Regional variations in early life stages response to a temperature gradient in the northern shrimp *Pandalus borealis* and vulnerability of the populations to ocean warming

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***In memory of our friend and colleague David Orr*

Abstract

In order to define the relative vulnerability of northern shrimp (*Pandalus borealis*) populations to the ongoing global warming, we compared the thermal performance curves for survival and growth in the first three pelagic larval stages from three populations of the Northwest Atlantic. Egg carrying females were obtained from different regions characterized by distinct sea surface temperature (SST) conditions for larval development in spring. Two independent experiments were conducted in two different years. In spring 2012, larvae from females captured in the Lower St Lawrence Estuary (LE) and in the Northeast Gulf of St Lawrence (GSL) were compared.

In spring 2014, larvae from females captured in the LE and on the Labrador–Newfoundland Shelf (Northwest Atlantic, NWA) were used. The LE larvae were used both years and served as the reference population for comparisons. In 2012 and 2014, groups of 25 newly hatched northern shrimp larvae from each source population were incubated at six temperatures (0, 3, 6, 9, 12, and 15 °C) to monitor and compare survival and growth at moult. Northern shrimp larvae from the LE (warmer May–June SST) had a higher optimal temperature range for survival compared to larvae from the GSL and the NWA (colder May–June SST) populations. However, in 2012 growth performance at moult was reduced at higher temperatures for the LE population compared to the GSL population. The differences in thermal performance curves observed may suggest the presence of a certain level of local adaptation in response to the different regional SST regimes in spring – early summer. Northern shrimp larvae in the Northeast Gulf of St Lawrence and Northwest Atlantic shelf could benefit from warmer early-spring temperatures; however, larvae from the Lower Estuary may be closer to their upper tolerance limits and thus more likely at risk of negative impact of future warming of surface water masses.

Keywords: Northern shrimp, larval survival, larval growth, macrophysiology, conservation physiology, climate change.

1.1 Introduction

Temperature is a dominant ecological factor influencing the biology of ecthothermic organisms (Angilletta, 2009). The current global warming trend will have a direct impact on the marine environment and on the biology of organisms such as fishes and marine invertebrates (Pörtner and Knust 2007). Acquiring an in depth understanding of the thermal windows and thermal tolerance limits of species—with particular reference to their early developmental stages—is needed to predict how they are likely to be impacted by the warming oceans (Sanford et al., 2006; Pörtner and Farrell, 2008; Walther et al., 2010; Small et al., 2015).

Persistent environmental gradients may impose divergent selection pressures such that populations of wide-ranging species could evolve different morphological, physiological, behavioural, or life-history traits (e.g., adaptation) that provide advantages under local conditions (e.g., Gaston et al., 2009; Bozinovic et al., 2011; Sanford and Kelly, 2011). Phenotypic variation and plasticity levels observed among populations living under different environmental regimes emerge from their adaptation to the prevalent local conditions (Williams, 1966). Whilst local adaptation maximise fitness under a given set of conditions, once the environmental landscape changes a spatially contained population may find itself in suboptimal conditions, either because it does not possess specific adaptations to deal with the new environmental conditions or/and because it does not possess sufficient plasticity to buffer the negative effects of the environment (Williams, 1966; Sanford and Kelly, 2011; Dam, 2013; Pespeni et al., 2013; Savolainen et al., 2013). In the short term, plasticity is possibly the principal factor that will determine the vulnerability or resilience of populations facing rapid climate change (Magozzi and Calosi, 2014; Foo and Byrne, 2016).

Northern shrimp (*Pandalus borealis,* Krøyer 1838) is a widespread crustacean in the northern Atlantic (Bergström, 2000). It is found over soft muddy bottoms along the continental shelves (at depths of ~50 to 500 m), ranging in latitude from the Barents Sea (Northern coast of Norway and Russia at ~82° N) to the Gulf of Maine (Eastern coast of North America at ~42° N) (Shumway et al., 1985; Bergström, 2000). It is an economically and ecologically important species over its entire range. In Canada, populations in the Gulf of St. Lawrence (GSL) and Labrador–Newfoundland Shelf in the Northwest Atlantic support important commercial fisheries (Savenkoff et al., 2007; Dawe et al., 2012). Recent studies have revealed genetically structured populations of northern shrimp at various spatial scales (Jordel et al., 2015; Knutsen et al., 2015). The existence of regional variations in local bottom and in sea-surface temperature (SST) is considered a key factor explaining the large-scale genetic pattern described to date (Jordel et al., 2015). Furthermore, spawning times of northern shrimp populations in the North Atlantic appear to be adapted to local bottom temperatures to favour larval hatching at the moment of the spring bloom and initiation of the biological production cycle for different regions (Koeller et al., 2009).

In the Northwest Atlantic, larvae hatch from late April to June, at a time of cold SST but also coincident with rapid vernal warming over the ocean surface (Koeller et al., 2009; Ouellet et al., 2011). However, strong differences in SST can exist among local populations during hatching. For example, differences as great as 4 °C on average can occur between the western region of the GSL and the Labrador–Newfoundland Shelf; considering both spatial and temporal differences (Figure 1; Ouellet et al., 2011). During the pelagic phase of the life cycle, northern shrimp development progresses through six larval stages, of which the first three (stages I to III) inhabit the upper layer of the water column, above the permanent thermocline (Ouellet and Allard, 2006). Therefore, the first three larval stages are more likely to face different thermal

regimes and temperature ranges during development, depending on the region and the time of hatching.

Acquiring a better understanding of the impacts of warming water masses on productivity in northern shrimp populations is required to evaluate the consequences of current changes in the thermal environment and to devise conservation objectives for these populations (e.g., Arnberg et al., 2012). The relationship between environmental variations and observed phenotypic variations is described by reaction norm curves (Schlichting and Pigliucci, 1998). Thermal performance or tolerance curves are types of continuous reaction norms describing the effects of temperature on biological rates (Izem and Kingsolver, 2005). Local adaptation, phenotypic plasticity and acclimatization potential can result in differences in the shape of the thermal performance curves among populations, reflecting differences in their vulnerability to climatic variations (e.g., Chevin et al., 2010). Our study addresses the question of the relative vulnerability of northern shrimp larvae from different populations to climate change. To accomplish this, temperature tolerance curves for survival and growth of the first three larval stages of northern shrimp are compared between populations from different thermal regions of the Northwest Atlantic characterized by distinct SST conditions in spring. Our null hypothesis is that the response of northern shrimp larvae to a temperature range is independent of the source populations.

2.1 Material and methods

2.1.1 Collection of larvae

Experiments were conducted over two years according to the availability of northern shrimp females from different regions of the GSL and from the Labrador–Newfoundland Shelf in the Northwest Atlantic. The selected populations differ especially in term of mean sea surface temperature susceptible to affect larvae development in the spring, with warmer conditions in the western region compared to colder surface water in the eastern region (Figure 1A). Live egg-bearing northern shrimp females were captured by dedicated bottom trawl tows in August 2011 and in September 2013 in the Lower St. Lawrence Estuary, in October 2011 in the Northeast GSL, and in November 2013 on the Labrador–Newfoundland Shelf (Table 1; Figure 1B). On each occasion, females were transferred to the aquaculture facilities of Maurice Lamontagne Institute, Fisheries and Oceans Canada (Mont-Joli, Quebec, Canada). They were held until larval hatching the following spring at temperatures close to the natural deep-water habitat (~4 °C) in large (1800 L) temperature-controlled tanks in semi-recirculated water, with filtration system of the re-used water.

Daily temperatures in the holding tank were slightly lower during winter 2013–2014 than in 2011–2012, resulting in fewer total degree-days (DD) accumulated by the embryos in 2014 (Figure 2A). In addition, technical issues of the temperature control units caused two sudden temperature increases in the holding tank in late winter 2014. The second incident, in early March 2014, rapidly increased the temperature in the tank, which peaked at about 10 ˚C before stabilizing at 6 ˚C for several days (Figure 2B). Although northern shrimp can be found at bottom temperatures higher than 6 ˚C (e.g., Bergström, 2000; Richards et al., 2016), the rapid temperature rise, and consequently the acceleration in the accumulation of DD, may have been responsible for the early hatching in March 2014 relative to spring 2012.

2.1.2 Selection of females and larvae

Two independent experiments were conducted in two different years. In spring 2012, larvae from females captured in the Lower Estuary in August 2011 (hereafter larval population LE12) and in the Northeast GSL in October 2011 (hereafter larval population GSL12) were compared. In spring 2014, larvae from females captured in the Lower Estuary in September 2013 (hereafter larval population LE14) and in late November 2013 on the Labrador–Newfoundland Shelf (hereafter larval population NWA14) were used. The Lower Estuary larvae were used both years and served as the reference population for comparisons.

