log_{10} AS and CS. However, we considered our analysis to be tolerant to deviations from the assumptions of normality and heteroscedasticity given our level of replication and structure of the experimental design used (Sokal and Rohlf, 1995; Underwood, 1997). Additionally, statistical (R package DHARMa, https://CRAN.R-project.org/package=DHARMa) and visual analyses of the residuals were performed to confirm the appropriateness of the models used.

Pearson's correlations between total and specific activity were calculated for all enzymes. Both measures of activity were significantly correlated for all enzymes measured in shrimp abdominal muscle for each origin (*R* between 0.56 and 0.98 depending on the enzyme and the origin, *P*<0.001 for all analyses), so only specific activity data are presented.

All the statistical analyses were performed using the software R 3.6.3 version (https://www.r-project.org/).

RESULTS
Survival
Mean survival rates decreased significantly at the highest temperature and at the low pH level tested (Table S3). In detail, mean survival was significantly lower at 10°C (approximately 77%) than at 2 and 6°C (approximately 92% and 88%, respectively), with the two colder temperatures being comparable to each other (Fig. 2A). In addition, a significant decrease of approximately 5% in mean survival was observed at low pH (Fig. 2B). Finally, shrimp from different origins showed comparable survival rates and none of the interactions were found to have a significant effect on survival (Table S3).

Metabolic traits
Standard metabolic rate (SMR)
Mean SMR increased differently with increasing temperature for shrimp from different origins, as indicated by the presence of a
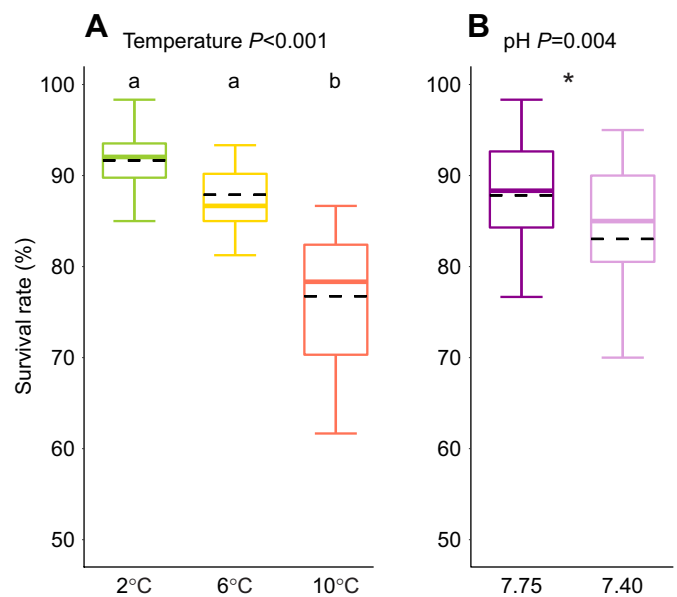

Fig. 2. The effects of exposure to isolated and combined seawater temperature and pH over 30 days on mean survival rate (%) of female northern shrimp *P. borealis*. Solid lines represent the median and dashed lines represent the mean. (A) Temperature treatments: 2°C (yellow), 6°C (green) and 10°C (red). Different lowercase letters indicate the presence of a significant difference (*P*<0.05) among temperature treatments. (B) pH treatments: 7.75 (purple) and 7.40 (light purple). The asterisk indicates the presence of a significant difference (*P*<0.05) between the two pH treatments. No significant differences among origins were found.

significant interaction between temperature and origin (Table S3, Fig. 3A). Specifically, for shrimp from all origins, mean SMR increased with increasing temperature along a linear trend, with the exception of shrimp from EC which showed an increase in mean SMR only between 2 and 6°C (Fig. 3A). In addition, mean SMR values of shrimp from different origins measured at the same temperature differed significantly at all temperatures tested (Fig. 3A). Specifically, mean SMR of shrimp from SLE were significantly higher than those of NNC, and among the highest, at all temperatures tested (Fig. 3A). Furthermore, the interaction between temperature and pH was found to be significant (Table S3) Mean SMR increased with increasing temperature within the same pH treatment (average increase of approximately 84% from 2 to 10°C), at both pH levels tested (Fig. 3B) and was comparable between the two pH levels tested at all temperatures (Fig. 3B), as the multiple comparisons tests for mean SMR values between different pH levels (at the same temperature) failed to detect significant differences.

