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

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Corresponding Author: Dr. Dounia Daoud,

Corresponding Author's Institution:

First Author: Dounia Daoud, PhD

Order of Authors: Dounia Daoud, PhD; Yvan Lambert, PhD; Celine Audet, PhD; Denis Chabot, PhD

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.

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

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4 DOUNIA DAOUD <sup>a, b, c\*</sup>, YVAN LAMBERT <sup>b</sup>, CELINE AUDET <sup>a</sup>, DENIS CHABOT <sup>b</sup>

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7 <sup>a</sup> Institut des Sciences de la Mer de Rimouski, Université du Québec à Rimouski, 310 des Ursulines,  
8 Rimouski (Qué.), Canada, G5L 3A1

9 <sup>b</sup> Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 route de la mer, Mont-Joli (Qué.),  
10 Canada, G5H 3Z4

11 <sup>c</sup> Coastal Zones Research Institute Inc., 232B av. de l'Église, Shippagan (N.-B.), Canada, E8S 1J2

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13 \* Corresponding author. Tel.: +1-506-336 6618; fax: +1-506-336 6601. E-mail address:

14 [dounia.daoud@irzc.umcs.ca](mailto:dounia.daoud@irzc.umcs.ca)

## 15 INTRODUCTION

16

17 Northern shrimp (*Pandalus borealis*), a commercially important species in Canadian waters, is a  
18 cold-water decapod widely distributed in the Northwest Atlantic and in the North Pacific (Bergström 2000).  
19 It is a protandric hermaphrodite species; each individual first matures and functions as a male, goes through  
20 a transition phase, and becomes a female. Along the latitudinal gradient extending from the Gulf of Maine  
21 to the Davis Strait, shrimp populations differ in abundance and in several life history traits (Apollonio et al.  
22 1986; Lysy and Dvinina 1991; Anderson 1999; Anderson and Piatt 1999; Koeller 2000). Longevity, length  
23 at sex change, and maximum length of males and females increase with latitude while growth rate and  
24 proportion of spawning females relative to non-spawning females decrease. Although some results may  
25 contradict this general observation (Koeller 2006), temperature appears to play a major role in structuring  
26 these populations through its influence on growth patterns, length at sex change, and ovigerous period  
27 which are all interrelated. These important latitudinal changes suggest future potential effects of climate  
28 changes on shrimp population dynamics (Koeller et al. 2009).

29 Growth in crustaceans is characterized by a succession of molts (ecdysis) separated by intermolt  
30 periods (IP), with each of these two phases often exhibiting very different responses to intrinsic and  
31 extrinsic factors (Hartnoll 1982). Size and temperature are generally seen as the most important parameters  
32 influencing IP and molt increment (MI) (Kinne 1970; Hartnoll 1982). Usually, small individuals molt more  
33 frequently (Benayoun and Fowler 1980) and have larger relative MI than larger individuals of the same  
34 species (Hartnoll 1982). Temperature or seasonal fluctuations in temperature directly influence IP but  
35 temperature effect on MI is less predictable (Comeau and Savoie 2001; Hartnoll 2001). In most studies, MI  
36 was weakly or not influenced by temperature (Hartnoll 1982; Iguchi and Ikeda 1995; Hart 2001; Sudo  
37 2003). However, decreases and increases in MI with increasing temperatures have been observed in  
38 different species (Paglianti and Gherardi 2004; Kulmiye and Mavuti 2005).

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

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

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

59

60

## MATERIAL AND METHODS

61

### 62 **Shrimp capture and rearing conditions**

63

64         Growth experiments were conducted at the aquaculture facilities of the Maurice Lamontagne  
65 Institute (Fisheries and Oceans Canada, Mont-Joli, Québec) between 2002 and 2005. Adult shrimp (15-30  
66 mm in cephalothorax length, CL) were caught using a rigid frame trawl in the St. Lawrence Estuary (80-  
67 160 m depth) near Rimouski (48°36'N 68°29.5'W) each year between 2001 and 2003. Following capture,  
68 shrimp were transported to the MLI and kept in 670 l rectangular tanks under natural photoperiod at a  
69 temperature of 5 °C and a salinity > 28 ‰. Male and female shrimp used for the adult growth experiment

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

76 Juveniles used in the experiments were raised in the laboratory. Ovigerous females caught in the  
77 St. Lawrence Estuary in the fall of 2002 and spring of 2003 and 2004 were isolated in May of 2003 and  
78 2004 in tanks until hatching of the larvae. Larvae were kept in 80 l plankton-Kreisel tanks (Aiken and  
79 Waddy 1989) at 5 °C and fed *ad libitum* with live brine shrimp nauplii (*Artemia salinas*) until they reached  
80 juvenile stages. Juveniles (4-12 mm CL) were then randomly assigned to 80 l Kreisel tanks adjusted to the  
81 three experimental temperature treatments (2, 5, and 8 °C) until the beginning of the experiments. The  
82 experiment on juveniles in their second year of live began in June 2004 and the one on juveniles in their  
83 first year of life in March 2005. Juveniles were fed three to five times a week depending on their age, using  
84 the same diet as for the adults. Remaining food was cleaned before each feeding period.