In March 2012 and 2014, three to four randomly selected females per population were isolated in 60 L flow-through tanks (two tanks per population and three or four females per tank) for larval hatching. The mean cephalothorax length (CL) of the selected females ranged from 23.11 mm (Northeast GSL in 2011) to 25.21 mm (Lower Estuary in 2013) (Supplementary material, Table S1). Actively swimming newly hatched larvae (less than 24 h old) were combined from the two tanks of a population for incubation at different temperatures. Mixing larvae from different females reduced the possible influence of maternal lineage, i.e., maternal effects, on the results.

2.1.3 Experimental setup

The equipment and protocol used to test the thermal performance of larvae were the same for the 2012 and the 2014 experiments. Six tanks (360 L, open circulation, i.e., no water reuse) were set up to monitor development at 0, 3, 6, 9, 12, and 15 °C (Supplementary material, Figure S1). Water temperature in each tank was monitored continuously and the targeted temperature maintained automatically by controlling the mixing of cold (chilled) and warm water. Groups of 25 larvae were held in closed 1.5 L jars, with multiple jars dispersed randomly in each tank. Considerable egg losses are observed for northern shrimp females in captivity

(Brillon et al., 2005), and even though the hatches of more than one female were combined, the number of newly hatched shrimp larvae was low on any given day. In 2012, the priority was to have three replicates, i.e., three jars of 25 larvae hatched the same day for every temperature, and it required larvae hatched on successive days to fill jars for all temperatures (Table 2). The number of larvae available each day for LE12 was very low, and up to 12 successive hatches were necessary to have multiple jars at each temperature level. In spring 2014, larvae available on a given day were allocated such that there was one jar of 25 larvae (no replicate per hatch) at each incubation temperature; this procedure was repeated on successive days (hatches). Overall, between two and five jars of 25 larvae were successfully incubated for each population by temperature combination (Table 2).

The water in the incubation jars was aerated with a continuous gentle flow of compressed air. Larvae were fed manually each day with a ration (1200 individuals L^{-1}) of enriched (EASY DHA Selco, INVE Aquaculture) *Artemia* sp. nauplii. At the same time, about half of the water in the jar was changed, the non-ingested food removed, the dead larvae counted, and the remaining larvae examined to detect evidence of moulting (i.e., to record the minimum number of days to the moult). After completion of a moult cycle (i.e., all larvae had moulted to the next stage), at least five live larvae were randomly selected in each jar to be measured, cephalothorax length (CL), manually under a binocular microscope. A jar was terminated either when all the larvae in the jar were dead or after the third moult was observed (i.e., at least one larvae was at stage IV). In 2014, an attempt was made to enhance the feeding and survival which was very low at the lower temperatures (< 6 ˚C) by adding commercially available microalgal cells, but that did not improve survival as intended: mortality was still high, probably due to the poor quality of the product or because these microalgae were not suitable for the diet of northern shrimp larvae.

2.1.4 Analyses: growth

Sample of 15 (2012) and 20 (2014) newly hatched larvae from each hatch used to set-up the jars were taken for measurement (CL – binocular microscope) and individual DW (after 24 hours at 70 ˚C). Growth was estimated as the relative (%) increase in CL at the moult, from hatching (stage I) to stage II and from stage II to stage III:

$$\%CL = ((\text{mean } CL_{stage\ i+1} - \text{mean } CL_{stage\ i})/\text{mean } CL_{stage\ i}) * 100$$

For an estimate of the growth increment at the first moult, the mean CL of stage II larvae sampled from each jar was compared to the mean CL of stage I larvae from the hatching event used to supply the jar. For an estimate of growth increment at the second moult, the mean stage III CL was compared to mean stage II CL for each jar.

Linear mixed effects models (LMM) were used to test the effect of incubation temperature, population (fixed effects), and their interaction on the relative growth increment at moult (%CL increase), with hatching (i.e., hatch number) as the random variable (random intercepts) in the 2014 experiment (LE14 and NWA14). In 2012, hatch and replicates (jars) nested in hatch were included as random variables. Because of this difference between years, both experiments were analyzed separately, even though northern shrimp from the Lower St Lawrence Estuary were used in both cases. In all cases, data met the criterion of homogeneity of variance (Levene's test, *p*-value > 0.05) and residuals were normally distributed (Supplementary material, Figure S2). LMM analyses were carried out with R (R Development Core Team, 2016) using the lmer function of the R packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2016).

2.1.5 Analyses: survival

A maximum of five larvae were sampled from a jar during incubation following each moult and some larvae were still alive when a jar was terminated (at the third moult). Hence, Kaplan-Meier estimates of the daily survival at each incubation temperature were obtained by non-parametric maximum likelihood (Turnbull method; Singh and Totawattage, 2013) for interval-censored data with the R package interval (Fay and Shaw, 2010). For the 2012 experiment, Logrank tests were applied to test for differences in survival estimate distributions among replicated jars at a given incubation temperature. When the difference was not significant ($p > 0.05$), data were pooled for further analyses of the survival trends.

For each population, the last Kaplan-Meier survival estimate, i.e., only one survivor in the jar or when the jar was terminated was plotted as a function of incubation temperature. The distributions of survival data were clearly asymmetrical, with higher values toward higher temperatures, and the skew-normal (SN) distribution was fitted to the survival data to account for the asymmetry (R package sn; Azzalini, 2016). The univariate SN density function of a random variable *z* is defined by

$$\int (z) = 2\phi(z)\Phi(\alpha z) \qquad (1)$$

where ø and Φ are the density and cumulative distribution functions of the standardized normal distribution, respectively (Azzalini, 1985).

The three parameters (location, scale, shape) of the SN density distribution address varying degrees of skewness and solve to the normal distribution when the skewness/shape parameter alpha is near zero. This approach is analogous to the method presented to compare common shape reaction norms among groups or populations by the development of an empirical three-parameter (location, height, width) function (i.e., Izem and Kingsolver, 2005). However, one advantage of fitting or modelling the observed survival data with a probability density function

having known properties is that robust estimates of the distribution parameters are obtained. Hence, where epsilon (ξ) is the location, omega (ω) is the scale, and alpha (α) is the shape parameter, the true mean and variance of the SN random variable *z* are obtained by

$$\mu(z) = \xi + \omega\delta\sqrt{2/\pi} \quad (2)$$

$$var(z) = \omega^2(1 - \frac{2\delta^2}{\pi}) \quad (3)$$

respectively, where $\delta = \alpha/\sqrt{(1+\alpha^2)}$.

The best SN fits according to Akaike's information criterion (AIC) were obtained after weights were applied to the survival estimates. Weights were chosen to account for the variability among replicates and the differences in relative survival observed for each incubation temperature (Supplementary material, Table S2). Subsequently, the parameters of the SN curves that best fit the distribution of survival data for each population were used to generate 1000 random SN density distributions. From these distributions, mean optimal temperatures for survival were estimated to compare (*t*-test for unequal variances) optimal temperatures for survival and growth between the populations.

3.1 Results

3.1.1 Growth

Mean cephalothorax length (CL) at hatching varied significantly between populations in 2012 but not among hatches (Table 3); mean (mm) ± 1SD = 1.399 ± 0.064, n = 135, and 1.384 ± 0.054, n = 170, for GSL12 and LE12, respectively. In 2014, mean CL at hatching was smaller and also varied significantly between populations; 1.274 ± 0.042 mm, n = 100, and 1.258 ± 0.039

mm, n = 135, for NWA14 and LE14, respectively. The effect of hatch on mean CL within a population was also found to be significant in 2014 (Table 3; Supplementary material, Figure S2). Mean dry weight (DW) at hatching did not vary significantly between populations in either experiment; however, the effect of hatch was significant in the 2014 experiments (Table 3), and overall larval DW at hatching was about 40% lower in 2014 compared to 2012 (Supplementary material, Figure S3). Time in days to the first and second moult was a function of the incubation temperatures only, but there was a significant interaction with the source populations at the second moult in 2014 (Supplementary material; Table S3, Figure S4).

For the 2012 experiments, comparison of the different LMM models revealed that the best model explaining the relationship between temperature and relative larval growth at moult (%CL increase) included both the fixed effects temperature and population and their interaction (Table 4). In 2012, change in %CL increase at the first moult increased with temperature but that effect was a function of the population of origin of the larvae (Table 5; Figure 3A). A post-hoc Tukey HSD (Honestly Significant Difference) test revealed few significant differences between the estimated means %CL increase. However, the maximum relative moult increment was estimated at 9 ˚C in GSL12 larvae and the minimum at 15 ˚C in the LE12 larvae (Figure 4). Relative moult increment was also larger in LE12 larvae at 3 ˚C when compared to GSL12 larvae (Figure 4). In 2014, the model with only population as fixed effect was not improved by adding the effects of incubation temperature or the interaction between temperature and population (Table 4). Regardless of temperature, only population had a significant effect (Table 6), and the increase in %CL increase at the first moult was greater for LE14 larvae than for NWA14 larvae (Figure 3A).