Additionally, mean SMR of shrimp from different origins measured at the same pH level differed significantly at the lowest pH tested only, as indicated by the presence of a significant interaction between origin and pH (Table S3, Fig. 3C). Specifically, mean SMR of shrimp from EC and NNC differed significantly from each other, being the highest (0.063 O_2 h^{-1} g^{-1}) and lowest (0.049 O_2 h^{-1} g^{-1}), respectively, whilst both being comparable to mean SMR of SLE and ESS shrimp (Fig. 3C). Mean SMR of each origin was comparable between the two pH levels tested (Fig. 3C), as the multiple comparisons tests for mean SMR values between different pH levels (for the same origin) failed to detect significant differences.

Finally, no effect of the interaction among temperature, pH and origin was found to be significant for this trait.
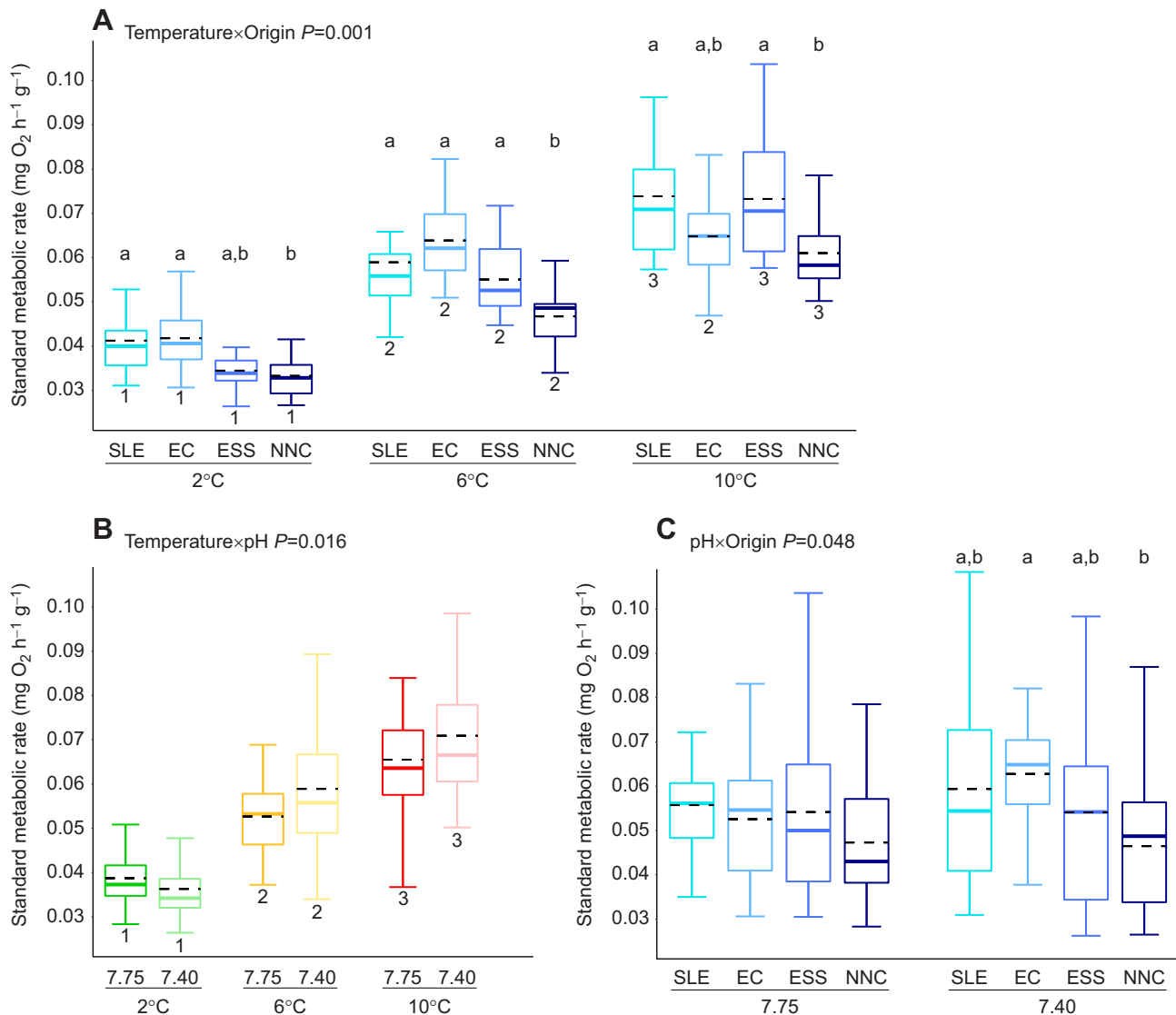
Fig. 3. The effects of exposure to isolated and combined seawater temperature and pH over 30 days on mean standard metabolic rate of female northern shrimp, *P. borealis,* from different origins. Solid lines represent the median and dashed lines represent the mean. (A) Treatments: temperatures (2, 6 and 10°C) and origins: SLE (azure), EC (light blue), ESS (blue) and NNC (dark blue). Different numbers indicate the presence of a significant difference (*P*<0.05) among temperature treatments for the same origin, and different lowercase letters indicate the presence of a significant difference (*P*<0.05) among origins at the same temperature treatment. (B) Treatments are: 2C (2°C, pH 7.75, green), 2A (2°C, pH 7.40, light green), 6C (6°C, pH 7.75, yellow), 6A (6°C, pH 7.40, light yellow), 10C (10°C, pH 7.75, red) and 10A (10°C, pH 7.40, light red). Different numbers indicate the presence of a significant difference (*P*<0.05) among temperature treatments at the same pH treatment. (C) Treatments: pH (7.75 and 7.40) and origins (SLE, ESS, EC and NNC). Different lowercase letters indicate the presence of a significant difference (*P*<0.05) among origins at the same pH treatment.

