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Abstract: Growth of Pandalus borealis post-larval stages was measured in relation to size and temperature. Growth characteristics, including intermolt period (IP), molt increment (MI) in size and mass, and tissue allocation in juvenile, male, and female shrimp, were evaluated at 2, 5, and 8°C, the temperature range where this species is generally found in the Northwest Atlantic. Significant variations in growth were associated with temperature and shrimp size. IP (days) increased significantly with shrimp size and was inversely related to temperature. Size (cephalothorax length in mm) and temperature effects were best described by: IP = 10^(0.67 log (CL) - 0.06 T - 1.34). The pronounced effect of temperature on IP while MIS changed little, indicated that the main influence of temperature on growth rate of P. borealis was through IP. Specific growth rate (SGRS) decreased rapidly with size to near zero values in females. Overall, juveniles were much more sensitive to temperature variations than adults, suggesting that temperatures encountered during the juvenile stage will largely influence the growth trajectory of the population.

SIZE AND TEMPERATURE-DEPENDENT VARIATIONS IN INTERMOLT DURATION AND SIZE INCREMENT AT MOLT OF NORTHERN SHRIMP, *PANDALUS BOREALIS*

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INTRODUCTION

Northern shrimp (*Pandalus borealis*), a commercially important species in Canadian waters, is a cold-water decapod widely distributed in the Northwest Atlantic and in the North Pacific (Bergström 2000). It is a protandric hermaphrodite species; each individual first matures and functions as a male, goes through a transition phase, and becomes a female. Along the latitudinal gradient extending from the Gulf of Maine to the Davis Strait, shrimp populations differ in abundance and in several life history traits (Apollonio et al. 1986; Lysy and Dvinina 1991; Anderson 1999; Anderson and Piatt 1999; Koeller 2000). Longevity, length at sex change, and maximum length of males and females increase with latitude while growth rate and proportion of spawning females relative to non-spawning females decrease. Although some results may contradict this general observation (Koeller 2006), temperature appears to play a major role in structuring these populations through its influence on growth patterns, length at sex change, and ovigerous period which are all interrelated. These important latitudinal changes suggest future potential effects of climate changes on shrimp population dynamics (Koeller et al. 2009).

Growth in crustaceans is characterized by a succession of molts (ecdycis) separated by intermolt periods (IP), with each of these two phases often exhibiting very different responses to intrinsic and extrinsic factors (Hartnoll 1982). Size and temperature are generally seen as the most important parameters influencing IP and molt increment (MI) (Kinne 1970; Hartnoll 1982). Usually, small individuals molt more frequently (Benayoun and Fowler 1980) and have larger relative MI than larger individuals of the same species (Hartnoll 1982). Temperature or seasonal fluctuations in temperature directly influence IP but temperature effect on MI is less predictable (Comeau and Savoie 2001; Hartnoll 2001). In most studies, MI was weakly or not influenced by temperature (Hartnoll 1982; Iguchi and Ikeda 1995; Hart 2001; Sudo 2003). However, decreases and increases in MI with increasing temperatures have been observed in different species (Paglianti and Gherardi 2004; Kulmiye and Mavuti 2005).

Different population and growth models have been developed for the study of shrimp population dynamics (Bergström 1992; Fu et al. 2001). However, no systematic study of the growth characteristics (IP and MI) of post-larval stages of *P. borealis* has been conducted in relation to important influential factors. Moreover, the absence of anatomical permanent structures that can be used to estimate age results in

uncertainties in age determination (i.e. growth) in shrimp, especially for older developmental stages (Apollonio et al. 1986; Savard et al. 1994; Aschan 2000; Hansen and Aschan 2000).

The development of growth models relies on precise measurements of both IP and MI at the individual level, which are hardly obtainable in natural environment. Experimental work may represent the best approach to develop models based on these two components, which characterize crustacean growth. For example, the growth rate of Antarctic krill, *Euphausia superba,* obtained from the measurement of IP and growth increment at molt in controlled experiments was central to the development of growth models in relation to sex, length and temperature for this species (Kawaguchi et al. 2006; Tarling et al. 2006). In the present study, laboratory experiments were used to measure growth of captive northern shrimp in relation to temperature. Growth of juveniles, males and females was assessed as ontogenetic changes in the distribution and vertical migration range influence the range of temperatures encountered by the different developmental stages of a population (Shumway et al. 1985). Growth characteristics, including IP, MI in size and mass, and tissue mass allocation in juvenile, male, and female shrimp were evaluated at three temperatures (2, 5, and 8 °C) corresponding to the temperature range where *P. borealis* is commonly found in Canadian waters. Predicted growth based on IP and MI at different temperatures was also compared to the growth of northern shrimp populations found in different temperature regimes.

MATERIAL AND METHODS

Shrimp capture and rearing conditions

Growth experiments were conducted at the aquaculture facilities of the Maurice Lamontagne Institute (Fisheries and Oceans Canada, Mont-Joli, Québec) between 2002 and 2005. Adult shrimp (15-30 mm in cephalothorax length, CL) were caught using a rigid frame trawl in the St. Lawrence Estuary (80-160 m depth) near Rimouski (48°36'N 68°29.5'W) each year between 2001 and 2003. Following capture, shrimp were transported to the MLI and kept in 670 l rectangular tanks under natural photoperiod at a temperature of 5 °C and a salinity > 28 ‰. Male and female shrimp used for the adult growth experiment

were caught in the spring of 2003 (April). They were maintained in stabulation until all females had released their larvae. In mid-July of 2003, male and non-ovigerous female shrimp were randomly assigned and acclimated to tanks that were gradually adjusted to the three experimental temperature treatments (2, 5, and 8 °C). The experiment began in August 2003. Shrimp were fed *ad libitum* three times a week with a diet consisting of equal parts of finely chopped Atlantic and Pacific krill, capelin and shrimp. Remaining food was cleaned before each feeding period.

Juveniles used in the experiments were raised in the laboratory. Ovigerous females caught in the St. Lawrence Estuary in the fall of 2002 and spring of 2003 and 2004 were isolated in May of 2003 and 2004 in tanks until hatching of the larvae. Larvae were kept in 80 l plankton-Kreisel tanks (Aiken and Waddy 1989) at 5 °C and fed *ad libitum* with live brine shrimp nauplii (*Artemia salinas*) until they reached juvenile stages. Juveniles (4-12 mm CL) were then randomly assigned to 80 l Kreisel tanks adjusted to the three experimental temperature treatments (2, 5, and 8 °C) until the beginning of the experiments. The experiment on juveniles in their second year of live began in June 2004 and the one on juveniles in their first year of life in March 2005. Juveniles were fed three to five times a week depending on their age, using the same diet as for the adults. Remaining food was cleaned before each feeding period.

Experimental setup

Experiments were conducted in 3 recirculated seawater tanks (1340 l); one for each of the three experimental temperatures. Each tank had a head tank with a capacity of 125 l, a sand filter and a heat pump to regulate water temperature. Seawater flow to the tank was ~ 30 l min^{-1}, whereas new seawater flow to the head tank was ~ 2.5 l min^{-1} (100% of seawater renewed every 10h). Experiments with juveniles (8-12 mm CL) and adults were conducted in compartmentalized baskets immersed in the tanks in order to follow individual shrimp. Compartments used for juveniles (8-12 mm CL) were 16.5 x 12 x 10 cm while those for adults were 35 x 30 x 35 cm. Vertical tray incubators connected to the seawater systems were used for the experiments with smaller juveniles in the 4-8 mm CL size range. Each incubator had 8 trays divided in 9 compartments (13 x 10 x 5.5 cm). Seawater inlet in tanks, baskets and compartments were

97 designed (openings and netting) and positioned to provide a uniform water circulation. Compartments were
98 used essentially to monitor individual shrimp. All statistical analyses were based on individual shrimp as
99 the experimental unit.

100 Two to four adults individually identified with a Visual Implant Tag (Northwest Marine
101 Technology, Shaw Island, Washington) fixed to the cephalothorax were placed together in each
102 compartment. Although tags were lost at molting, the low number of shrimp per compartment allowed
103 individual identification and post-molt tagging. CL (± 0.01 mm), total mass (M ± 0.001 g), sex, and tag
104 number were noted when shrimp were introduced in the compartments. Experiments with juveniles were
105 conducted with only one specimen per compartment. No manipulations (tagging and measurements) were
106 made on live juveniles. All shrimp were fed in excess during the experiments with the diet previously
107 described.

108 Between 2003 and 2005, IP, CL and mass increments as well as the distribution of total mass
109 between the different tissues (hepatopancreas, muscle, gonads, and remaining tissues, mostly carapace,
110 collectively referred to as carcass) were measured for juvenile and adult shirmp during a molt cycle.
111 Growth characteristics were measured at 2, 5, and 8 °C for adult males (15-22 mm CL; n=70) and females
112 (21-27 mm CL; n=45) and for juveniles in their first (5-8 mm CL; n = 69) and second (7-11 mm CL; n =
113 41) year of life.

114 A sample of juvenile and adult shrimp was taken in order to determine initial CL-mass
115 relationships and initial relative contribution of tissue masses (hepatopancreas, muscle, gonad, and carcass)
116 to the total mass of shrimp. For this group representing initial conditions, adults were randomly selected
117 from each tank at all temperatures (total n = 135) prior to the beginning of the experiment (i.e. transfer of
118 shrimp into compartments). Juveniles (total n = 58) of the initial sample were individually raised at each
119 temperature and euthanized 15 days after the first molt that occurred in the compartments. CL, M, and
120 tissue masses were noted for juveniles with CL > 8 mm while CL and M only were noted for smaller
121 juveniles (i.e. CL < 8 mm). CL was measured (± 0.01 mm) with a calliper for adults or with image analysis
122 for juveniles (video camera [SPOT INSIGHT V 3.2] mounted on a stereomicroscope [WILD
123 HEERBRUGG] and connected to a frame grabber, used together with image analysis software [Image-Pro

Plus, ver. 4.1.1.2]).