By the time larvae reached stage III (second moult) in both experiments, high mortality at the upper and lower incubation temperatures, especially for GSL12 larvae (Figure 3B) reduced the amount of data available for the statistical analyses. With the available data, the LMMs revealed no statistically significant effect of temperature on %CL increase at the second moult (these non-significant statistical results are not shown).

The thermal performance curves for growth at the first moult were obtained by fitting regression lines to %CL increases at each temperature (Table 7). Although the confidence intervals overlap over the temperature range, the thermal performance curve for GSL12 starts lower at 3 ˚C but tend to depart from the LE12 curve at higher temperatures (above 9 °C) (Figure 5A). In 2012, higher growth (maxima on the regression lines) were observed at 6 and 9 ˚C for LE12 and GSL12 larvae, respectively (Figure 5A). The thermal performance curves show that there was no effect of temperature on %CL increases for the LE14 population (horizontal line), but a small increase (positive slope) in %CL increase with temperature for the NWA14 population (Figure 5B). Nonetheless, %CL increase was higher, especially at temperatures below 9 ˚C, for LE14 larvae relative to NWA14.

3.1.2 Survival

Overall, mean survival across temperatures was not statistically different between populations for either experiment (Table 8). Nonetheless, survival was not uniform over the incubation temperatures, and temperature had a significant effect on survival. Each year and for all populations, survival increased with temperature except for the highest incubation temperatures (15 °C), and a skew-normal (SN) distribution function provided a good fit for the estimated survival data (Table 9; Figure 6A). However, the residuals were clearly not normally distributed in some cases (e.g., GSL12; Supplementary material, Figure S6).

The highest survival estimates observed and the maximum of the fitted density distribution occurred between ~9 and ~14 °C for all populations (Table 8, Figure 6A). The main differences between the fitted curves for GSL12 and LE12 survival were in the scale (i.e., dispersion) and shape parameters of the distribution (Table 9). The fitted curve was more centered over the incubation temperature range and showed higher survival values at lower temperatures in GSL12 (Figure 6A). The fitted curve for LE12 showed stronger skewness, probably driven by the lower variability in the observed survival estimates at 12 ˚C, and a narrower range of relatively high survival values (Figure 6A). In 2014, the main difference between populations was in the shape parameter, with the distribution more strongly skewed toward higher temperatures in LE14 compared to NWA14 (Table 9, Figure 6A).

The results described above were from only one experiment each year. In an effort to assess the reliability of these conclusions and to have an estimation of the variability and differences between populations, the SN coefficients with their standard errors were used to generate 1000 random SN density distributions for each population. The results of the simulations reflected not only the higher uncertainty around the estimations for the GSL12 and NWA14 populations, but also the clear skewness of the density distribution toward higher temperatures for the Lower Estuary population in both years (Figure 6B). According to the simulations, the estimated mean optimal temperatures for survival were significantly higher for the Lower Estuary larvae than for the alternative population in both experiments (Figure 7).

4.1 Discussion

These experiments were a first attempt to investigate possible significant differences in thermal performance curves (thermal reaction norms) at the larval stage among different populations of northern shrimp inhabiting different thermal regions. Overall, we found that

northern shrimp larvae from different populations showed significant differences in survival and possibly in growth during early development over a temperature range, and these can be related to different natural habitat conditions. Larvae from the small population isolated in the Lower St Lawrence Estuary—a population experiencing relatively warm early-spring SST—were significantly different (better survival at high temperature) from larvae from the more eastern populations inhabiting regions of colder early-spring SST. The results suggest phenotypic variability that can be consistent with the presence of local adaptation in response to different thermal regimes.

4.1.1 Survival

In spring 2012 and 2014, and for all northern shrimp larval populations, survival increased slowly with incubation temperature but declined rapidly past 12 ˚C. The estimated temperatures for best survival were in the range that has been reported before for northern shrimp larvae reared under constant temperature conditions (Wienberg, 1982; Nunes and Nishiyama, 1984; Ouellet and Chabot, 2005).

Various mathematical functions have been proposed to describe or model thermal performance curves (Logan et al., 1976; Izem and Kingsolver, 2005; Angilletta, 2006; Klepsatel et al., 2013). The skew-normal distribution used here is well suited to the analysis of continuous distributions, where the errors are not normally distributed (e.g., skewness, tails), and it is a more robust model for estimating the distribution parameters in these situations (e.g., Contreras-Reyes and Arellano-Valle, 2013). Nevertheless, the limited number of data points and large variations in the observed survival data among larval groups influence the precision of the optimal temperature estimates obtained by fitting theoretical curves to observed data. For example, survival values were still relatively high at 15 °C for LE14, giving a

very high value for the shape parameter. The fitted curve in this case dropped almost vertically between 12 and 15 °C; however, examination of the Kaplan-Meier survival estimates suggests an optimal temperature between 11 and 12 °C. The fitted curve for NWA14 suggested that 12 °C is optimal for survival; however, there were only two successful incubations (jars) and survival was highly variable at that temperature. These uncertainties were accounted for in the simulations of SN density distributions for each population and the consistent result for both experiments was that larvae from the Lower Estuary—a population experiencing relatively warm early-spring SST—showed a higher optimum temperature for survival than did larvae from GSL12 and NWA14 populations, which are characterized by colder early-spring SST conditions (see Figure 8).

Better survival at low temperatures was expected for the larvae from the colder regions. Although the fitted survival curve shows better survival at the lower temperatures in GSL12 larvae, the Kaplan-Meier estimates would suggest that survival was better on average—but also more variable among hatches—at 3 °C and 6 ˚C for the Lower Estuary in LE12 larvae. Difficult rearing conditions at low temperatures might explain the inconsistent results. At 0, 3, and even at 6 °C, the mobile prey (*Artemia* sp. nauplii) and the northern shrimp larvae showed low activity (the larvae were observed to remain close to the bottom of the jars), which may have impaired feeding success and led to starvation and mass mortality. Indeed, the pattern of mortality over time at 0 °C observed in 2012 and 2014 (mass mortality after a given time; data not shown) suggests mortality by starvation in the jars. On the other hand, feeding success appears to have been good at warmer temperatures, and the results more reliable. Therefore, we conclude that northern shrimp larvae from the Lower St. Lawrence Estuary survived better at the upper limit of the temperature range used. Overall, northern shrimp larvae from

359 different populations showed different responses to temperature during development, and
360 these can be related to natural habitat conditions.

361 While female shrimp were captured in similar benthic thermal environments, there were
362 strong differences among the regions in SST conditions at the time of larval hatch at sea.
363 Although the scale of interannual variability is about the same for all three regions, SST at the
364 end of April and early May is much higher in the Lower Estuary than in the Northeast GSL or on
365 Labrador-Newfoundland Shelf (Figure 8). However, vernal warming occurs more rapidly for the
366 Northeast GSL population, and SST is equal to or higher than SST in the Lower Estuary by early
367 July. In contrast, spring and early summer SSTs are always lower in the Northwest Atlantic.
368 Earlier investigations of environmental influences on northern shrimp recruitment in these
369 regions concluded that mean SST at hatching and SST warming rates following hatching
370 influence larval survival and recruitment to the populations (Ouellet et al., 2007, 2011). In all
371 populations, above-average recruitment levels were associated with higher SST warming rates
372 in spring (Ouellet et al., 2011), but relatively high SST early in the spring—at hatching—had a
373 negative effect on recruitment in the western GSL (Ouellet et al., 2007). This suggests that in
374 cases of warmer spring, relatively warm SST early in the year, subsequent warming may result
375 in water temperatures that are too high and detrimental to larval survival. The 2012 results for
376 LE12 support this scenario: survival was lower and size at moult smaller at 15 °C, which is above
377 the climatological SST maxima in the Lower Estuary (Figure 8). In the Northeast GSL, on the
378 other hand, SST is on average colder at hatching and presumably limits early growth rates. In
379 2012, the GSL12 larvae appear able to compensate, with higher growth performance when
380 temperature conditions improve.