Maximum metabolic rate (MMR)

Mean MMR significantly increased with temperature along a linear trend, rising from 0.157 to 0.240 mg O_2 h^{-1} g^{-1} from 2 to 10°C (Table S3, Fig. 4A). In addition, a significant decrease of approximately 12% in mean MMR was observed at low pH (Table S3, Fig. 4B). Moreover, different origins differed in mean MMR (Table S3, Fig. 4C). Specifically, mean MMR of shrimp from SLE was the highest (0.213 mg O_2 h^{-1} g^{-1}) when compared with all other origins and significantly differed from mean MMR of shrimp from ESS (0.190 mg O_2 h^{-1} g^{-1}), which was the lowest (Fig. 4C). In addition, mean MMRs reported for shrimp from EC and NNC were comparable to mean MMRs reported for shrimp from all other origins (Fig. 4C).

Finally, none of the interactions had a significant effect on mean MMR (Table S3).

Aerobic scope (AS)

Mean AS increased with increasing temperature differently for shrimp from different origins, as indicated by the presence of a significant interaction between temperature and origin (Table S3, Fig. 5A). Specifically, for shrimp from EC and NNC, mean AS increased significantly with increasing temperature (increase of approximately 81% and 43%, respectively, from 2 to 10°C), whereas for shrimp from SLE and ESS, mean AS was similar among all temperatures (Fig. 5A). Moreover, mean AS values of shrimp from different origins measured at the same temperature were comparable at each temperature tested (Fig. 5A), as the multiple comparisons tests for mean AS values between different origins (at the same temperature) failed to detect significant differences.