Compartments were checked daily for molts. At the first ecdysis, the exuvia was discarded and the date noted as the starting time of the IP of interest. Adults were weighed 15 days following the first ecdysis (premolt mass for determination of the growth in mass between two molts). Premolt mass of juveniles was not measured directly to minimize the influence of manipulations on growth performance, considering the shorter IP in juveniles. Following the second ecdysis, the exuvia was recovered, measured, and the size was used as premolt CL. Initial M of juveniles was estimated from their premolt CL, using the relationship between CL and M obtained from the initial group sampled at the start of the experiment. Juveniles and adults were killed and dissected 15 days after the second ecdysis. For each shrimp, final CL, M, as well as muscle, hepatopancreas, gonad and carcass masses were measured. The only exception was for juveniles in the 4-8 mm CL range for which only CL and M were measured.

Data calculation and statistical analyses

IP was defined as the duration in days between two successive molts.

The relative size increment at molt (MI_S) was calculated as:

$$MI_S = 100 \times (CL_2-CL_1) / CL_1$$

where CL_1 and CL_2 are the premolt and postmolt CL, respectively.

The relative mass increment at molt (MI_M) was calculated as.

$$MI_M = 100 \times (M_2-M_1) / M_1$$

where M_1 and M_2 are the pre-molt and post-molt values of total mass, obtained 15 days following the first and second ecdysis, respectively. M_1 was measured directly in adults and estimated for juveniles with the M-CL relationship of the initial juvenile group.

The specific growth rate (Ricker 1975) in size (SGR_S) and mass (SGR_M) were also calculated as:

$$SGR_S = (\log CL_2-\log CL_1) / IP$$

149 $SGR_M = (\log M_2 - \log M_1) / IP$

150 The distribution of total mass in the different tissues was examined by calculating relative mass
151 indices as described in Brillon *et al.* (2005). Hepatopancreas (HSI), muscle (MSI), gonads (GSI) and
152 carcass (CSI) masses were expressed as percentage of somatic mass (total mass less the mass of the
153 gonads).

154 Values of IP, MI, SGR and relative tissue mass indices (HSI, MSI, GSI and CSI) were compared
155 between temperatures and developmental stages (juvenile, male, and female) using 2-way ANOVA with
156 interaction followed by Tukey's multiple comparisons (Sokal and Rohlf 1995). When the interaction was
157 significant, the comparisons of adjusted means that were of interest (i.e. stages at each temperature and
158 temperatures at each stage, 18 comparisons) were done by a series of one-degree-of-freedom tests (t-test),
159 and the significance level was adjusted for the number of comparisons of interest (critical value = 0.0028
160 $((1-0.95)^{1/18})$ according to the Dunn-Sidák method (Sokal and Rohlf 1995). Graphical examination of the
161 data and Brown-Forsythe tests were used to examine homogeneity of variances. When normality of data
162 and homogeneity of variances were not met, ANOVA were performed on log-transformed, square root-
163 transformed or rank-transformed data (Quinn and Keough 2002). If these transformations were not
164 sufficient to meet the criteria for an ANOVA, separate 1-way ANOVAs were performed for each stage to
165 compare the three temperatures. In this case, the criteria for an ANOVA were met after log-
166 transformations.

167 Regression analysis was used to estimate IP and MI_S in relation to pre-molt size (CL in mm) and
168 temperature. Multiple regression models were used to predict the evolution of size at age at fixed
169 temperatures of 2, 5, and 8°C. Mean size at age (CL) with confidence intervals for each temperature were
170 generated with a Monte Carlo analysis using 1000 iterations of random values from a normal distribution of
171 the parameter estimates of the regression models (parameter estimates ± SE) for IP and MI_S. The
172 projections of size at age began with age 1. The starting values for sizes at age 1 at each temperature were
173 based on various studies reported by Bergström (2000). These values were fixed at 7.3, 8.8, and 11.0 mm at
174 2, 5, and 8 °C, respectively. In the projections, it was assumed that sex change was initiated when shrimp
175 reached sizes of approximately 21-23 mm in the last quarter of the year (Skuladottir et al. 2005; Koeller

2006). At the female stage, the ovigerous period was taken into account by setting spawning time between day of the year 200 and 250 (Koeller et al. 2009) and using as IP, the duration of the ovigerous period at the different temperatures. The duration of the ovigerous period was fixed at 236, 177, and 135 days at 2, 5, and 8 °C based on a laboratory study in controlled conditions at these 3 temperatures (Brillon et al. 2005).

Finally, estimations of sizes at age for populations of northern shrimp in different locations and subjected to variable bottom temperatures were compared to the projections of size at age obtained from the multiple regressions models for IP and MI_S. Age, which is usually based on hatching date in the different populations, was standardized using January 1st as starting date.

All statistical analyses were carried out with SAS software (SAS Institute version 8.2, Cary, NC). Monte Carlo analyses were done using PopTools, an add-in tool for PC versions of Microsoft Excel downloadable from: http://www.cse.csiro.au/poptools/.

RESULTS

Growth in size and mass during a molt cycle

For each developmental stage, mean initial CL was similar (1-way ANOVA, $p \geq 0.67$) between temperatures (Table 1). Mean initial mass of male and female shrimp was also identical (1-way ANOVA, $p \geq 0.56$) between temperatures. No comparison was done for the initial masses of the juveniles as these were obtained from the following relationship between initial CL (range = 6.17 – 9.01 mm) and M :

$$\text{Log (M)} = -3.103 + 2.882 \text{ Log (CL)} \qquad (n= 146, r^2=0.94)$$

Significant effects of temperature and developmental stage on IP and MI were observed for shrimp monitored during a complete molt cycle. IP was influenced by both temperature and developmental stage and the interaction was significant (2-way ANOVA, Temp x Stage, $F_{4,\ 219} = 8.68$, $p < 0.0001$). IP significantly decreased with increasing temperature for juveniles, males, and females (Fig. 1). Pairwise comparisons for each developmental stage indicated significant differences between each temperature ($p <$

0.0001). The only exception was observed for males where IP did not differ between 5 and 8 °C (Dunn-Sidak test; $p = 0.0038$). For all developmental stages, a higher decrease in IP was observed between 2 °C and 5 °C than between 5 °C and 8 °C. IP was 32-37% shorter at 5 °C than at 2 °C for both males and females and 20% shorter at 8 °C than at 5 °C for females. In juveniles, differences in IP were less important, IP being 40% and 32% shorter at 5 °C than at 2 °C and at 8 °C than at 5 °C, respectively. IP was identical for males and females at the 3 temperatures ($p > 0.33$) but approximately twice as long as in juveniles for each temperature (Pairwise comparisons $p < 0.0001$).

Increases in CL and M at the 3 temperatures were different for juveniles, males, and females (Fig. 2) with significant interactions between developmental stage and temperature for both CL and M (2-way ANOVA, MI_S: $F_{4, 164} = 2.48$, $p < 0.05$; MI_M: $F_{4, 164} = 7.10$, $p < 0.0001$). Mean MI_S ranged between 3.5 and 5.3% for juveniles and males without any significant effect of temperature. In females, MI_S ranged between 1.4 and 3.7% and was significantly lower at 2 °C than at 5 °C ($p = 0.0008$) and 8 °C ($p = 0.0015$). A significant increase in MI_M from 18.6 to 27.2% was observed for juvenile shrimp raised at temperatures between 2 and 8 °C ($p = 0.0001$) (Fig. 2). In males, mean MI_M ranged between 3.9 and 7.7% with a significant increase between 2 and 5 °C ($p = 0.0012$) while in females, MI_M was lower (1.1 to 4.2%) and not different between temperatures ($p > 0.016$) (Fig. 2). No difference in MI_S was observed between juveniles, males and females at 5 and 8 °C (pairwise comparisons: $p \geq 0.031$) but at 2 °C, MI_S was lower in females than in juveniles and males ($p < 0.0023$). At each temperature, MI_M differed between developmental stages (pairwise comparisons: $p < 0.0001$) with the exception of males and females which had similar MI_S at 2 °C ($p = 0.36$) and 8 °C ($p = 0.03$).

Specific growth rate obtained from CL and mass increments at molt and IP were used to describe the combined effects of these two components of growth. There was a significant interaction between temperature and developmental stage for both SGR_S and SGR_M (2-way ANOVA, Temp x Stage, $F_{4, 164} =$ 2.91 and 26.64, $p < 0.05$ and 0.0001, respectively). In juvenile shrimp, both SGR_S and SGR_M increased with temperature (Fig. 3) with significant differences between each of the three temperatures (pairwise comparisons: $p < 0.0001$). In males, a significant increase in SGR_S was observed between 2 and 8 °C ($p <$ 0.0015). However, no difference in SGR_S between 2 and 5 °C ($p = 0.0030$) and 5 and 8 °C ($p = 0.63$) was detected (Fig. 3). SGR_M for males was similar at the 3 temperatures ($p > 0.02$), whereas SGR_S and SGR_M

for females were not influenced by temperature ($p > 0.0068$). At each temperature, SGR_S and SGR_M were also significantly higher in juveniles than in adults ($p < 0.0003$).

Hepatopancreas, muscle and carcass masses constituted 5.8-8.3%, 34.7-43.7% and 43.4-50.5% of the shrimp mass, respectively (Table 2). Gonad mass represented less than 0.3-0.4% of male mass while female GSI ranged between 1 and 2.6% at the beginning of the experiment and was below 0.8% at the end of the experiment.

Analysis of variance on the different tissue masses indicated significant interactions between temperature and developmental stages for initial HSI (2-way ANOVA, Temp x Stage, $F_{4, 182} = 2.43$, $p < 0.05$), initial CSI ($F_{4, 179} = 2.99$, $p < 0.03$), final MSI ($F_{4, 106} = 3.85$, $p < 0.006$), and final CSI (Temp x Stage, $F_{4, 105} = 7.28$, $p < 0.0001$). Thus, *a posteriori* comparisons were conducted among temperatures at each developmental stage and among stages for each temperature for these variables. Initial HSI differed significantly between temperatures for females at 2 and 8 °C ($p = 0.0004$) and HSI was higher in females than in juveniles at each temperature ($p < 0.001$) (Table 2). Initial MSI was not different between temperatures (2-way ANOVA, $F_{2, 182} = 2.46$, $p > 0.08$) but was significantly influenced by developmental stage (2-way ANOVA, $F_{2, 182} = 248.96$, $p < 0.0001$) with MSI being lower in juveniles than in adults. Initial CSI only differed between temperatures for males with a significant difference between 2 and 8 °C ($p = 0.0003$) and between 5 and 8 °C ($p = 0.0009$). However, at each temperature, initial CSI was significantly higher in juveniles than in adults ($p < 0.0001$). Initial GSI for adult shrimp was significantly influenced by sex (2-way ANOVA, $F_{1, 128} = 424.32$, $p < 0.0001$) with initial female GSI being 3.3 to 7.8 times higher than in males at the different temperatures (Table 2).