Our results suggest that larvae from the small northern shrimp population isolated in the Lower Estuary were significantly different from larvae from the more eastern populations, showing phenotypic variability or suggesting local adaptations in response to different thermal regimes. Local adaptation may lead to greater inter-population variations in thermal physiology in species with a large geographical range (e.g., Calosi et al., 2010, 2016). However, to demonstrate adaptation, it must be shown that natural selection influences phenotypic variability and that this variability has, at least in part, a genetic basis. There are no genomic studies or information on the genetic structure of the northern shrimp populations investigated here. Nonetheless, the fact that northern shrimp from these locations show variability in biological traits and abundance trends would suggest that the populations are isolated. For instance, female cephalothorax length tends to be larger in the Lower Estuary compared to the Northeast GSL, but in recent years they have been decreasing in the Lower Estuary while increasing in the Northeast GSL, suggesting isolation between the two populations. Since about 2011, male northern shrimp biomass has been decreasing in the Lower Estuary whereas the biomass of adult shrimp, males and females, has remained stable in the Northeast GSL (Orr and Sullivan, 2013; Bourdages and Marquis, 2014a; 2014b).

Further, circulation patterns do not favour mixing of larvae from these three populations. The general circulation pattern in the GSL shows westward (upstream) circulation along the north shore, but numerical simulations have shown that events of upstream advection from the northern GSL to the Lower Estuary are stronger and more frequent in summer and autumn, whereas shrimp larvae are present in late winter and spring (Ouellet et al., 2013; Maps et al., 2014). The Northwest Atlantic population is part of a more or less continuous band of northern shrimp aggregations from Hudson Strait to the Grand Banks that are under the influence of the deep coastal Labrador Current running along the shelf break. Although there are intrusions of

coastal Labrador water into the Northeast GSL via the Strait of Belle Isle, those fluxes are strongest in winter (e.g., Galbraith, 2006) and are unlikely to constitute a source of larvae for the Northeast GSL in late spring. In fact, it is more likely that some larvae from the Northeast GSL might be exported to the Labrador Shelf by surface outflow at the Strait of Belle Isle.

4.1.2 Growth, and comparing results from the 2012 and 2014 experiments

The highest growth increment at the first moult occurred around 6 and 9 °C in the GSL12 and LE12 populations, but better survival at higher temperatures was associated with lower growth performance in Lower Estuary larvae (growth was significantly reduced at 15 °C). On the other hand, larvae from a region with low SST in early spring (i.e., GSL12) had better growth performance at high temperatures compared to the Lower Estuary larvae, though this was significant only at 15 °C. Larvae from the Lower Estuary population appear to have developed a strategy that favours growth at the average temperature observed at hatching (see above) and favours survival when temperature increases, whereas larvae from the cold region (e.g., Northeast GSL) appear to favour growth when temperatures become more favourable in spring. However, both populations used in the 2012 experiment showed decreased growth rate and survival at 15 °C.

It has been proposed that the thermal niche of species and populations is limited by their ability to supply their tissues with oxygen for respiration (Pörtner, 2001; Pörtner and Knust, 2007). This agrees with early observations that the aerobic scope (the difference between the maximum and the standard metabolic rates) of water-breathing animals usually declines when temperature decreases below or increases above an optimal temperature (Fry and Hart, 1948; Fry, 1971). Reduced growth at temperatures greater than 9 °C in 2012 may be the result of a declining aerobic scope. Chabot and Ouellet (2005) obtained a continuously increasing

428 metabolic scope from 3 to 8 °C in stage I larvae from the Lower Estuary population. A large
429 metabolic scope at 9 °C and a decline at higher temperatures is therefore possible. However,
430 even though growth rate was significantly correlated with metabolic scope, Chabot and Ouellet
431 (2005) concluded that metabolic scope was not limiting for growth (within the temperature
432 range they studied) as it explained only 39% of the variability in growth rate. Because aerobic
433 scope of stage I larvae has not been measured at temperatures exceeding 8 °C for the Lower
434 Estuary population—and not measured at all for the GSL population—it is impossible to
435 attribute the better growth rate at high temperatures of the GSL12 population, relative to the
436 LE12 population, to differences in aerobic scope.

437 In 2014, growth rate was little affected by temperature for both the Lower Estuary and
438 Northwest Atlantic populations. However, the percent size increases at the first moult were
439 higher at all temperatures relative to 2012 and higher for the Lower Estuary relative to the
440 Northwest Atlantic larvae. The presumed link between temperature and aerobic scope, a
441 characteristic of species or possibly of populations, appears weak considering the differences in
442 growth rates obtained at the same temperatures in 2012 and 2014. However, a warming that
443 occurred late during the incubation seems to have provoked early hatching in 2014. In
444 crustacean decapods, embryonic growth may be highest in the final phase of development
445 (Sibert et al., 2004), and this early hatching was likely responsible for the smaller larval CL and
446 especially dry mass at hatching compared with 2012 larvae (Brillion et al., 2005). Chabot and
447 Ouellet (2005) obtained different relationship between aerobic scope and body mass at 3, 5,
448 and 8 °C, which may partly explain the strange pattern in growth rate as a function of
449 temperature for the small larvae of 2014. More importantly, Chabot and Ouellet (2005) found
450 that aerobic scope accounted for only 39% of the variability in growth rate of stage I larvae,
451 which leaves room for other variables to influence growth rate in 2014 and does not mean that

aerobic scope was not affected by temperature in this year. Thus, the small dry mass at hatching appears to have influenced the pattern of growth of stage I larvae in 2014. Interestingly, the mean CL of stage II larvae was quite comparable between 2012 and 2014 (Supplementary material, Figure S7). Therefore, high growth performance in 2014 despite small initial size and the fact that the survival distribution pattern over temperatures was very similar between 2012 and 2014 provide some confidence in the 2014 results. However, under the laboratory rearing conditions, the 2014 larvae were not able to sustain high growth rates, as revealed by the smaller %CL increases at the second moult (see Figure 3) and smaller mean CL of stage III larvae relative to 2012 (Supplementary material, Figure S8).

5.1 Conclusion

Although the difficulty of capturing live shrimp by trawling in deep water and transporting them alive and in good condition over a large distance limited the number of females (hence of larvae) for the experiments, and weaken the power of the analyses, we were able to show significant differences in the thermal performance curves for survival and possibly in growth among the larval populations. Variations in the thermal performance curves and different slopes in reaction norms can indicate phenotypic variability, adaptation to temperature, and/or genetic–environment interactions (e.g., Angilletta et al., 2002; Yamahira et al., 2007). Exchanges of pelagic larval stages among the regions are highly unlikely, and juvenile and adult northern shrimp are not known to make large displacements or migrations. Therefore, restricted gene flow suggests that the potential for local adaptations exists, even though an earlier study based on the investigation of allozymes showed no evidence of genetic distinctions between shrimp populations of the GSL and Northwest Atlantic (Sévigny et al.,

2000). It would be appropriate to re-examine the question of genetic differentiation among those northern shrimp populations using more powerful modern techniques (Jordel et al., 2014).

Significant differences in reaction norms among the larval populations would indicate at least a degree of inter-population plasticity that can provide information on the relative vulnerability of northern shrimp populations in the Northwest Atlantic to environmental changes (Dam, 2013; Calosi et al., 2016; Calosi et al., 2017). The Lower Estuary is downstream of a zone of intense vertical mixing at the head of the Laurentian Channel, which produces higher SST in winter–spring but lower SST in summer compared to the more stratified Northeast GSL (e.g., Galbraith et al., 2012). The estimated temperature for maximum survival for the Lower Estuary larvae is close to the maximum observed in the SST climatology for this region. Thus higher SST in the future in the Lower Estuary in late spring or summer could have a negative effect on larval growth and recruitment success in this population. In the Northeast GSL and Northwest Atlantic Shelf, larvae hatch at colder SST, and development is expected to be slow until the later rapid rise in water temperature. Although more work should be conducted on those populations, our results suggest that the larvae in the Northeast GSL and Northwest Atlantic Shelf may react positively and could benefit from future moderate warming in early spring.

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681 Table 1. Sampling dates of northern shrimp females and characteristics of the regions where source populations were sampled for the 2012 and
682 2014 experiments.