Finally, exposure to low seawater pH caused a significant decrease of approximately 18% in mean AS (Table S3, Fig. 5B), and
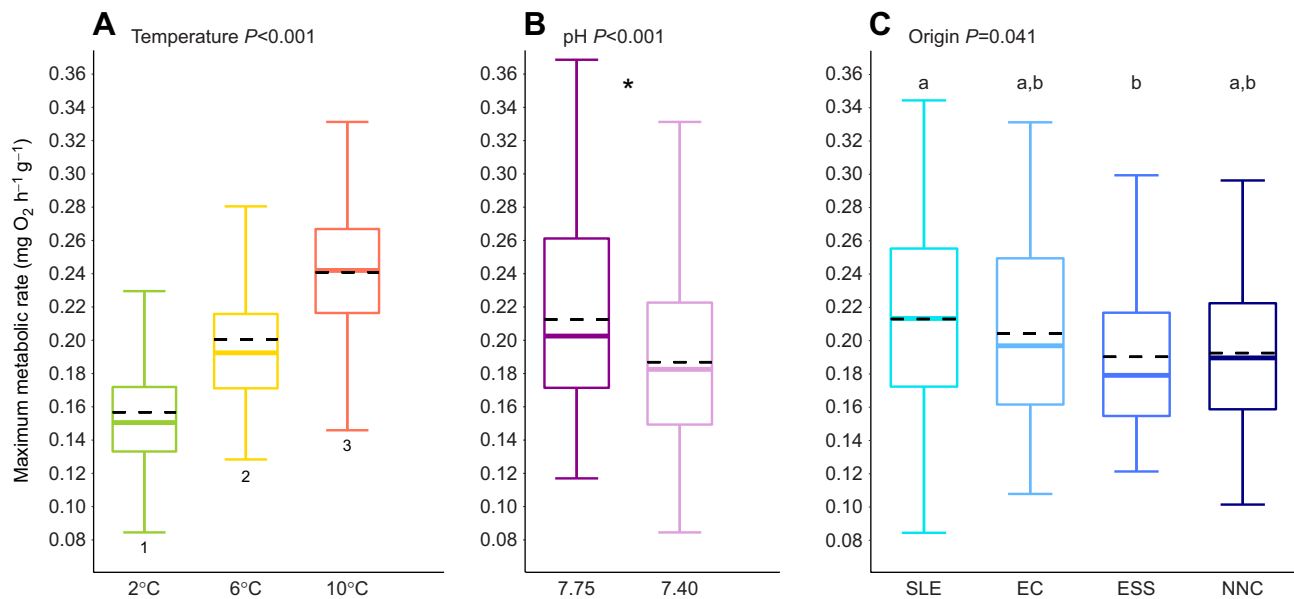
Fig. 4. The effects of exposure to isolated and combined seawater temperature and pH over 30 days on mean maximum metabolic rate of female northern shrimp, *P. borealis*, from different origins. Solid lines represent the median and dashed lines represent the mean. (A) Temperature treatments: 2°C (yellow), 6°C (green) and 10°C (red). Different numbers indicate the presence of a significant difference (*P*<0.05) among temperature treatments. (B) pH treatments: 7.75 (purple) and 7.40 (light purple). The asterisk indicates the presence of a significant difference (*P*<0.05) between the two pH treatments. (C) Origins: SLE (azure), EC (light blue), ESS (blue) and NNC (dark blue). Different lowercase letters indicate the presence of a significant difference (*P*<0.05) among origins.

the remaining interactions in our analyses were not significant (Table S3).

Cellular energetic capacity

Mean enzyme activities and their ratios differed significantly for shrimp from different origins (Table S3, Fig. 6). Specifically, mean CS, COX and LDH of shrimp from SLE were the lowest measured (5.9, 2.6 and 338.8 U g^{-1} of proteins, respectively)

when compared with those of shrimp from other origins (Fig. 6A–C). In addition, shrimp from ESS and NNC showed the highest mean CS and COX, respectively, when compared with shrimp from all other origins, and approximately double the mean values of shrimp from SLE (Fig. 6A,B). Furthermore, mean enzyme activities of shrimp from SLE always differed significantly from those of shrimp from ESS and NNC (Fig. 6A–C).
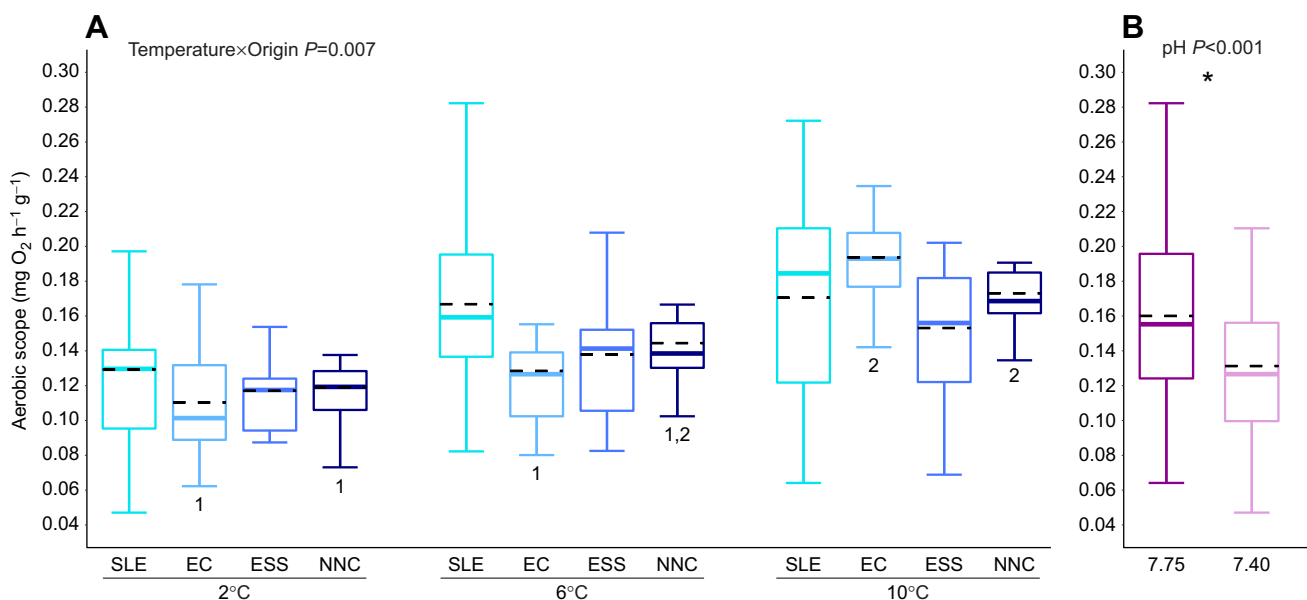