At the end of the experiment, HSI was similar across temperatures and developmental stages (2-way ANOVA, $p > 0.76$). Some differences were observed in final MSI and final CSI. However, no significant distinct pattern associated with either temperature or developmental stage was detected. Final GSI in males decreased with temperature (1-way ANOVA, $F_{2,46} = 4.27$, $p = 0.02$) with a significant difference between 2 and 8 °C. In females, final GSI was affected by temperature (1-way ANOVA, $F_{2,34} = 4.17$, $p = 0.024$) with a significant difference between 2 and 5 °C ($p = 0.018$) and between 5 and 8 °C ($p = 0.016$).

257

258 **Growth models**

259 Significant relationships were observed between intermolt duration and shrimp size at the 3
260 temperatures (Fig. 4). The slopes of the regressions on log transformed data differed between all
261 temperatures ($p>0.0001$), the steepness of slopes increasing with temperature (Table 3). Comparisons of
262 intermolt duration for CL of 7, 19, and 25 mm indicated more important differences in IP between 2 °C and
263 5 °C than between 5 °C and 8 °C. Furthermore, temperature-induced differences in IP were proportionally
264 greater for smaller shrimp. While a 2.5 fold difference in IP was observed in juvenile shrimp (7 mm CL)
265 between 8 °C and 2 °C, IP was 1.8 times shorter at 8 °C than at 2 °C in adult shrimp (25 mm in CL). A
266 multiple regression model using size (i.e. pre-molt CL) and temperature as dependent variables explained
267 87% of the variability in intermolt duration (Table 4). Size and temperature explained 52% and 35%
268 (partial r^2) of the variability in IP, respectively.

269 MI_S was less dependent on pre-molt size and temperature. A significant relationship ($p<0.05$)
270 between MI_S and pre-molt CL was only observed at 2 °C (Fig. 4). Nevertheless, in a multiple regression
271 model, both size (i.e. pre-molt CL) and temperature had a significant effect on size increment at molt
272 although explaining only 12% of the variability in MI_S (9.4% for Cl_I and 2.3% for temperature, Table 4).

273 Projections of size at age based on IP and MI_S indicated that at 8 °C, shrimp reached a size of 30
274 mm in CL at the age of 5 while the same size was reached at the age of 8 at 5 °C. At 2 °C, a size between
275 21 and 25 mm was only reached at the age of 9 (Fig. 5). Variations in the size at age estimated from modal
276 analysis of length frequency distributions for populations found in different temperature conditions (Table
277 5) are in good agreement with the projections based on IP and MI_S for the different temperatures (Fig. 6).
278 Growth for populations in the temperature range between 1 and 4.5 °C are largely included in the interval
279 for the projections of growth at 2 and 5 °C. Populations found at higher maximum temperatures (6 to 6.5
280 °C) had sizes at age similar to those obtained from the projection at 8 °C. Some discrepancies between
281 observed and projected size at age are observed for younger ages (below age 2 to 3); growth rates appearing
282 faster in the natural populations. Predicted sizes at age for older ages (> age 4) at 2 °C also tended to be
283 lower compared to sizes at age for natural populations exposed to the lowest temperatures (Barents Sea and
284 Davis Strait populations).

DISCUSSION

This study represents the first assessment of the growth characteristics of *P. borealis* over most of its size range. The laboratory experiments allowed the determination of the growth parameters MI and IP for juvenile and adult *P. borealis* in the size range of 5 to 27 mm CL at temperatures (2–8 °C) largely covering the temperature range where *P. borealis* is usually found (Shumway et al. 1985; Bergström 2000). Observed patterns of variations in IP and MI with size and temperature corroborate the general results observed in many crustacean species. IP decreased with increasing temperature at all developmental stages and increased with pre-molt size in all treatments, juveniles showing the highest molting frequency. MI was also influenced by shrimp size, with greater size increments in juveniles than in males and females. However, temperature had a smaller effect on MI and this effect was different between developmental stages. MI_M was 4-fold higher in juveniles than in males and females whereas MI_S only differed significantly between juveniles and females at 2 °C. Variation in MI_S of *P. borealis* was also of relatively small amplitude over the range of temperature conditions tested. Variations in specific growth rates, which integrate both IP and MI, with developmental stages, clearly demonstrate the positive effect of temperature on the growth of *P. borealis* and the decrease in growth with increasing size. SGR_S for juveniles and males significantly increased with temperature and SGR_S of juveniles was significantly higher than in adults.

The present study indicates a pronounced effect of temperature on IP while MI_S changed little, indicating that the main influence of temperature on growth rate of *P. borealis* is through IP. Hence, the shortening of IP results in a faster growth at higher temperature. Hartnoll (1982) reported various examples of crustaceans in which an increase in temperature shortened IP and decreased or had no effect on CL increments per molt. Wainwright and Armstrong (1993) showed a declining probability of molt for mature Dungeness crab, *Cancer magister*, compared to juveniles. Temperature has been shown to strongly influence IP and to have a negligible influence on MI for *C. magister*. Moreover, higher temperature may result in faster growth even in cases when MI decreases with increasing temperature, if higher molt frequency compensates for reduced MI (Paglianti and Gherardi 2004). This lengthened IP duration with lower temperature may reflect the greater time needed for the accumulation of sufficient energy reserves for molting. A similar response in growth was observed in the arctic-boreal species, *Sclerocrangon boreas.*

313 Size-specific MI did not vary with temperature (6.3 and 9.1 °C) whereas IP was approximately 50 %
314 shorter at the highest temperature regime (Ingram 1979 in Sainte-Marie et al. 2006). In *Neomysis integer*
315 (2-12 mm) a decrease of IP from 20 to 5 days and a increase of MI_S from 4 to 12 % were observed between
316 10 and 15 °C (Winkler and Greve 2002). Studying the impact of temperature on growth rates along the
317 developmental stages of this species, the authors concluded that temperature affected growth of *N. integer*
318 by principally controlling intermolt periods. In juvenile tiger prawn, *Penaeus esculentus*, and mysid,
319 *Acanthomysis robusta*, it was also concluded that the increase of IP with decreasing temperature was the
320 major factor controlling juvenile growth rate (O'Brien 1994).

321 Increases in mass at the different temperatures were not associated with differential investment in
322 hepatopancreas, muscle, gonads or carcass. Even if differences were observed in some of the tissue mass
323 indices, there was no systematic pattern of variation with temperature indicating potential variations in
324 seasonal energy allocation or reproductive investment associated with temperature in the present study.
325 Initial GSI values for females indicate that many females were maturing whereas GSI values at the end of
326 the experiment indicate that most of the females were in a recovery phase. Although this observation might
327 suggest that captivity inhibited maturation, we hypothesized that many of the maturing females ended
328 maturation, made their nuptial molt and spawned during the experiment. As females and males were
329 separated during the experiments, eggs could not be fertilized. Visual observations made in our laboratory
330 indicate that the females do not retain unfertilized eggs. As spawning occurs just after molting (Brillon et
331 al. 2005), the egg mass spawn by mature females was most probably lost before the sampling and weighing
332 of the shrimp (15 days after the molt).

333 The multiple regression models examining size and temperature effects on the growth of *P.*
334 *borealis* explained significant proportions of the variation in IP and MI_S. Both temperature and pre-molt
335 size accounted for important proportions of the variation in IP (35% and 52%, respectively). However, both
336 factors only accounted for 12% of the variation in MI_S. Other factors not measured in the present study may
337 influence size increment at molt. For example, food supply, which may influence growth (Hartnoll 2001),
338 was not specifically measured in the present study. In our experiments, shrimp were always fed in excess.
339 In Antarctic krill, growth rates have been related to food quantity and quality (Ross et al. 2000; Atkinson et
340 al. 2006). However, it was demonstrated that food did not influence the IP (Tarling et al. 2006). In *P.*

341 *borealis* which feeds on pelagic organisms, benthic polychaetes, and detritus from sediments, lipid content
342 exhibited marked seasonal oscillations while growth in carapace length showed only comparatively weak
343 seasonality (Hopkins et al. 1993). This suggests that in natural environment, temperature may have a larger
344 influence on IP and MI_S than food availability in northern shrimp but further studies are necessary to assess
345 their relative importance.

346 Regression models indicate that the growth trajectory of individual shrimp should largely be
347 influenced by environmental conditions during the juvenile stage. The juvenile stage is the most sensitive to
348 variations in temperature conditions, differences in IP with temperature being more important for smaller
349 shrimp sizes. The slower growth observed for females at all temperatures in the present study, the costs of
350 energy maintenance for females during the ovigerous period (Brillon et al. 2005), and energy investment in
351 the gonads during the vitellogenesis period would suggest that the growth of shrimp following sex change
352 will be reduced and almost independent of temperature (for the temperature range studied). Molting events
353 in females are limited by the reproductive cycle. Females of *P. borealis* molt in fall just before mating and
354 spawning, carry their eggs for a period of 6 to 10 months and molt again in spring following the release of
355 the larvae (Shumway et al. 1985; Koeller et al. 2009). The duration of the ovigerous period which varies
356 from 236 to 135 days at temperatures between 2 °C and 8 °C (Brillon et al. 2005) is twice as long as IP of
357 non-ovigerous females at the same temperatures. Moreover, based on our measurements of IP, reproducing
358 females could not complete more than 1 or 2 molt cycles during the 2 to 6 months when they do not carry
359 eggs. The reproductive cycle therefore limits molting frequency to 2 or 3 cycles per year in reproducing
360 females, and hence limits their growth rate. Thus, the asymptotic female size of the population (i.e.
361 maximum size) could be largely determined by the size of shrimp following sex change. Shumway et al.
362 (1985) suggested that growth rate increased during sex change. However, no specific study compared the
363 growth of males in the process of sex change to that of males of similar size delaying the initiation of sex
364 change.