Population →	Lower St. Lawrence Estuary		Northeast Gulf of St. Lawrence	Northwest Atlantic (Labrador-Nfld shelf)
Larva ID →	LE12	LE14	GSL12	NWA14
Capture date	6–11 Aug 2011	27–30 Oct 2013	27–28 Oct 2011	18–23 Nov 2013
Capture depth (m)				
mean	150	146	266	304
range	80–258	76–201	257–276	199–461
Bottom temperature[a] (°C)				
mean	3.0	3.0	3.8	2.5
range	2.7–3.4	2.6–3.5	3.3–5.1	0.4–4.0
Hatching time[b]				
mid-point (H50%), DOY/week	131.1/20		117.9/18	112.8/17
SST weekly mean ± 1SD (°C)				
at initiation (min–max)[c]	2.8 ± 0.8 (1.1–4.1)		-0.3 ± 0.4 (-1.1–0.2)	0.3 ± 1.0 (-0.7–1.4)
at H50% (min–max)	5.8 ± 1.0 (4.0–7.4)		0.9 ± 1.3 (-1.1–3.8)	0.0 ± 0.7 (-1.2–1.3)
SST maximum (°C)				
mean ± 1SD/week	12.6 ± 1.2/30		13.9 ± 1.7/31	12.9 ± 2.1/32
SST warming rate (°C d^{-1})[d]	0.09 (91 days)		0.12 (124 days)	0.08 (125 days)

683 [a] No temperature data were recorded along with the shrimp catches in the Lower Estuary in 2011 and 2013 or in the Northeast GSL in 2011. The mean
684 temperatures at depth for populations LE12, LE14, and GSL12 were estimated from conductivity, temperature, density (CTD) profiles recorded during different
685 cruises around the same period in the same areas.
686 [b] From Ouellet et al., 2011.
687 [c] Initiation of hatch for each population was set at three weeks before mid-hatching (H50%) time.
688 [d] Number of days from hatching initiation to maximum SST

Table 2. Experimental setup showing the number of hatches, replicates (jars) per hatch (in 2012), and the number of successful incubations for each population and incubation temperature combination in 2012 and 2014. H(R) = a given hatch (H) from 1 to *n* and the number of jars (i.e., replicates - R) for the given hatch at the given incubation temperature; S = the number of successful incubations (jars) at the given temperature providing data for the subsequent analyses.

(˚C)	Year / Population							
	2012				2014			
	GSL12		LE12		LE14		NWA14	
	H(R)	S	H(R)	S	H	S	H	S
0	1(3); 9(2)	4	1(1); 2(2)	3	1; 2; 3; 4	4	5; 6; 7; 8	4
3	1(2); 2(1); 8(1)	4	3(1); 4(1); 5(1)	3	2; 3; 4; 5; 6; 7	5	4; 5; 6	3
6	2(3); 7(1)	4	6(1); 7(2)	3	1; 2; 3; 4; 7	5	5; 6	2
9	3(3); 8(1)	4	7(1); 8(2); 12(1)	4	1; 2; 3; 4	4	4; 5; 6	3
12	4(3); 8(1)	4	9(2); 10(1); 12(1)	4	1; 2; 3; 4	4	4; 5; 6	2
15	5(2); 6(1); 7(2)	5	10(1); 11(2)	3	1; 2; 3; 4	4	4; 5; 6; 7	3

Table 3. ANOVA results for the effects of origin (source population, Pop) and successive hatching (Hatch) on stage I northern shrimp larva cephalothorax length (CL, mm) and dry weight (DW, mg) at hatching for each experimental year. Bold characters indicate significant effects.

Year	VD	Sources	SS	df	F value	*p* (>F)
2012	CL	**Pop**	**0.015**	**1**	**4.415**	**0.037**
		Pop(Hatch)	0.062	19	0.927	0.550
		Residuals	0.994	284		
	DW	Pop	0.009	1	2.359	0.126
		Pop(Hatch)	0.089	19	1.233	0.230
		Residuals	1.058	278		
2014	CL	**Pop**	**0.015**	**1**	**11.413**	**0.001**
		Pop(Hatch)	**0.088**	**10**	**6.568**	**0.000**
		Residuals	0.298	223		
	DW	Pop	0.000	1	0.137	0.711
		Pop(Hatch)	**0.028**	**10**	**13.583**	**0.000**
		Residuals	0.046	218		

Table 4. Comparison of linear mixed models (LMM) for the effect of incubation temperature and population on larval growth performance at the moult. Dependent variable (DV): %CL increase at the moult.

2012
Fixed effects: Pop (Lower Estuary [LE12], Northeast GSL [GSL12]), incubation temperature (T_{incub})
Random effects: Hatch, Jar (i.e., replicate), and the residuals [ε]

Model	DF	AIC	BIC	Log-Lik	Dev	Chi_Sq	df	P (>Chi_Sq)
DV ~ Pop + (1 | Hatch /Jar) + ε	5	207.04	214.21	-98.52	197.04			
DV ~ T_{incub} + (1 | Hatch /Jar) + ε	8	196.86	208.33	-90.43	180.86	16.17	3	0.001
DV ~ T_{incub} + Pop + T_{incub}*Pop +(1 | Hatch /Jar) + ε	13	191.98	210.62	-82.99	165.98	14.88	5	0.011

2014
Fixed effects: Pop (Lower Estuary [LE14], Northwest Atlantic [NWA14]), incubation temperature (T_{incub})
Random effects: Hatch, and the residuals [ε]

Model	DF	AIC	BIC	Log-Lik	Dev	Chi_Sq	df	P (>Chi_Sq)
DV ~ Pop + (1 | Hatch) + ε	4	156.85	161.98	-74.26	148.51			
DV ~ T_{incub} + (1 | Hatch) + ε	7	167.85	177.42	-76.92	153.85	0.00	3	1.000
DV ~ T_{incub} + Pop + T_{incub}*Pop +(1 | Hatch) + ε	12	168.22	184.63	-72.11	144.22	9.62	5	0.086

706 Table 5. Summary table for the significance of fixed effects and variance in the random factors from
707 the linear mixed model applied to %CL increases at the first moult in 2012.

Factor	F	df	df (residuals)	*p*-value
T_{incub}	7.055	4	14.7	0.002
Pop	0.132	1	9.1	0.724
T_{incub}*Pop	3.697	4	15.1	0.027

Random effects:		Variance	Standard deviation	% of total variance
Hatch/Jar	(Intercept)	10.120	3.181	44.5
Residual		12.620	3.553	55.5

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709

710

711 Table 6. Summary table for the significance of fixed effect and variance in the random factor from
712 the linear mixed model applied to %CL increases at the first moult in 2014.

Factor	F	df	df (residuals)	*p*-value
Pop	7.216	1	26.615	0.012

Random effects:		Variance	Standard deviation	% of total variance
Hatch	(Intercept)	0.619	0.787	5.8
Residual		10.061	3.172	94.2

713

714 Table 7. Regression models for %CL increases at the first moult as a function of incubation
715 temperature (T_{incub}). For GSL12 and LE12, the thermal performance curves are second-
716 degree polynomials; for NWA14 and LE14, the thermal performance curves are straight
717 lines (no effect of temperature).

Population	Predictor variable	Estimate	Estimate std err	*t*-value	*p*-value	adj r^2
GSL12	Intercept	-3.367	4.795	-0.702	0.496	0.493
	T_{incub}	4.689	1.296	3.618	0.004	
	T_{incub}^2	-0.239	0.074	-3.227	0.007	
LE12	Intercept	5.291	5.400	0.980	0.345	0.469
	T_{incub}	3.414	1.344	2.541	0.025	
	T_{incub}^2	-0.226	0.073	-3.086	0.009	
NWA14	Intercept	18.939	2.342	8.086	0.000	0.078
	T_{incub}	0.322	0.214	1.504	0.155	
LE14	Intercept	25.597	2.299	11.135	0.000	0.000
	T_{incub}	-0.043	0.219	-0.195	0.848	

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720 Table 8. Mean and variance of the Kaplan-Meier survival estimates across all temperatures and
721 comparison (*t*-test, *p*-value) between populations for each year. The optimal temperature
722 (Optimal T) for survival was estimated from the location of the maximum density
723 distribution (see Figure 6A).

		Survival				
Year	Population	Mean	Variance	*t*-value (df)	*p*-value (one-tailed)	Optimal T (°C)
2012	GSL12	0.202	0.018	1.45 (34)	0.080	8.89
	LE12	0.289	0.047			11.36
2014	NWA14	0.167	0.014	0.76 (47)	0.225	12.06
	LE14	0.196	0.018			13.76
	LE12 vs. LE14			1.60 (43)	0.060	
	GSL12 vs. NWA14			0.87 (38)	0.194	

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726 Table 9. Parameters (with standard error) and log-likelihood of the best-fit skew-normal curve

727 fitted to the survival data for both years and each population.

Population	Location (ξ)	Scale (ω)	Shape (α)	Log-Likelihood
2012				
GSL12	0.0841 (0.0077)	0.1779 (0.0528)	-1.5015 (1.7266)	15.8897
LE12	0.0323 (0.0097)	0.3358 (0.0521)	-3.4186 (2.1020)	3.4622
2014				
NWA14	0.0209 (0.0084)	0.1887 (0.0360)	-4.2490 (4.8812)	11.2575
LE14	0.0204 (0.0028)	0.2218 (0.0218)	-8.2163 (3.2973)	37.3585

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730 Figures captions

731 Figure 1. A- May and June sea-surface temperature (SST) from a 25-year climatology showing the
732 longitudinal gradient in SST from west to east over the study area (refer to Supplementary material
733 for references and explanation on the construction of SST climatology maps). B- Sampling locations
734 (red squares) for northern shrimp females in 2011 and 2013 (see also Table 1) and the polygons
735 (black lines) used to construct the SST climatology for each region of hatching larvae.