Fig. 5. The effects of exposure to isolated and combined seawater temperature and pH over 30 days on mean aerobic scope of females of the northern shrimp, *P. borealis*, from different origins. Solid lines represent the median and dashed lines represent the mean. (A) Treatments: temperatures (2, 6 and 10°C) and origins: SLE (azure), EC (light blue), ESS (blue) and NNC (dark blue). Different numbers indicate the presence of a significant difference (*P*<0.05) among temperature treatments for the same origin. (B) pH treatments: 7.75 (purple) and 7.40 (light purple). The asterisk indicates the presence of a significant difference (*P*<0.05) between the two pH treatments.
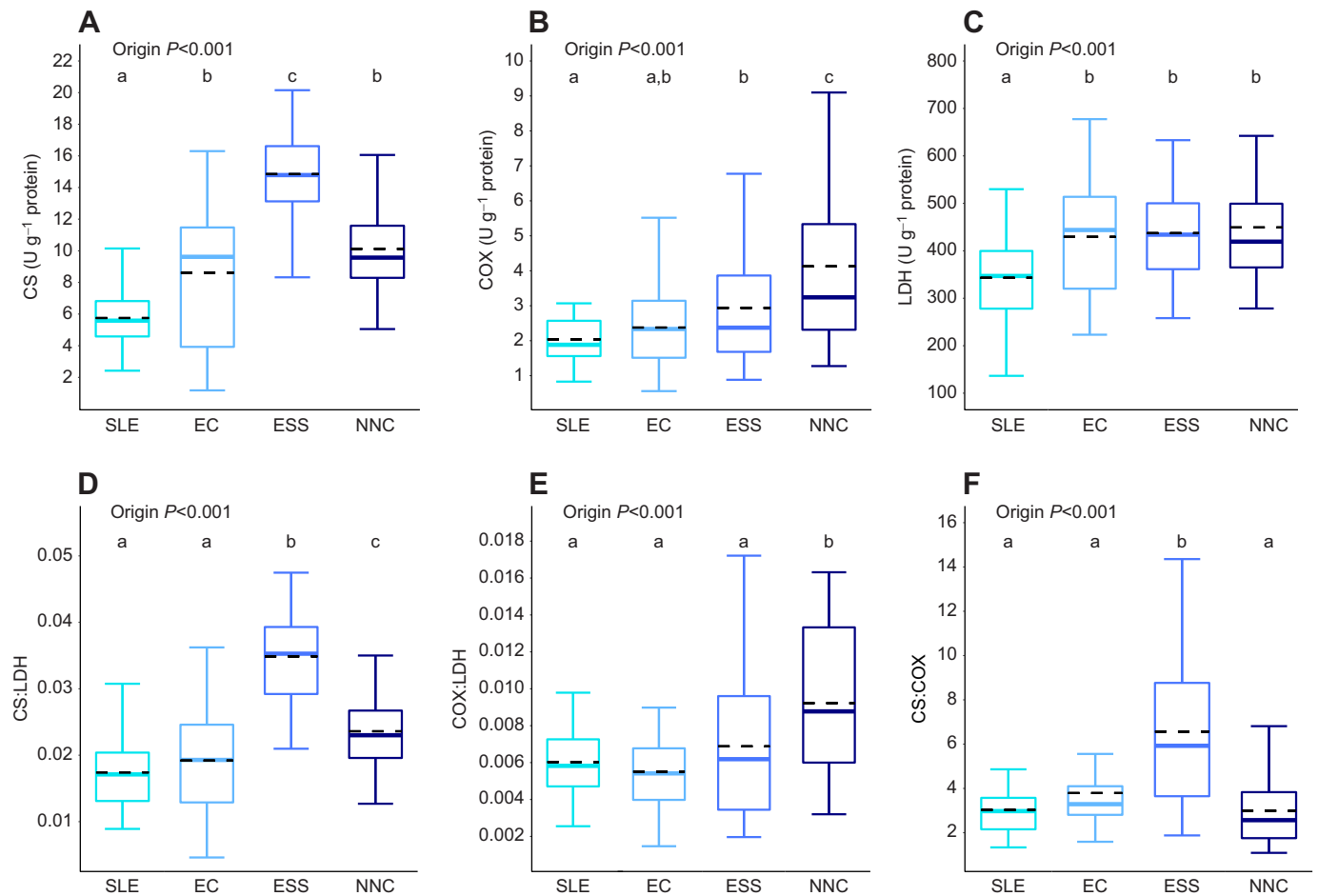
Fig. 6. Specific enzyme activities and their ratios in the muscle of female northern shrimp, *P. borealis*, from different origins after 30 days exposure to isolated and combined seawater temperature and pH. (A) citrate synthase (CS), (B) cytochrome C oxidase (COX), (C) lactate dehydrogenase (LDH), (D) citrate synthase to lactate dehydrogenase ratio (CS:LDH), (E) cytochrome C oxidase to lactate dehydrogenase ratio (COX:LDH) and (F) citrate synthase to cytochrome C oxidase ratio (CS:COX). Solid lines represent the median and dashed lines represent the mean. Origins are: SLE (azure), EC (light blue), ESS (blue) and NNC (dark blue). Different lowercase letters indicate the presence of a significant difference (*P*<0.05) among origins. No effects of temperature or pH were found to be significant.