365 Most studies on the growth of northern shrimp have been carried out on populations in the open
366 sea by the identification and tracking of modes (cohorts) using length-frequency distributions (Skuladottir
367 et al. 1991; Bergström 1992; Hansen and Aschan 2000). As in most crustaceans, the difficulty of separating
368 the components of growth (MI and frequency) has prevented the complete description of this fundamental

process in natural populations (Ehrhardt 2008). Although laboratory work cannot completely mimic natural conditions, the present study clearly delineate the relative importance of IP and MI in the growth of northern shrimp. Moreover, projections of size at age at different temperatures based on regression models relating IP and MI_S to size and temperature are in good agreement with sizes at age estimated from modal analysis of length distributions of populations in different temperature regimes.

Apparent divergence in observed growth rate for age 2 and 3 shrimp in natural populations and predicted growth using IP and MI_S was examined by comparing predicted growth of juveniles in the present study to annual length increment of juvenile shrimp found at different bottom temperatures in West Greenland (Wieland 2005). In West Greenland, annual length increments for age 2 and 3 showed considerable variability and were not influenced by bottom temperature in the range of 1 to 5 °C. Increments ranged from 2.7 to 4.7 mm CL per year at age 2 (11-14 mm CL) and from 1.5 to 3.7 mm CL per year at age 3 (15-19 mm CL) (Wieland 2005). Predicted size increments for juveniles of the same sizes at 2 °C and 5 °C in the present study varied between 1.9 and 3.5 mm CL per year for age 2 and 1.7 to 3.2 mm CL per year for age 3. Thus, predicted increments for sizes below 14 mm CL may have been slightly underestimated in the present study. Comparable or higher size increments for juveniles of that size are only observed at 8 °C (5.2 to 5.7 mm CL per year). However, for larger juvenile sizes, a very good correspondence in increments per year is observed.

Specific comparisons between estimated sizes at age in natural populations and projected sizes at age at a constant temperature are difficult to interpret. In natural populations, ontogenetic, seasonal, and diurnal migration patterns can result in large differences between temperatures experienced by free-ranging shrimp in different parts of their life cycle and the mean temperatures used as selected temperatures by the populations. Moreover, as already mentioned, uncertainties in age determination of shrimp in natural conditions can lead to inaccuracies in the determination of size at age.

Temperature regimes reported for the different populations represent mean bottom temperatures encountered during annual surveys. These temperatures may differ from average ambient conditions to which northern shrimp are subjected, as they do not account for diurnal vertical migration, seasonal, spatial and ontogenetic migrations. In the natural environment, differential distribution of juveniles, males and

396 females has often been observed. In most areas, juvenile shrimp are usually observed inshore in shallower
397 waters where they are exposed to different and more variable temperatures (Shumway et al. 1985; Simard
398 and Savard 1990). In Flemish Cap, many studies reviewed by Skuladottir et al. (2005) noted the prevalence
399 of smaller males at shallower depth and females at greater depths. In some populations, ovigerous females
400 also migrate during fall and winter from offshore to nearshore colder waters (Bergström 2000; Clark et al.
401 2000). This behaviour is suggested to be an adaptation to improve the match between egg hatching and the
402 phytoplankton bloom (Koeller et al. 2009). Diurnal vertical migration has also been observed in many
403 populations with some differences in the extent of the migration depending on shrimp size (Shumway et al.
404 1985; Bergström 2000).

405 Sampling bias due to the ontogenetic distribution pattern of shrimp and inaccuracies in the
406 methods used to determine size at age may also explain some of the differences between predicted and
407 observed sizes at age. For example, differences in the length of shrimp from the same cohort sampled in
408 different depth in the Barents Sea indicate the importance of sampling design to accurately reflect size
409 frequency distribution which is used to determine size at age (Aschan 2000). Moreover, the absence of
410 permanent anatomical structure allowing individual determination of age is increasing the difficulty in
411 determining and interpreting age and growth.

412 Given all the uncertainties in determining size at age and the influence of temperature on growth
413 derived from these measures in natural populations, the present study offers an alternative in predicting
414 growth response of shrimp populations to modifications of their environment. In the context of large-scale
415 climatic change it has already been anticipated that *P. borealis* will be affected by changes in both the
416 timing of spring bloom and bottom temperatures (Koeller et al. 2009). The present study clearly shows the
417 influence of temperature on growth, which will have direct impacts on many life history characteristics of
418 the populations. Growth rate will influence maximum size of males, size at sex change, maximum female
419 size, and fecundity. Moreover, temperature through its influence on intermolt duration might affect the
420 timing of spawning as well.

421 Our results provide insights for the interpretation of growth patterns of populations in the wild. In
422 seasonally and annually varying environments, different cohorts of postlarvae, settling at different times of

the year (different temperatures), will contribute differentially to the recruitment of shrimp (Staples and Heales 1991). The temperature regime encountered during the juvenile stage (i.e. first 2-3 years) should drive the growth trajectory of the population as temperature effects on intermolt duration and size increment at molt are more important for juvenile than adult stages. Further studies of juvenile growth in controlled conditions (i.e. CL between 5-15 mm) are necessary to validate growth measured in the present study for that size range. Moreover, a better knowledge of juvenile distribution and migration is necessary to understand growth trajectories of shrimp populations in natural environment and predict the impact of large-scale change in the environment on shrimp population dynamics.

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444 **BIBLIOGRAPHY**

445

446 Aiken DE, Waddy SL (1989) Culture of the American lobster, *Homarus americanus*. In: Bogden AD (ed)
447 Cold-water aquaculture in Canada. The Canadian Institute for Research on Regional Development,
448 Moncton, Canada, pp 79-122
449 Anderson PJ (1999) Pandalid shrimp as indicator of ocean climate regime shift. NAFO SCR doc. 99/80 No.
450 N4152.
451 Anderson PJ, Piatt JF. 1999. Community reorganization in the Gulf of Alaska following ocean climate
452 regime shift. Mar. Ecol. Prog. Ser. 189: 117-123. doi: 10.3354/meps189117.
453 Apollonio S, Stevenson DK, Dunton EE (1986) Effects of temperature on the biology of the northern
454 shrimp, *Pandalus borealis*, in the Gulf of Maine. NOAA Tech. Rep. 42: 22 pp
455 Aschan M (2000) Spatial variability in length frequency distribution and growth of shrimp (*Pandalus*
456 *borealis* Kroyer 1838) in the Barents Sea. J Northwest Atl Fish Sci 27: 93-105
457 Atkinson A, Shreeve RS, Hirst AG, Rothery P, Tarling TA, Pond DW, Korb RE, Murphy EJ, and Watkins
458 JL (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based
459 on food, temperature, body length, sex, and maturity stage. Limnol Oceanogr 51: 973-987
460 Benayoun G, Fowler SW (1980) Long-term observation on the moulting frequency of the shrimp *Lysmata*
461 *seticaudata*. Mar Biol 59: 219-223
462 Bergström BI (1992) Growth, growth modelling and age determination of *Pandalus borealis*. Mar Ecol
463 Prog Ser 83: 167-183
464 Bergström BI (2000) The biology of *Pandalus*. Adv Mar Biol 38: 55-245
465 Brillon S, Lambert Y, Dodson J (2005) Egg survival, embryonic development, and larval characteristics of
466 northern shrimp (*Pandalus borealis*) females subject to different temperature and feeding
467 conditions. Mar Biol 147: 895-911
468 Clark SH, Cadrin SX, Schick DF, Diodati PJ, Armstrong MP, McCarron D (2000) The Gulf of Maine
469 northern shrimp (*Pandalus borealis*) fishery: a review of the record. J Northw Atl Fish Sci 27:
470 193-226
471 Comeau M, Savoie F (2001) Growth increment and molt frequency of the American lobster (*Homarus*

americanus) in the southwestern Gulf of St. Lawrence. J Crustac Biol 21: 923-936

Ehrhardt NM (2008) Estimating growth of the Florida spiny lobster, *Panulirus argus*, from molt frequency and size increment data derived from tag and recapture experiments. Fish Res 93: 332-337

Fu C, Quinn TJ, Shirley TC (2001) The role of sex change, growth and mortality in *Pandalus* population dynamics and management. ICES J Mar Sci 58: 607-621

Hansen HO, Aschan M (2000) Growth, size- and age-at-maturity of shrimp, *Pandalus borealis*, at Svalbard related to environmental parameters. J Northw Atl Fish Sci 27: 83-91

Hart RC (2001) Rapid estimation of in situ growth rates of *Caridina nilotica* (Crustacea: Decapoda) in Lake Victoria: Description and pilot application of a simple, field-compatible technique. Limnol Oceanogr 46: 692-698

Hartnoll RG (1982) Growth. In: Abele LG (ed) The biology of Crustacea. Academic Press, New York, pp 11-96

Hartnoll RG (2001) Growth in Crustacea - twenty years on. Hydrobiologia 449: 111-122

Hopkins CCE, Sargent JR, and Nilssen EM (1993) Total lipid content, and lipid and fatty acid composition of the deep-water prawn *Pandalus borealis* from Balsfjord, northern Norway: growth and feeding relationships. Mar Ecol Prog Ser 96: 217-228

Iguchi N, Ikeda T (1995) Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the southern Japan Sea, as influenced by temperature. J Plankton Res 17: 1757-1769

Kawaguchi S, Candy SG, King R,Naganobu M, and Nicol S (2006) Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. Mar Ecol Prog Ser 306: 1-15

Kinne O (1970) Environmental factors, part 2. In: Ecology M (ed) Temperature, animals, invertebrates. Wiley Interscience, London, U.K., pp 443-486

Koeller P (2006) Inferring shrimp (*Pandalus borealis*) growth characteristics from life history stage structure analysis. J Shellfish Res 25: 595-608

Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S, Richards A, Ouellet P, Orr D, Skuladottir U, Wieland K, Savard L, Aschan M. 2009. Basin-scale coherence in phenology of shrimps and phytoplankton in the north Atlantic Ocean. Science (Wash D C) 324: 791-793. doi: 10.1126/science.1170987.