736 Figure 2. A- Accumulated degree-days (DD) of females northern shrimp from 1 December to the
737 first observation of hatching for each experimental year (2011–2012 and 2013–2014). B- Mean
738 daily temperatures in the holding tank from 1 December to the first observation of hatching for
739 each experimental year (2011–2012 and 2013–2014).

740 Figure 3. Percent cephalothorax length increase (%CL increase) as a function of incubation
741 temperature for each larval group (jars) and population. A- Hatching to the first moult (stage II), B-
742 from stage II to stage III (second moult).

743 Figure 4. Comparison of relative growth at the first moult (estimated means %CL increase and ±
744 Standard Error) for each combination of temperatures and populations for 2012, and results of
745 Tukey HSD multiple comparisons. Values with same letters are not statistically different.

746 Figure 5. Thermal performance curves (solid line) and 95% confidence intervals for growth (%CL
747 increase) at the first moult for each population. A- for 2012 larvae, B- for 2014 larvae.

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Figure 6. A- Estimated survival (open circles) at the last observation of a live larva in the jar or when the jar was terminated at the third moult as function of incubation temperature. The curves represent the density distribution obtained from the parameters of the best-fit skew-normal curve (see Table 5). B- Mean (solid line) and spread (shaded area) between the first and third quartiles (25%, 75%) of the distribution, and the mean ± 1SD optimal temperature for survival estimated from 1000 random skew-normal density distributions.

Figure 7. Comparisons of optimal temperature for survival in populations of northern shrimp larvae from the Northeast Gulf of St. Lawrence (GSL), Northwest Atlantic (NWA), and the Lower St. Lawrence Estuary (LE). The vertical bars show the mean temperature and standard deviation at the probability density function (pdf) maximum of the 1000 simulated skew-normal density distributions (see Figure 6B). The X-axis labels are the sea-surface temperature (SST) ranges observed at %50 hatching for each population / region (see Table 1; Figure 8). The parameters of *t*-tests for unequal variances between populations are shown for 2012 and 2014 experiments.

Figure 8. Sea-surface temperature (SST) climatology (1985–2010) during ice-free months for each region considered in the study based on weekly composites. The shaded areas represent the interannual variability, ± 1SD about the mean.

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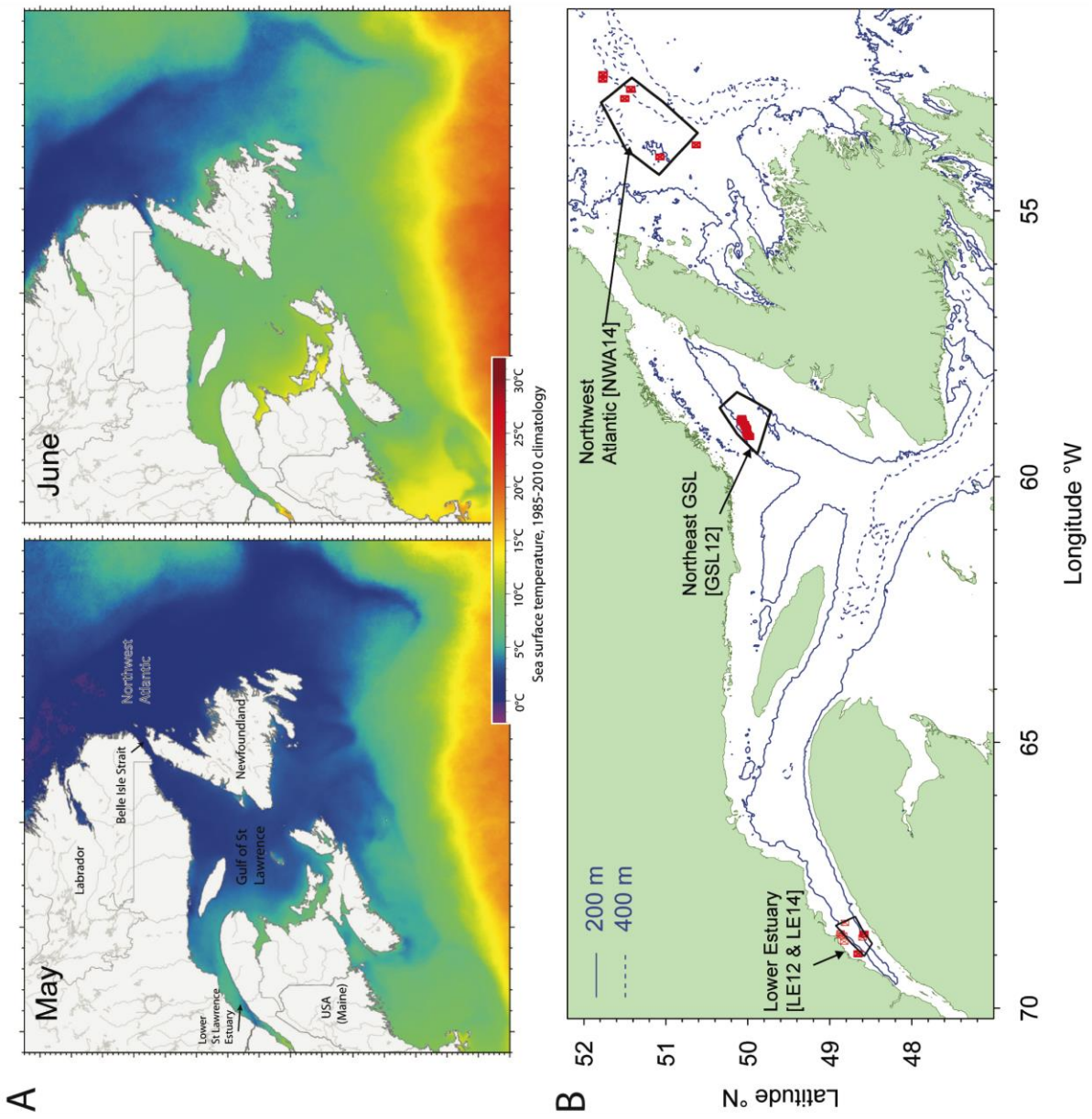

769

770 Figure 1.

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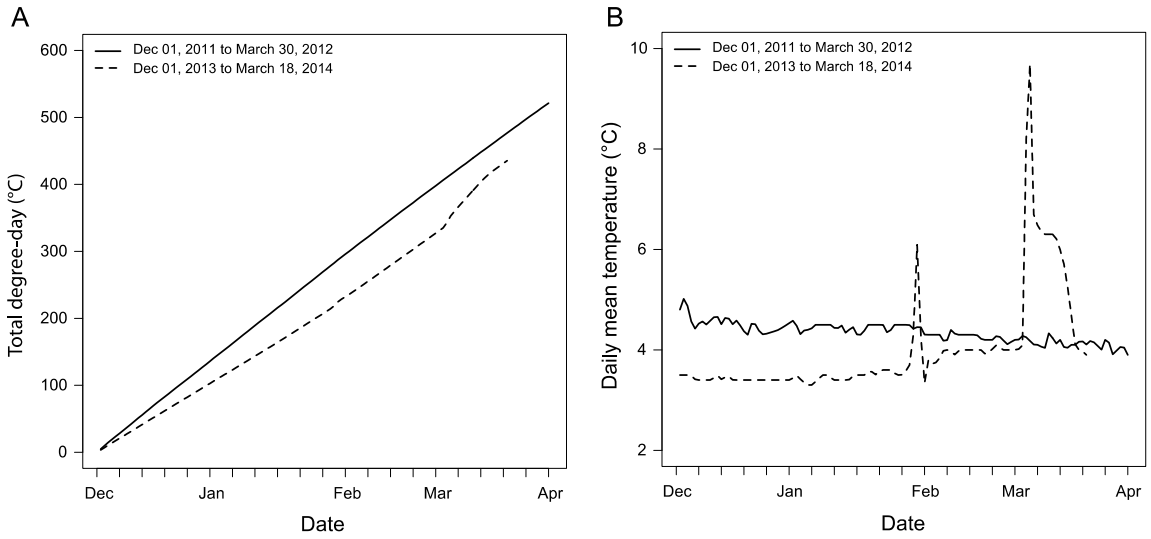