Finally, shrimp from ESS showed the highest mean CS:LDH and CS:COX compared with those of shrimp from all other origins (Fig. 6D,F), and shrimp from NNC showed the highest mean COX: LDH (6.37) compared with an average of 3.30 shown from shrimp from all other origins (Fig. 6E).

All other terms in our analyses were found to be non-significant (Table S3).

DISCUSSION

Altogether, our results show that *P. borealis* is overall relatively tolerant to the combined exposure to OW and OA conditions predicted to occur at the end of the century. Indeed, OW and OA are shown to moderately reduce shrimp survival rates under short exposure to laboratory conditions and increase their whole-organism aerobic performance. Interestingly, small differences in metabolic rates among origins do not appear to impact the overall AS of shrimp, which, along with survival rates, is comparable among shrimp from different origins. This suggests that northern shrimp sensitivity to OW and OA is highly comparable among individuals from different geographic origins close to the southern edge of its distribution. Moreover, isolated and combined OW and OA do not alter shrimp cellular enzyme activities, either because there is little plasticity associated with short-term changes in environmental conditions or because there is no need

of compensation. However, it is noteworthy that shrimp cellular aerobic capacity (CS and COX activities) differs among origins, suggesting signs of regional long-term acclimatization or adaptation at the cellular level. This highlights the importance of testing multiple levels of biological hierarchy (Bartholomew, 1964; Harvey et al., 2014) whilst investigating the responses of organisms from different geographic origins (Gaston et al., 2009) when attempting to define species' sensitivity to combined global changes, to ensure we avoid overestimating or underestimating global change impacts.

Overall, the northern shrimp is more sensitive to OW than to OA, confirming that temperature is a major controlling factor in ectotherms at the whole-organism level (Fry, 1971). Indeed, shrimp SMR increases only with increasing temperatures. OW also leads to an increase of approximately 53% in shrimp MMR, whilst pH alone causes a more moderate decrease of this trait (~12%). An increase in SMR means that more energy is required for maintenance (Brett and Groves, 1979; Chabot et al., 2016b), but shrimp appear to be able to support the increased energy demand as their capacity to transport oxygen to the tissues (MMR) also increases. Shrimp AS increases with OW, and moderately decreases with OA. This confirms previous findings that shrimp can tolerate temperature increases, as well as the pH decreases, predicted to occur by the year 2100 in the northwest Atlantic (Chemel et al.,

2020; Lavoie et al., 2020), as long as the increased metabolic demand is fuelled by an adequate prey supply.