500 Koeller PA (2000) Relative importance of abiotic and biotic factors to the management of the northern
501 shrimp (*Pandalus borealis*) fishery on the Scotian Shelf. J Northw Atl Fish Sci 27: 21-33
502 Kulmiye AJ, Mavuti KM (2005) Growth and moulting of captive *Panulirus homarus homarus* in Kenya,
503 western Indian Ocean. N Z J Mar Freshw Res 39: 539-549
504 Lysy AY, Dvinina EA (1991) On relation of the deep sea shrimp size with oceanographic conditions in the
505 Barents sea. ICES CM. 1991/k :52
506 O'Brien CJ (1994) The effects of temperature and salinity on growth and survival of juvenile tiger prawns
507 *Penaeus esculentus* (Haswell). J Exp Mar Biol Ecol 183: 133-145
508 Paglianti A, Gherardi F (2004) Combined effects of temperature and diet on growth and survival of young-
509 of-year crayfish: a comparison between indigenous and invasive species. J Crustac Biol 24: 140-
510 148
511 Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University
512 Press, Cambridge, UK
513 Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bull Fish Res
514 Board Can 191: 382 pp.
515 Ross RM, Quetin LB, Baker KS, Vernet M, and Smith RC (2000) Growth limitation in young *Euphausia*
516 *superba* under field conditions. Limnol Oceanogr 45: 31-43
517 Sainte-Marie B, Bérubé I, Brillon S, Hazel F (2006) Observations on the growth of the sculptured shrimp,
518 *Sclerocrangon boreas* (Decapoda: Caridea). J Crustac Biol 26: 55-62
519 Savard L, Parsons DG, Carlsson DM (1994) Estimation of age and growth of northern shrimp (*Pandalus*
520 *borealis*) in Davis Strait (NAFO subareas 0+1) using cluster and modal analyses. J Northw Atl
521 Fish Sci 16: 63-74
522 Shumway SE, Perkins HC, Schick DF, Stickney AP (1985) Synopsis of biological data on the pink shrimp,
523 *Pandalus borealis* Kroeyer, 1838. FAO Fisheries Synopsis 144: 57 pp.
524 Simard Y, Savard L. 1990. Variability, spatial patterns and scales of similarity in size-frequency
525 distributions of the northern shrimp (*Pandalus borealis*) and its migrations in the Gulf of St.
526 Lawrence. Can J Fish Aquat Sci 47(4): 794-804. doi: 10.1139/f90-092.
527 Skuladottir U, Palsson J, Bragason GS, Brynjolfsson S (1991) The variation in size and age at change of

528 sex, maximum length and length of ovigerous period of the shrimp, *Pandalus borealis*, at different
529 temperatures in the Icelandic waters. ICES CM 1991/k : 5
530 Skuladottir U, Petursson G, Brynjolfsson SH (2005). The biology of northern shrimp (*Pandalus borealis*)
531 on the Flemish Cap. J Northw Atl Fish Sci 37: 147-164. doi: 10.2960/J.v37.m571.
532 Sokal RR, Rohlf FJ (1995) Biometry—The principles and practice of statistics in biological research.
533 Freeman and Co., New York
534 Staples DJ, Heales DS (1991) Temperature and salinity optima for growth and survival of juvenile banana
535 prawns *Penaeus merguiensis*. J Exp Mar Biol Ecol 154: 251-274
536 Sudo H (2003) Effect of temperature on growth, sexual maturity and reproduction of *Acanthomysis robusta*
537 (Crustacea: Mysidacea) reared in the laboratory. Mar biol 143: 1095-1107
538 Tarling TA, Shreeve RS, Hirst AG, Atkinson A, Pond DW, Murphy EJ, and Watkins JL (2006) Natural
539 growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting
540 intermolt period. Limnol Oceanogr 51: 959-972
541 Wainwright TC, Armstrong DA (1993) Growth patterns in the dungeness crab (*Cancer magister* Dana):
542 synthesis of data and comparison of models. J Crustac Biol 13: 36-50
543 Wieland K (2005) Changes in recruitment, growth, and stock size of northern shrimp (*Pandalus borealis*)
544 at West Greenland: temperature and density-dependent effects at released predation pressure.
545 ICES J Mar Sci 62: 1454-1462
546 Winkler G, Greve W. 2002. Laboratory studies of the effect of temperature on growth, moulting and
547 reproduction in the co-occurring mysids *Neomysis integer* and *Praunus flexuosus*. Mar Ecol Prog
548 Ser 235: 177-188. doi: 10.3354/meps235177.
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552 **Fig. 1** Box-plots of intermolt period (IP) for juvenile, male and female northern shrimp *P. borealis* at 2, 5,
553 and 8 °C. The median and the 25th and the 75th percentiles are represented. Whiskers below and above the
554 box indicate the 10th and the 90th percentiles. Different letters indicate significant ($p < 0.05$) differences
555 between temperatures for each developmental stage.
556 **Fig. 2** Box-plots of molt increment in CL (MI_S) and in total mass (MI_M) for juvenile, male and female
557 northern shrimp *P. borealis* at 2, 5, and 8 °C. The median and the 25th and the 75th percentiles are
558 represented. Whiskers below and above the box indicate the 10th and the 90th percentiles. Different letters
559 indicate significant ($p < 0.05$) differences between temperatures for each developmental stage.
560 **Fig. 3** Box-plots of specific growth rates in CL (SGR_S) and in total mass (SGR_M) for juvenile, male and
561 female northern shrimp, *P. borealis* at 2, 5, and 8 °C. The median and the 25th and the 75th percentiles are
562 represented. Whiskers below and above the box indicate the 10th and the 90th percentiles. Different letters
563 indicate significant ($p < 0.05$) differences between temperatures for each developmental stage.
564 **Fig. 4** Relationships between intermolt duration (IP), size increment at molt (MI_S) and pre-molt
565 cephalothorax length (CL) at 2, 5, and 8 °C for northern shrimp *P. borealis*. Relationships between IP and
566 CL are presented as power functions ($Y=aX^b$) and the relationship between MI and CL as a linear
567 regression ($Y=a+bX$). The relationship between MI_S and CL was significant ($p < 0.05$) only at 2 °C.
568 **Fig. 5** Predicted size at age (CL in mm) for northern shrimp *P. borealis* using multiple regression equations
569 relating intermolt duration and size increment at molt to pre-molt size and temperature for constant
570 temperatures of 2, 5 and 8 °C. Mean size at age and upper and lower 95% confidence intervals estimated
571 with the Monte Carlo analysis are presented.
572 **Fig. 6** Size at age for populations of northern shrimp, *P. borealis*, found in different locations and
573 temperature regimes. Numbers correspond to locations and average bottom temperatures for different
574 populations presented in table 5. Projections of sizes at age at 2, 5, and 8 °C are also represented by light
575 grey curves.
576

Figure 1

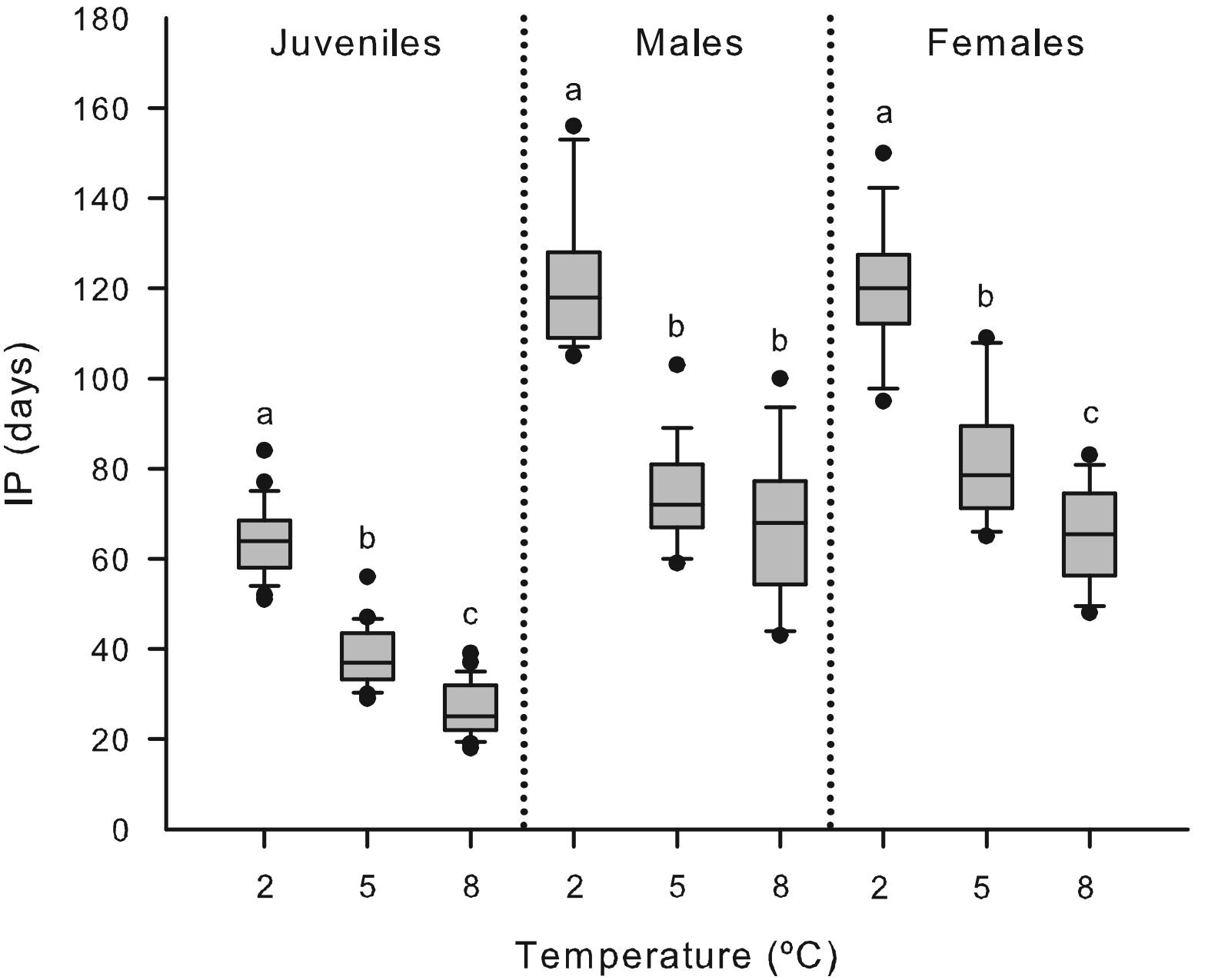

Juveniles
Males
Females
IP (days)
0
20
40
60
80
100
120
140
160
180
a
b
c
a
b
b
a
b
c
2
5
8
2
5
8
2
5
8
Temperature (ºC)