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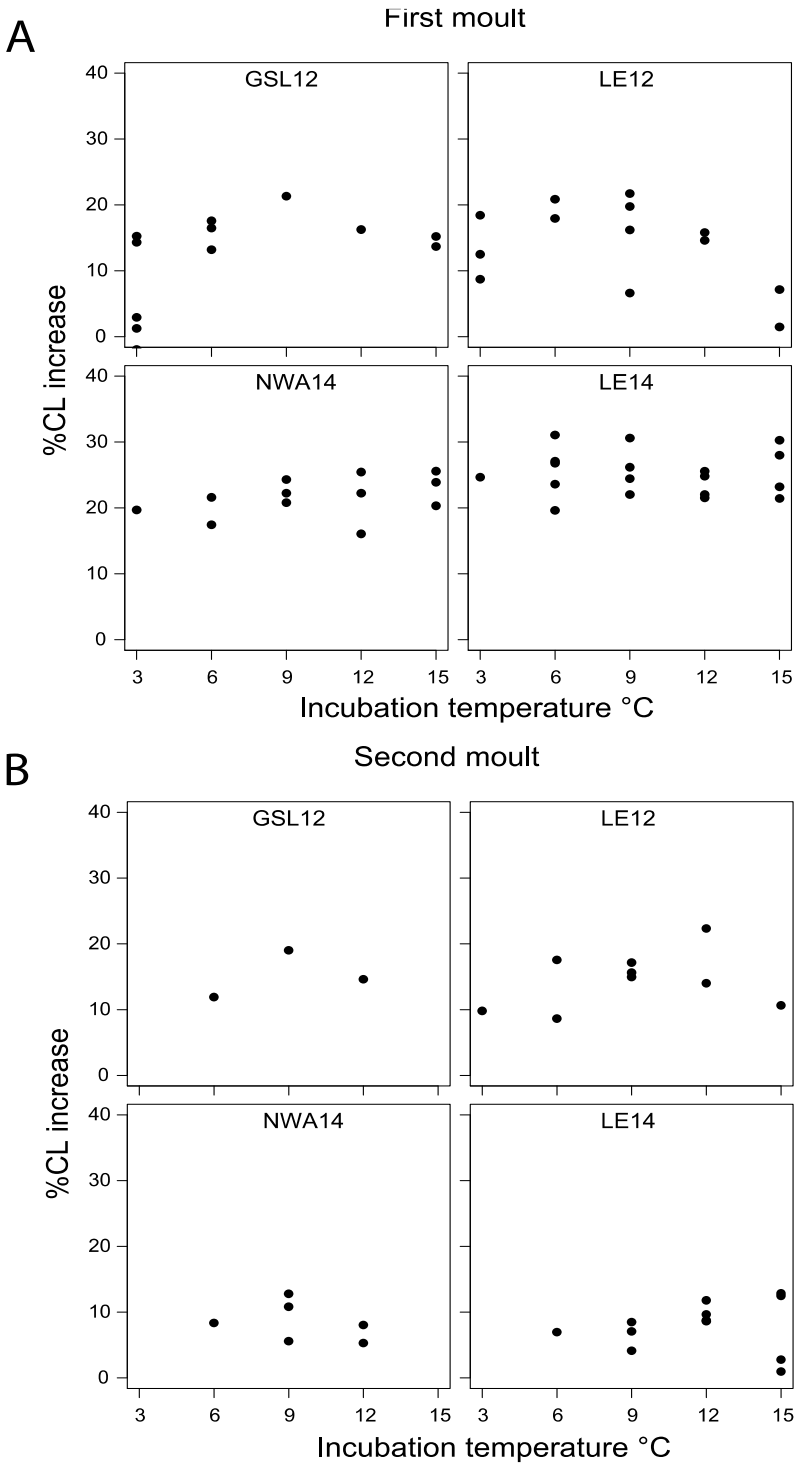

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777 Figure 3.

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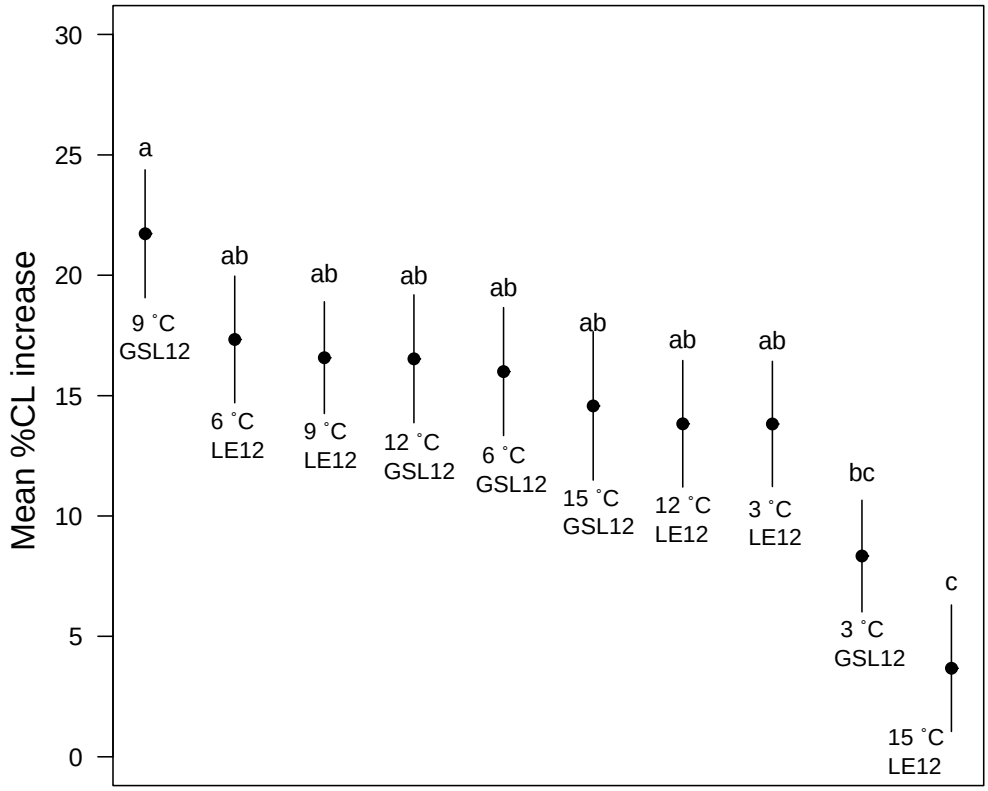

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781 Figure 4.

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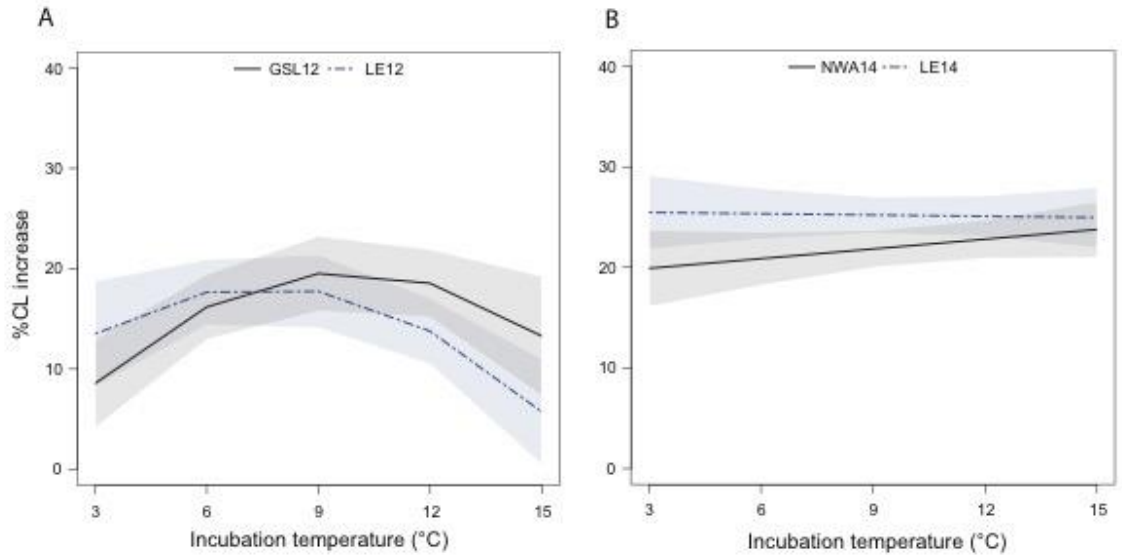

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786 Figure 5.