Interestingly, our results show the presence of differences among shrimp from different origins, considered as indicators of low levels of intraspecific variation, for both SMR and MMR. Specifically, maintenance and repair costs of shrimp from SLE are among the highest compared with those from other origins, and are always higher than those of shrimp from NNC. In fish, individuals with a higher SMR tend to have a higher MMR and often show a greater AS (Metcalfe et al., 2016). We suggest that the differences observed in maintenance costs and oxygen transport capacity among shrimp from different origins, captured by SMR and MMR variations, respectively, do not impact the whole-organism performance of individuals that survived the experimental exposure, as shrimp from different origins show comparable AS at each temperature tested and within the duration of exposure used in this study. Nonetheless, energy allocation and partitioning could differ among shrimp from different origins based on their different needs. However, further studies on energy allocation and partitioning, for example using modelling approaches (such as dynamic energy budget models), are needed to unravel further potential differences among origins.

Altogether, similar whole-organism aerobic performances among shrimp origins suggest that sensitivity of shrimp to predicted OW and OA is comparable among origins. In contrast, other marine species have shown geographically specific metabolic responses to these drivers, showing an increased response to OW and OA (Calosi et al., 2017; Lardies et al., 2014; Thor et al., 2018; Vargas et al., 2017). At the cellular level, OW and OA do not affect the activity of enzymes involved in energy metabolism, suggesting either low plasticity of metabolic apparatus or no requirement for compensation. The cellular energetic capacity, however, varies among shrimp from different origins, showing a high level of intraspecific variation and supporting the idea that long-term acclimatization or adaptation to regional environmental conditions has occurred at the cellular level. Indeed, shrimp from ESS and NNC have the greatest aerobic capacity compared with shrimp from other origins, as their CS and COX activities and their ratios to LDH are the highest, respectively. In fish, higher mitochondrial densities (i.e. higher CS activity) have been associated with cold acclimation (Battersby and Moyes, 1998; Lannig et al., 2003; Lucassen et al., 2003), supporting the suggestion that *P. borealis* could be regionally acclimatized or adapted to differing temperatures. Differences in metabolic enzyme activities among populations as a consequence of acclimatization or adaptation have also been shown in other marine species inhabiting different environmental regimes and latitudes (Liu et al., 2013; Rodríguez et al., 2019; Sokolova and Pörtner, 2001). Moreover, ESS and NNC enzyme activities always differ from those of shrimp from SLE, which can be considered to show the worst general physiological condition as they show the lowest aerobic and anaerobic enzyme activities, and the highest MMR. Furthermore, shrimp from SLE are more sensitive to OW and OA, at the molecular level, when compared with shrimp from other origins (Guscelli et al., 2023). This suggests that shrimp from SLE might already operate close to the limit of their aerobic capacity, which can be detrimental. Indeed, it can promote oxidative stress and leaves little room for increasing aerobic capacity meaning faster and higher mobilization of anaerobic glycolysis and metabolic fatigue. Conversely, shrimp from ESS have the highest CS to COX ratio, suggesting that mitochondria have a greater reducing capacity because CS is an enzyme located in the mitochondrial matrix that catalyses the

reaction at the entry to the Krebs cycle pathway, promoting the aerobic metabolism (Wiegand and Remington, 1986), despite ATP concentrations not differing among different origins (Guscelli et al., 2023).