Figure 2

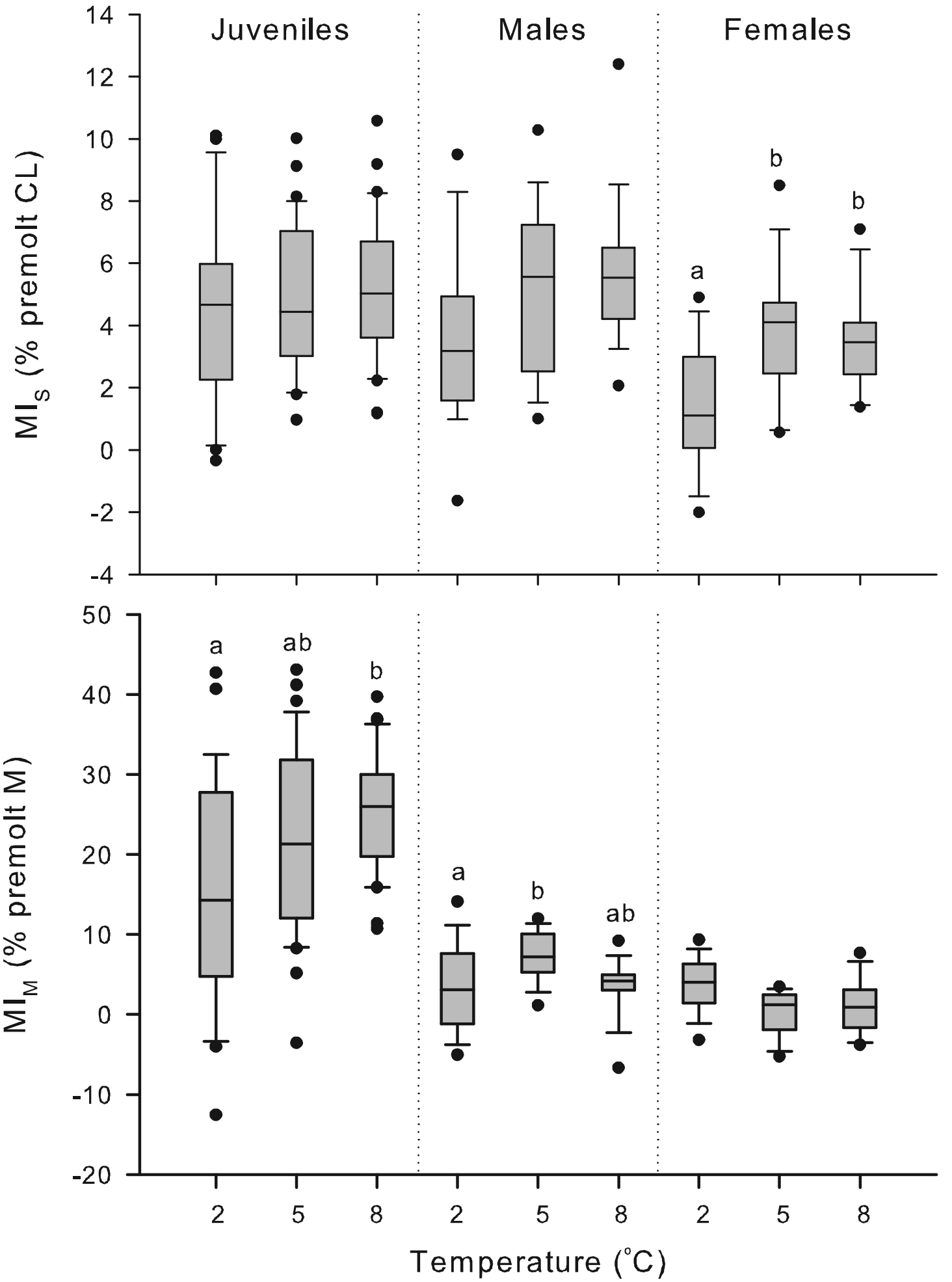

Juveniles
Males
Females
MI_S (% premolt CL)
MI_M (% premolt M)
Temperature (°C)
a
ab
b
a
b
ab
a
b
b
2
5
8

Figure 3

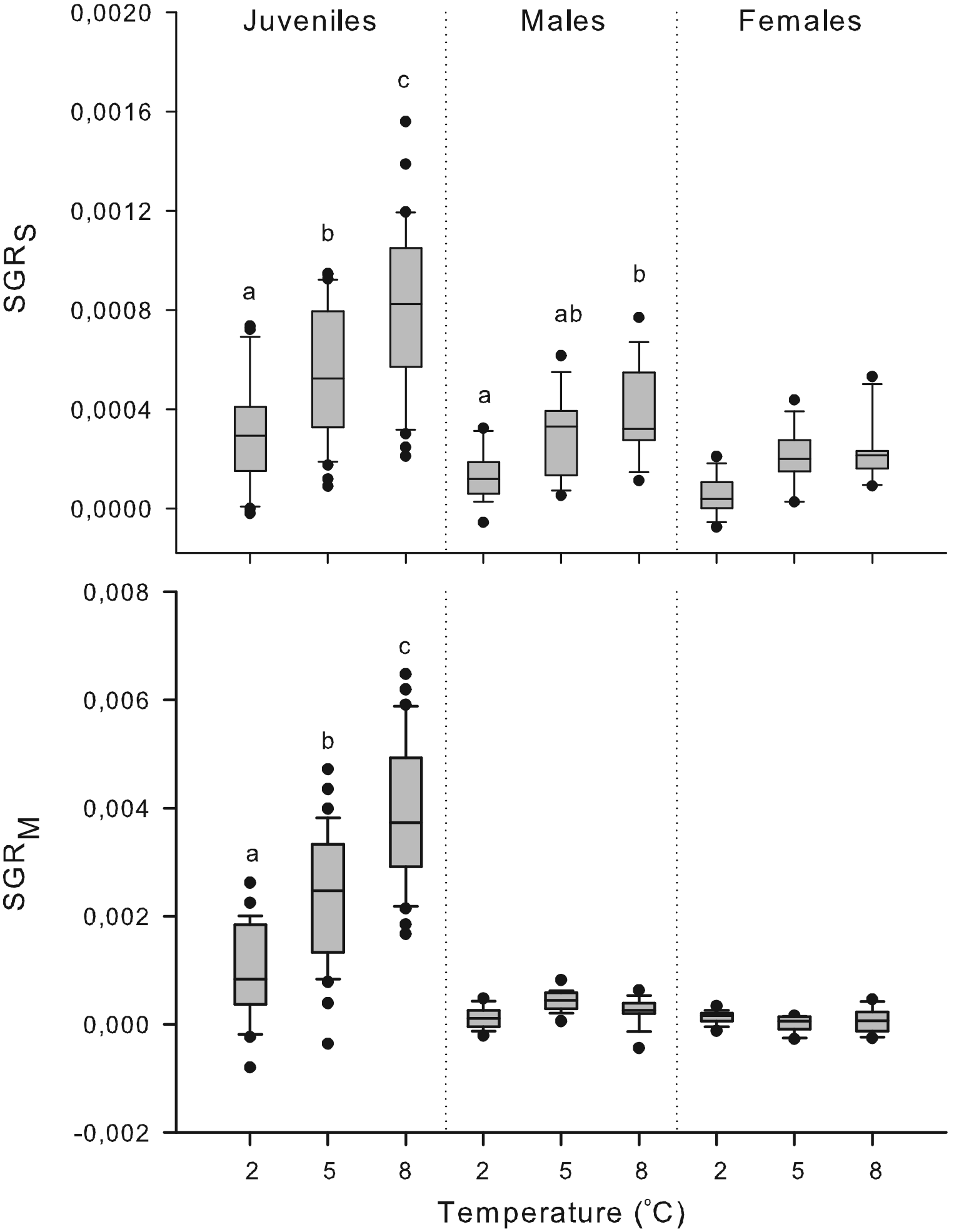
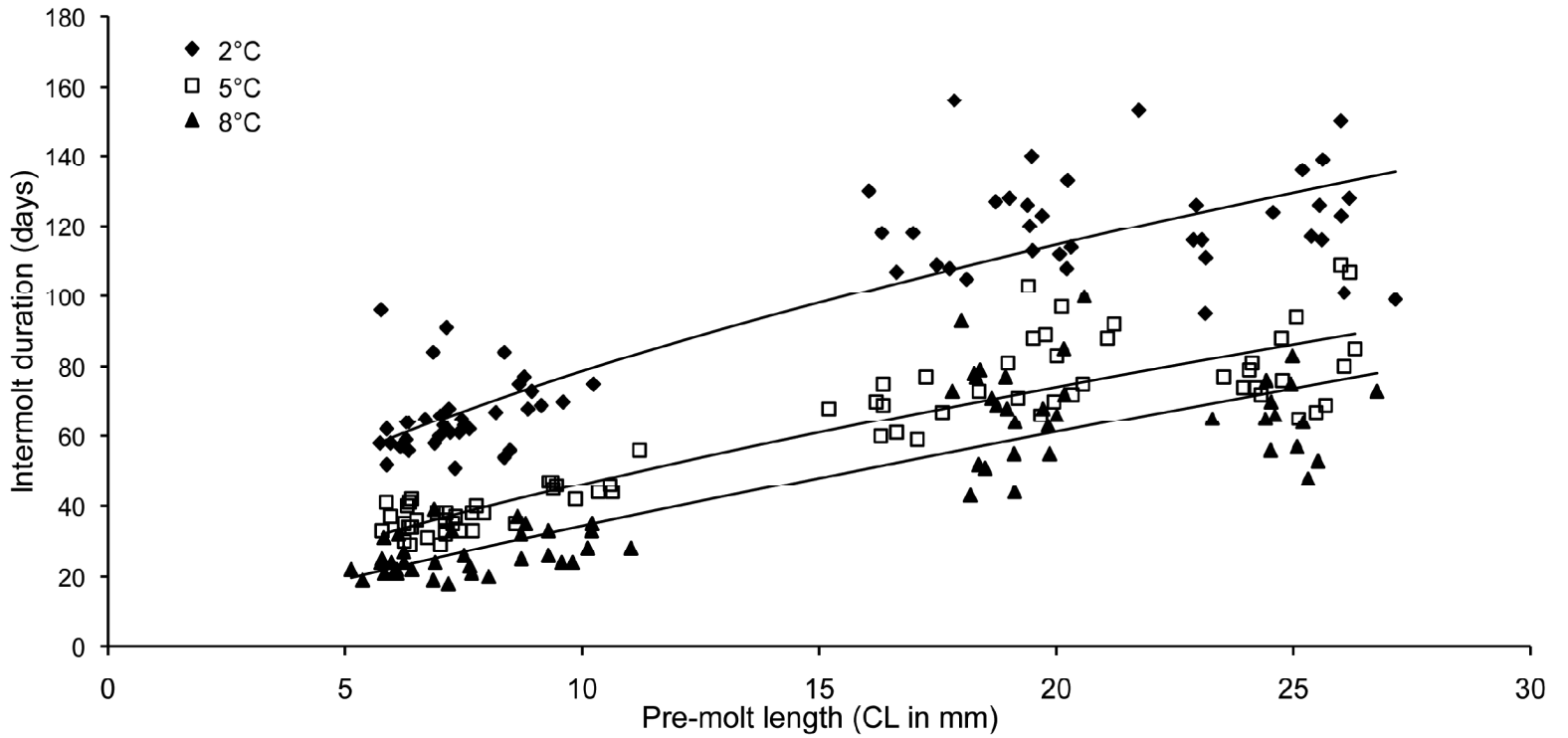