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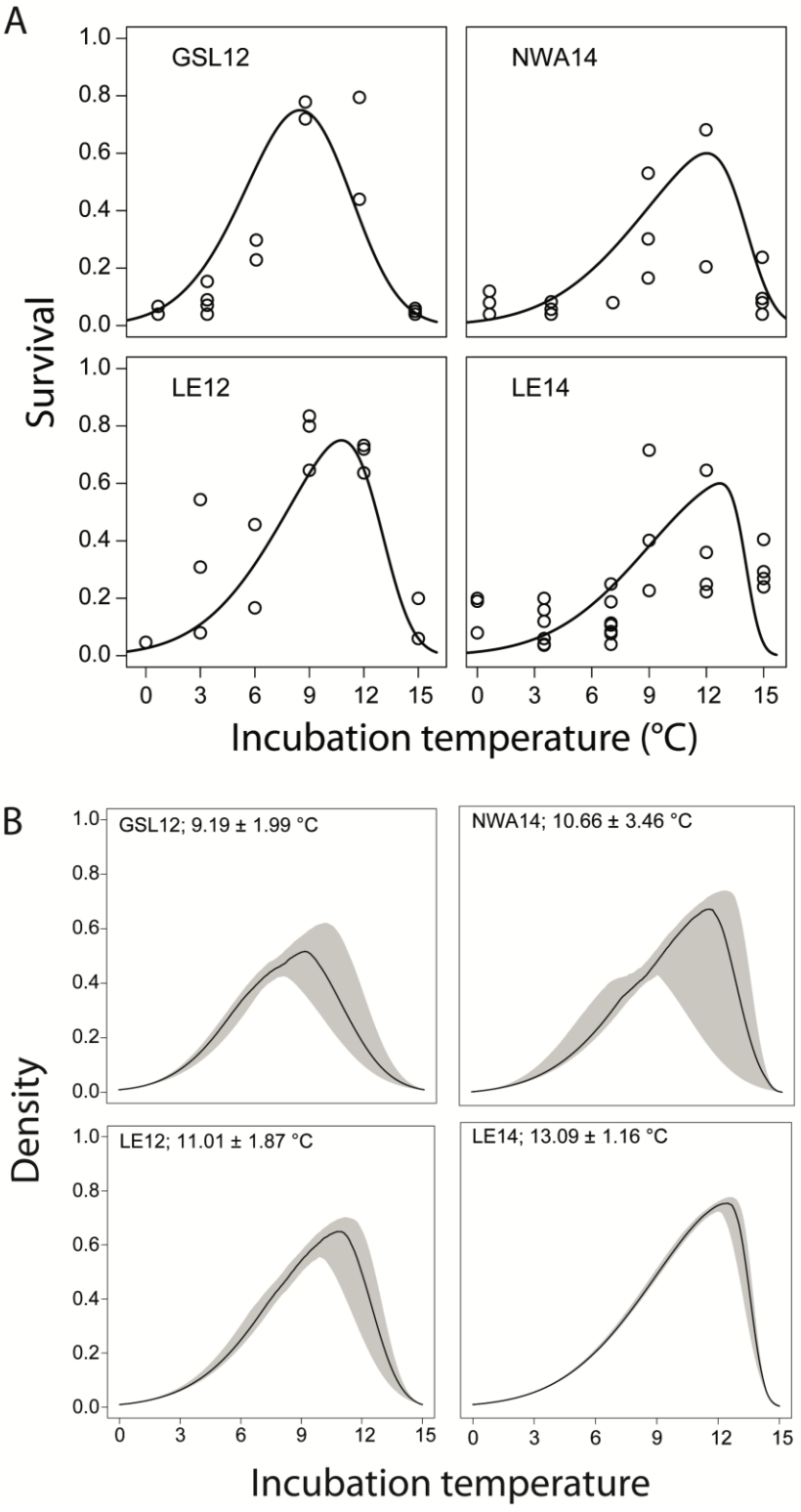

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789 Figure 6.

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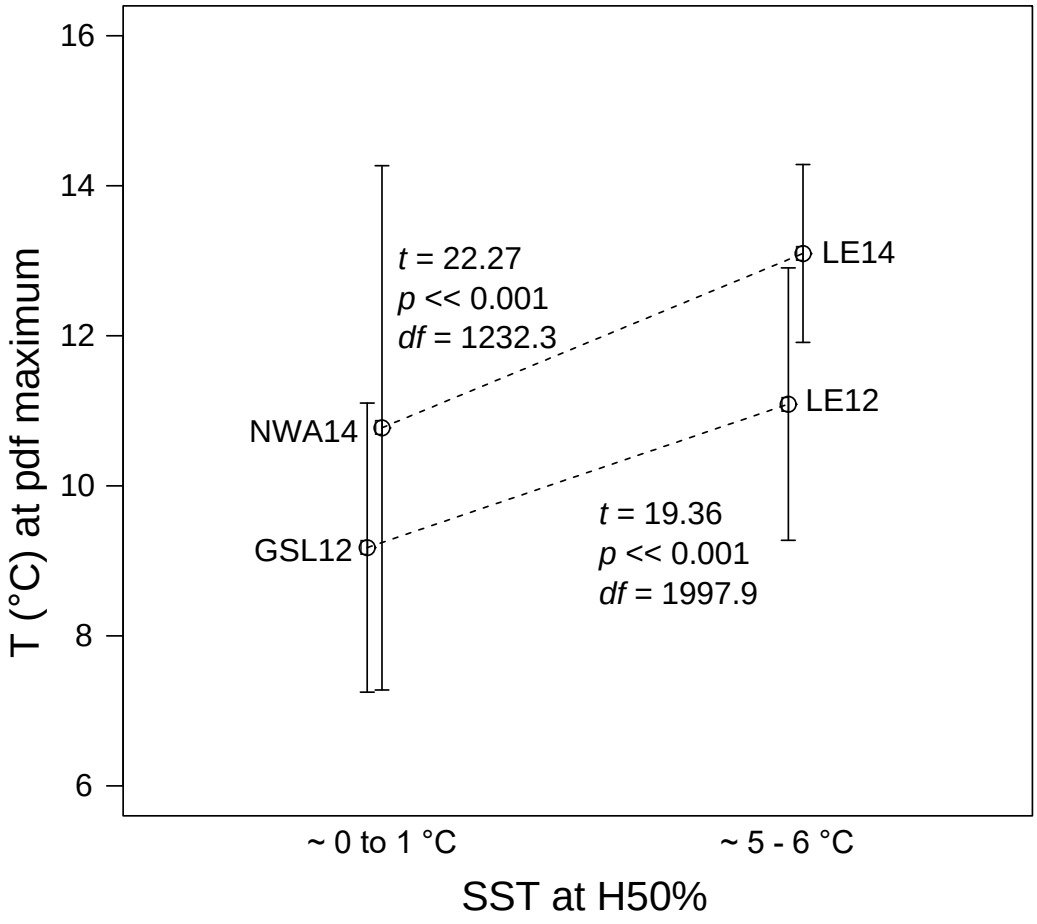

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792 Figure 7.

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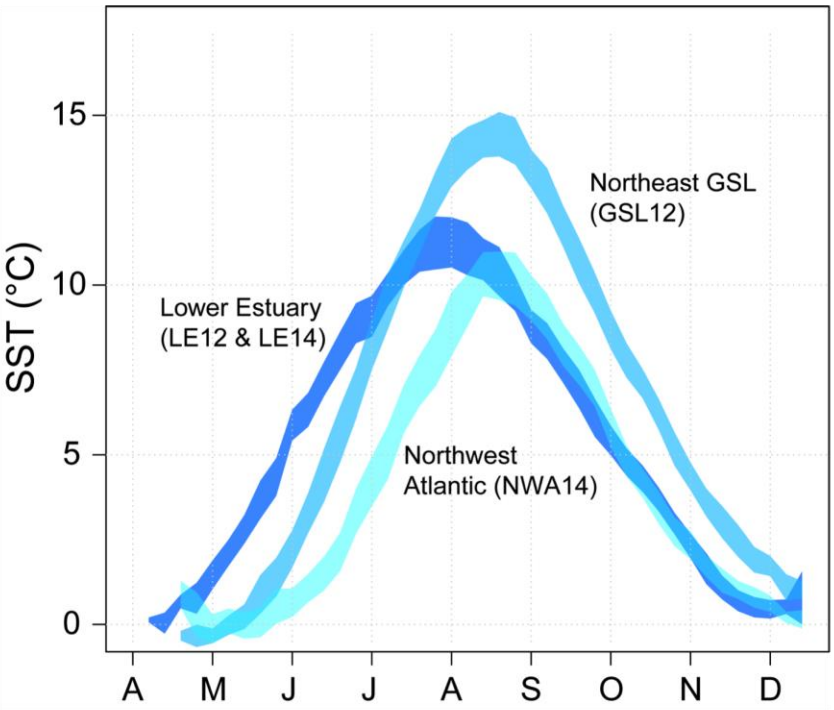

796

797 Figure 8.

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