Altogether, our study demonstrates that shrimp from different origins show different cellular aerobic and anaerobic capacities, whereas their whole-organism performance and survival rates are comparable. Additionally, OW and OA have a moderate effect on survival rate, as observed at the highest temperature and at the lowest pH tested, after 30 days of exposure. However, we should consider that over longer exposure periods *in situ*, and under exposure to additional co-occurrent global change drivers, such as decreasing dissolved oxygen, mortality levels might be significantly higher (>60%; Chemel et al., 2020). We confirm here that shrimp are relatively tolerant to OW and OA, as suggested before (Chemel et al., 2020; Dupont et al., 2014). Despite our results showing that the sensitivity to OW and OA of shrimp from different origins is comparable, their vulnerability to environmental conditions predicted for the end of the century could still differ owing to the environmental regime they are currently exposed to. In fact, shrimp experience contrasting regional environmental conditions in the northwest Atlantic: in some regions they already experience temperatures and pH levels close to those predicted to occur locally by the year 2100 (Lavoie et al., 2020). Recently, mean temperatures in EC increased from ~5–6 to ~6–7°C at ~250 m deep, where shrimp are most abundant (DFO, 2022a). Across the ESS, bottom temperatures range from −1 to 6°C year-round (DFO, 2022c), and in the last decade they have been observed to be at least 3°C in spring (May–June), and increasing annually since 2017 (DFO, 2022c). During the same period, NNC average bottom temperatures have ranged from 0.2 to 3.4°C following decadal cycles, with a general warming from the 1980s to 2020 (Cyr et al., 2022). In the SLE, waters are most severely hypoxic (18–26% saturation between 1990 and 2008; Gilbert et al., 2005) and dissolved oxygen (DO) levels of deep waters decreased even further in recent years (down to 14–16% O_2 saturation; Blais et al., 2021; Jutras et al., 2020), reaching levels close to the hypoxia tolerance level of shrimp (16% O_2 saturation for females at 5°C; Dupont-Prinet et al., 2013). The decrease in DO likely caused the recent shift to shallower (<150 m), colder (2–3°C) and better-oxygenated (50–60% O_2 saturation) waters observed for shrimp from the SLE (Bourdages et al., 2022, their fig. 18). Hypoxia has also been shown to compromise shrimp physiology, and strongly reduce their survival when combined with OW and OA (Chemel et al., 2020); thus, DO needs to be taken into account when trying to define the vulnerability of shrimp among origins. The NNC near-bottom DO ranges from 60 to 100%, and is generally above 80%, whereas the overall ESS DO is above 60% and has remained relatively stable since 2014. However, the northern parts of the ESS are influenced by the lower DO levels observed in the Laurentian Channel, and show a decrease to 40 to 50% O_2 saturation (DFO, 2021c). Hypoxia is more severe in the EC, where shrimp experience DO levels of ~30% O_2 saturation at 6.5°C (DFO, 2022a). Unlike shrimp from SLE, EC shrimp have not moved to shallower depths, either because the conditions in deep water were not extreme enough or there is not enough habitat with appropriate sediments available at shallower depths. Similarly, seawater pH differs among regions. The most recent surveys in the SLE show bottom pH varying between 7.4 and 7.6, these values being a little lower when compared with those from the EC (DFO, 2021c). Furthermore, in the ESS and the NNC, bottom-water pH is higher and ranges from 7.8 to above 8 (DFO, 2021c, 2022b). Considering that shrimp from EC already

experience the highest temperatures and the lowest DO levels compared with shrimp from other origins, based on recent findings their survival at the end of the century could be reduced to as low as 40% (Chemel et al., 2020). This will likely have important consequences for shrimp abundance and hence fisheries, suggesting risks of local commercial extinction.

In conclusion, our study shows that the level of intraspecific variation can differ among biological compartments, highlighting the importance of measuring the physiological responses of organisms at multiple levels of biological organization to avoid overestimating or underestimating the sensitivity of species to future complex environmental conditions (Calosi et al., 2017). In addition, the high level of intraspecific variation reported for cellular responses underlines the importance of conducting multi-population studies instead of considering species as a single homogeneous unit (Gaston et al., 2009), confirming previous findings on the metabolomics reprogramming variation among shrimp from different origins (Guscelli et al., 2023). This study also confirms that using a macrophysiological–macroecological approach when attempting to define the sensitivity of species to combined global changes is paramount, to avoid overestimation or underestimation, particularly for ectotherms of ecological, commercial and socio-economic value, such as the northern shrimp. Finally, our results indicate that despite the comparable responses of shrimp from the four distinctive origins, current differences in environmental conditions at different locations will yield different environmental conditions at the end of the century, this having important implications for management and conservation of *P. borealis* and its stocks.

Author contributions
Conceptualization: E.G., F.N., D.C., P.U.B., P.C.; Methodology: E.G., F.N., D.C., P.U.B., T.H., P.C.; Validation: E.G., F.N., D.C., P.U.B., P.C.; Formal analysis: E.G., D.C.; Investigation: E.G., T.H.; Resources: F.N., D.C., P.U.B., P.C.; Data curation: E.G., D.C.; Writing - original draft: E.G.; Writing - review & editing: E.G., F.N., D.C., P.U.B., T.H., M.C., P.P., K.R.S., P.C.; Visualization: E.G.; Supervision: E.G., F.N., D.C., P.U.B., P.C.; Project administration: F.N., D.C., P.U.B., P.C.; Funding acquisition: F.N., D.C., P.U.B., P.C.

Data availability
The data that support the findings of this study are available on PANGAEA® Data Publisher, under OA-ICC data compilation.

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