Juveniles
Males
Females
SGRS
SGRM
0,0020
0,0016
0,0012
0,0008
0,0004
0,0000
0,008
0,006
0,004
0,002
0,000
-0,002
a
b
c
a
ab
b
a
b
c
2
5
8
Temperature (°C)

Figure 4


2°C
5°C
8°C
Intermolt duration (days)
Pre-molt length (CL in mm)

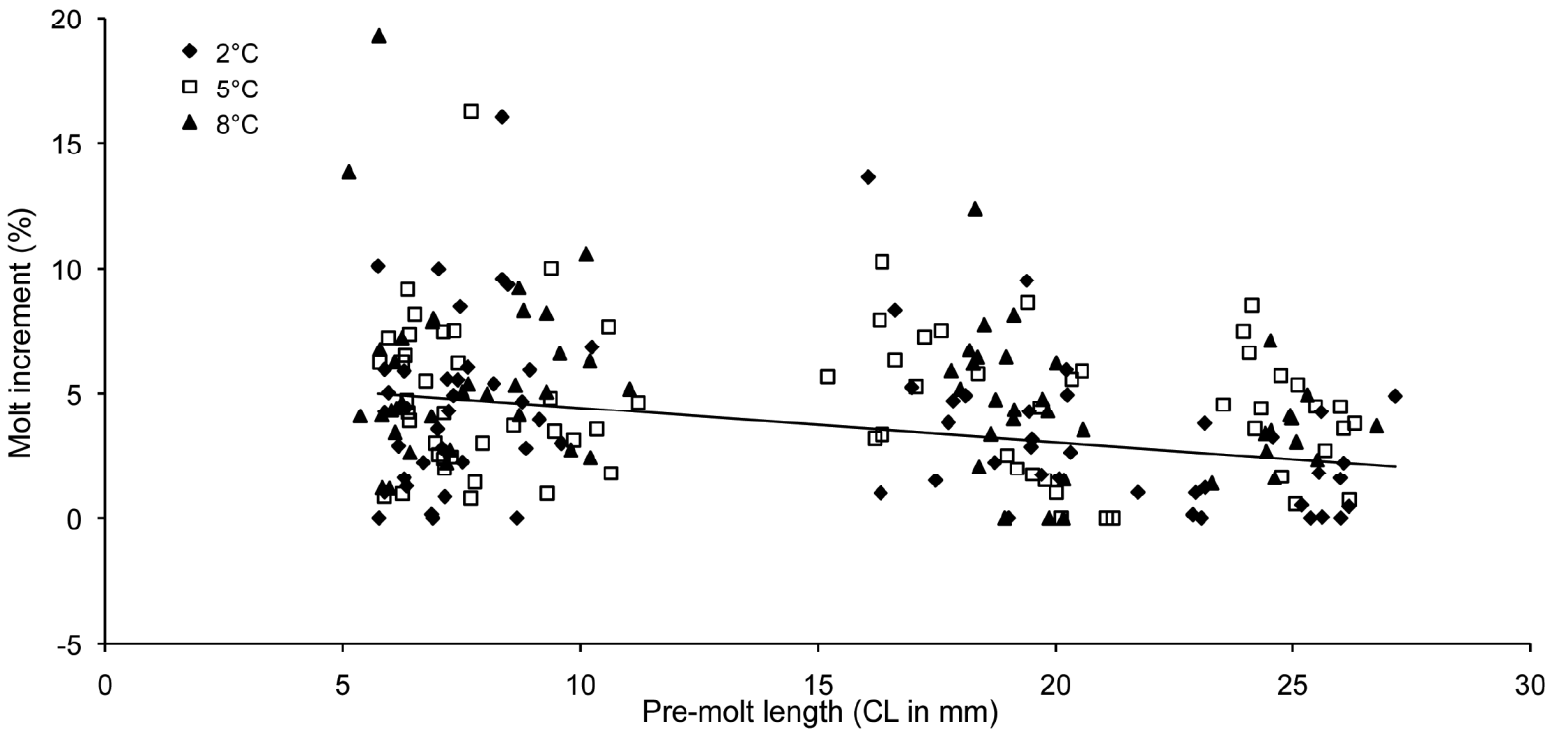

2°C
5°C
8°C
Molt increment (%)
Pre-molt length (CL in mm)

Figure 5

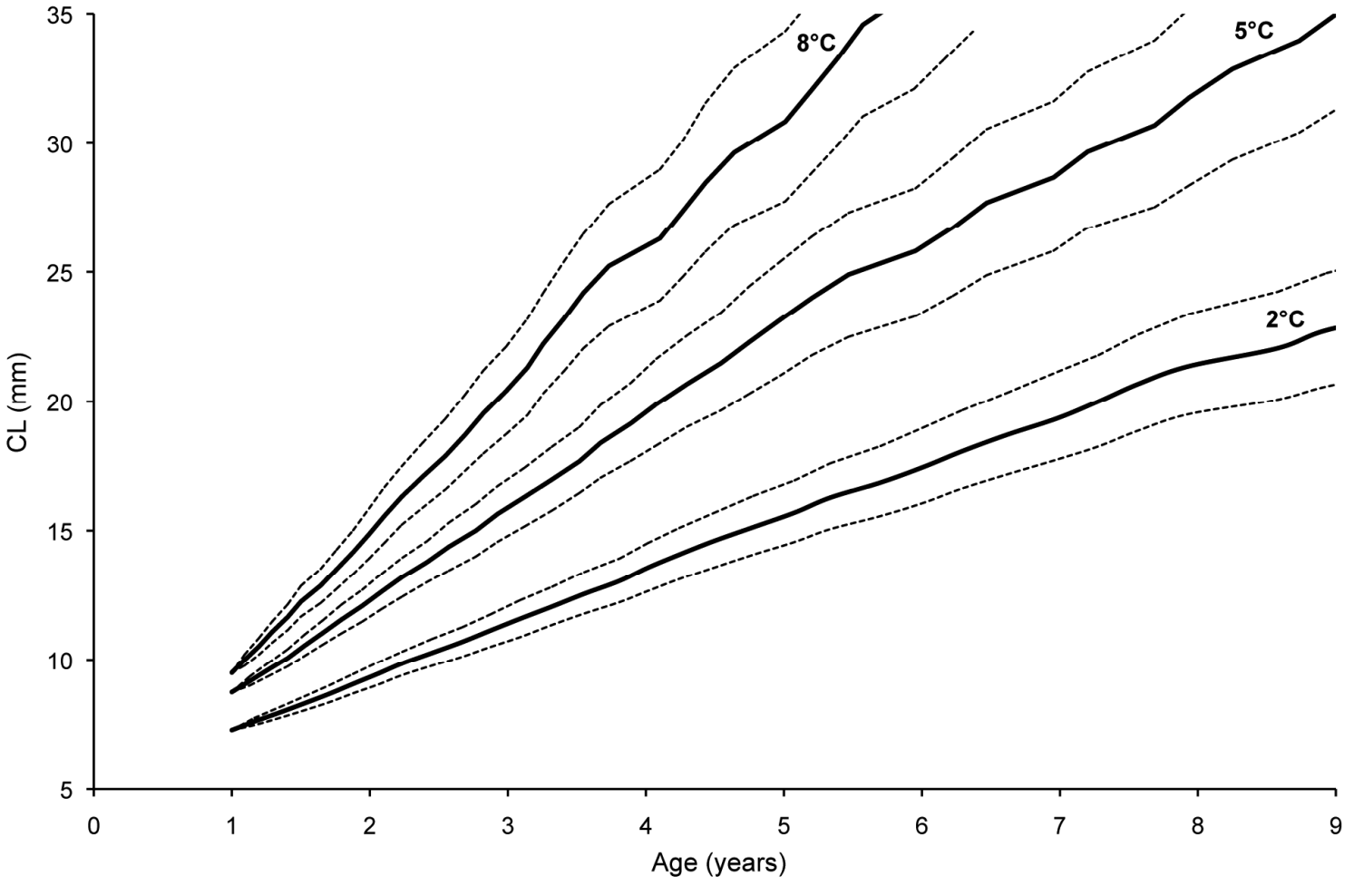
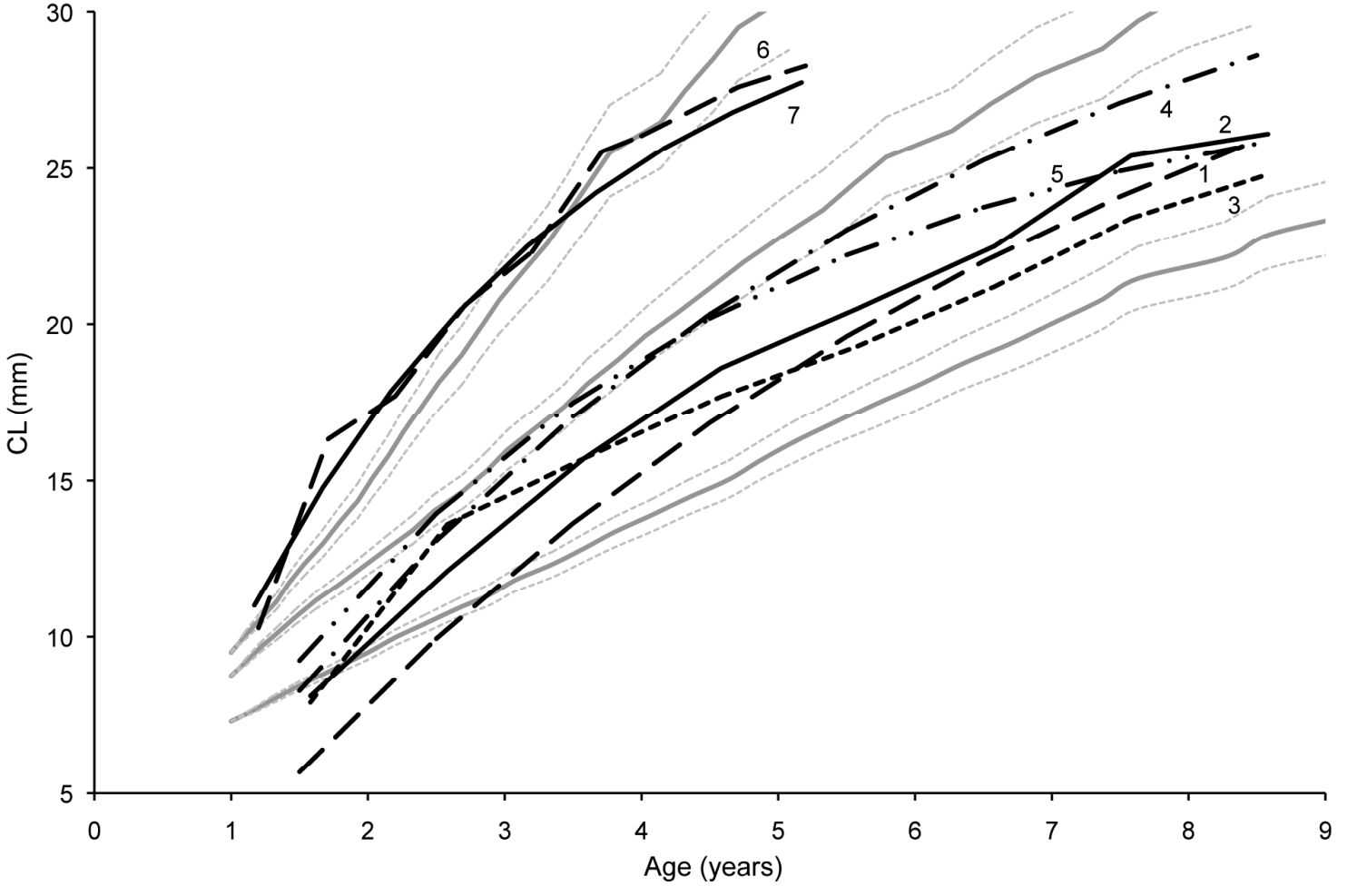


Figure 6



Table

Table 1. Size (CL_i) and mass (M_i) of juveniles, males and females at the beginning of the intermolt period. Mean values, SD, range of values, and number of samples in parenthesis are presented. For both CL_i and M_i, no significant differences were observed ($p > 0.05$) between temperatures at each developmental stage.

Temperature		**2°C**	**5°C**	**8°C**
Juvenile	CL_i (mm)	7.45 ± 1.24 (25)	7.62 ± 1.54 (31)	7.59 ± 1.56 (30)
	CL_i range (mm)	5.74 – 10.24	5.78 – 11.21	5.37 – 10.21
	M_i (g)*	0.276 ± 0.137	0.305 ± 0.193	0.302 ± 0.176
	M_i range(g)*	0.119 – 0.665	0.122 – 0.870	0.098 – 0.659
Male	CL_i (mm)	18.94 ± 1.47 (18)	18.07 ± 1.70 (18)	19.09 ± 0.76 (13)
	CL_i range (mm)	16.32 - 21.74	15.20 - 20.56	18.00 - 20.59
	M_i (g)	4.435 ± 0.824	3.900 ± 1.022	4.572 ± 0.564
	M_i range(g)	3.135 – 5.910	2.245 – 5.640	3.923 – 5.431
Female	CL_i (mm)	25.02 ± 1.37 (15)	24.93 ± 0.81 (12)	24.89 ± 0.86 (11)
	CL_i range (mm)	22.89 – 27.15	23.53 – 26.19	23.29 – 26.76
	M_i (g)	9.437 ± 1.580	9.657 ± 0.938	9.724 ± 1.098
	M_i range(g)	6.832 – 12.645	8.392 – 11.675	7.805 – 12.193

*values estimated with the CL-mass relationship: $Log(M) = -3.103 + 2.882\ Log(CL)$, $n = 146$, $r^2 = 0.94$.

Table 2. Changes in relative masses of body compartments (%) observed during one complete molt cycle at three temperatures for juvenile, male and female shrimp. Mean values, SD, and number of samples in parenthesis are presented for the hepatopancreas (HSI), muscle (MSI), gonads (GSI), and carcass (CSI) indices. Different letters indicate significant differences between temperatures for each developmental stage.

Indices		HSI	MSI	CSI	GSI
	Initial				
Juvenile	2°C	5.75 ± 0.88 (14)	34.71 ± 2.07 (15)	50.45 ± 2.13 (15)	
	5°C	6.51 ± 0.97 (22)	35.61± 2.50 (22)	49.88 ± 2.15 (22)	
	8°C	5.81 ± 0.85 (20)	35.10 ± 2.25 (21)	49.91 ± 1.92 (21)	
Male	2°C	7.11 ± 1.29 (25)^{b}	42.52 ± 2.08 (23)	43.35 ± 2.17 (24)^{a}	0.36 ± 0.13 (25)
	5°C	6.89 ± 0.91 (22)^{b}	43.71 ± 2.46 (22)	43.48 ± 2.76 (21)^{a}	0.33 ± 0.12 (22)
	8°C	6.22 ± 1.11 (22)^{a}	42.69 ± 1.89 (22)	45.44 ± 1.99 (22)^{b}	0.31 ± 0.10 (22)
Female	2°C	8.30 ± 1.50 (19)^{b}	40.60 ± 1.62 (20)	46.58 ± 1.63 (20)	1.50 ± 1.01 (20)^{ab}
	5°C	7.61 ± 0.99 (23)^{b}	40.91 ± 1.53 (22)	45.98 ± 1.77 (20)	2.57 ± 1.84 (23)^{b}
	8°C	7.01 ± 0.98 (24)^{a}	41.58 ± 1.32 (24)	46.27 ± 1.40 (23)	1.03 ± 0.43 (22)^{a}
	Final				
Juvenile	2°C	5.97 ± 0.95 (9)	35.99 ± 2.24 (9)^{a}	50.11 ± 2.16 (9)	
	5°C	6.38 ± 1.21 (9)	38.72 ± 1.56 (9)^{b}	48.18 ± 1.86 (8)	
	8°C	6.39 ± 1.61 (11)	38.53 ± 1.32 (11)^{b}	48.58 ± 1.86 (11)	
Male	2°C	5.84 ± 0.67 (18)	39.72 ± 1.79 (18)	46.46 ± 1.69 (17)^{a}	0.41 ± 0.10 (18)^{b}
	5°C	6.21 ± 1.09 (18)	41.00 ± 1.40 (18)	47.81 ± 1.37 (18)^{b}	0.36 ± 0.09 (18)^{ab}
	8°C	5.80 ± 0.85 (13)	39.80 ± 1.66 (13)	48.95 ± 1.63 (13)^{b}	0.31 ± 0.06 (13)^{a}
Female	2°C	6.40 ± 1.20 (15)	39.99 ± 1.70 (15)	45.62 ± 1.84 (15)^{a}	0.61 ± 0.13 (14)^{b}
	5°C	5.86 ± 1.25 (12)	39.58 ± 1.28 (12)	48.27 ± 1.26 (12)^{b}	0.42 ± 0.07 (12)^{a}
	8°C	6.58 ± 1.05 (11)	39.63 ± 1.49 (11)	48.22 ± 1.43 (11)^{b}	0.73 ± 0.45 (11)^{b}

Table 3. Regression parameters of the relationships between intermolt duration and pre-molt CL (log transformed data) at 2, 5, and 8°C. For each relationship, temperature, the slope (b), the intercept (a), the coefficient of determination (r^2), probability level of significance (p), number of fish (n), and intermolt duration (days) at specific CL of 7, 19, and 25 mm are presented.

Temperature	b	a	r^2	p	n	7 mm	19 mm	25 mm
2°C	0.579	1.305	0.86	<0.0001	58	62	111	130
5°C	0.675	0.989	0.89	<0.0001	61	36	71	86
8°C	0.811	0.719	0.81	<0.0001	54	25	57	71

Table 4. Multiple regression models relating intermolt duration (IP) and size increment at molt (MI_S) to pre-molt cephalothorax length (CL_I) and temperature (T). For each variable, coefficient estimate, standard error (SE) of the coefficient, F value, and probability level (p) are presented. Model r^2 and the partial r^2 are also presented.

	Coefficient	SE	F	p	Partial r^2	Model r^2
Log IP						
Intercept	1.2961	0.0289	13.91	< 0.0001		
Log CL_I	0.6806	0.0236	5.77	< 0.0001	0.515	0.515
T	-0.0555	0.0023	3.94	< 0.0001	0.353	0.868
MI_s						
Intercept	5.0458	0.5646	79.87	< 0.0001		
CL_I	-0.0988	0.0244	16.36	< 0.0001	0.094	0.094
T	0.1715	0.0749	5.24	0.0233	0.027	0.122

Table 5. Bottom temperature range (°C) observed in different locations where *P. borealis* is distributed. In the different studies, bottom temperatures were obtained from annual shrimp surveys usually conducted at the same time of the year.

Location	Years	Temperature	Reference
Barents Sea [1]	1990-1993	1-2°C	Skuladottir et al. (2005)
Davis Strait [2]	1978-1986	1-4°C	Parsons et al. (1989)
Hopedale Channel [3]	1981-1987	2-4°C	Parsons et al. (1989)
Flemish Cap [4]	1993-1999	3.2°C	Skuladottir et al. (2005)
Iceland [5]	1981-1989	4.5°C	Skuladottir et al. (2005)
Gullmarsfjorden [6]	1980-1985	4-6°C	Bergstrom (1992)
Gulf of Maine [7]	1969-1986-1990-1991	5.5-6.5°C	Clark et al. (2000)