85

## 86 **Experimental setup**

87

88 Experiments were conducted in 3 recirculated seawater tanks (1340 l); one for each of the three  
89 experimental temperatures. Each tank had a head tank with a capacity of 125 l, a sand filter and a heat  
90 pump to regulate water temperature. Seawater flow to the tank was  $\sim 30 \text{ l min}^{-1}$ , whereas new seawater  
91 flow to the head tank was  $\sim 2.5 \text{ l min}^{-1}$  (100% of seawater renewed every 10h). Experiments with juveniles  
92 (8-12 mm CL) and adults were conducted in compartmentalized baskets immersed in the tanks in order to  
93 follow individual shrimp. Compartments used for juveniles (8-12 mm CL) were 16.5 x 12 x 10 cm while  
94 those for adults were 35 x 30 x 35 cm. Vertical tray incubators connected to the seawater systems were  
95 used for the experiments with smaller juveniles in the 4-8 mm CL size range. Each incubator had 8 trays  
96 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 ( $\pm 0.01$  mm), total mass ( $M \pm 0.001$  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 shrimp 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 ( $\pm 0.01$  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

124 Plus, ver. 4.1.1.2]).

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

135

#### 136 **Data calculation and statistical analyses**

137

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

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

$$140 \quad MI_S = 100 \times (CL_2 - CL_1) / CL_1$$

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

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

$$143 \quad MI_M = 100 \times (M_2 - M_1) / M_1$$

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

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

$$148 \quad SGR_S = (\log CL_2 - \log CL_1) / IP$$

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  $\pm$  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



176 2006). At the female stage, the ovigerous period was taken into account by setting spawning time between  
177 day of the year 200 and 250 (Koeller et al. 2009) and using as IP, the duration of the ovigerous period at the  
178 different temperatures. The duration of the ovigerous period was fixed at 236, 177, and 135 days at 2, 5,  
179 and 8 °C based on a laboratory study in controlled conditions at these 3 temperatures (Brillon et al. 2005).

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

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

187

## 188 RESULTS

189

### 190 Growth in size and mass during a molt cycle

191

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

$$196 \quad \text{Log (M)} = -3.103 + 2.882 \text{ Log (CL)} \quad (\text{n}= 146, \text{r}^2=0.94)$$

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

202 0.0001). The only exception was observed for males where IP did not differ between 5 and 8 °C (Dunn-  
203 Sidak test;  $p = 0.0038$ ). For all developmental stages, a higher decrease in IP was observed between 2 °C  
204 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  
205 females and 20% shorter at 8 °C than at 5 °C for females. In juveniles, differences in IP were less  
206 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  
207 identical for males and females at the 3 temperatures ( $p > 0.33$ ) but approximately twice as long as in  
208 juveniles for each temperature (Pairwise comparisons  $p < 0.0001$ ).

209         Increases in CL and M at the 3 temperatures were different for juveniles, males, and females (Fig.  
210 2) with significant interactions between developmental stage and temperature for both CL and M (2-way  
211 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  
212 5.3% for juveniles and males without any significant effect of temperature. In females,  $MI_S$  ranged between  
213 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  
214 significant increase in  $MI_M$  from 18.6 to 27.2% was observed for juvenile shrimp raised at temperatures  
215 between 2 and 8 °C ( $p = 0.0001$ ) (Fig. 2). In males, mean  $MI_M$  ranged between 3.9 and 7.7% with a  
216 significant increase between 2 and 5 °C ( $p = 0.0012$ ) while in females,  $MI_M$  was lower (1.1 to 4.2%) and  
217 not different between temperatures ( $p > 0.016$ ) (Fig. 2). No difference in  $MI_S$  was observed between  
218 juveniles, males and females at 5 and 8 °C (pairwise comparisons:  $p \geq 0.031$ ) but at 2 °C,  $MI_S$  was lower in  
219 females than in juveniles and males ( $p < 0.0023$ ). At each temperature,  $MI_M$  differed between  
220 developmental stages (pairwise comparisons:  $p < 0.0001$ ) with the exception of males and females which  
221 had similar  $MI_S$  at 2 °C ( $p = 0.36$ ) and 8 °C ( $p = 0.03$ ).

222         Specific growth rate obtained from CL and mass increments at molt and IP were used to describe  
223 the combined effects of these two components of growth. There was a significant interaction between  
224 temperature and developmental stage for both  $SGR_S$  and  $SGR_M$  (2-way ANOVA, Temp x Stage,  $F_{4, 164} =$   
225 2.91 and 26.64,  $p < 0.05$  and 0.0001, respectively). In juvenile shrimp, both  $SGR_S$  and  $SGR_M$  increased  
226 with temperature (Fig. 3) with significant differences between each of the three temperatures (pairwise  
227 comparisons:  $p < 0.0001$ ). In males, a significant increase in  $SGR_S$  was observed between 2 and 8 °C ( $p <$   
228 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  
229 detected (Fig. 3).  $SGR_M$  for males was similar at the 3 temperatures ( $p > 0.02$ ), whereas  $SGR_S$  and  $SGR_M$

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

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

236 Analysis of variance on the different tissue masses indicated significant interactions between  
237 temperature and developmental stages for initial HSI (2-way ANOVA, Temp x Stage,  $F_{4, 182} = 2.43$ ,  $p <$   
238  $0.05$ ), 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  
239 Stage,  $F_{4, 105} = 7.28$ ,  $p < 0.0001$ ). Thus, *a posteriori* comparisons were conducted among temperatures at  
240 each developmental stage and among stages for each temperature for these variables. Initial HSI differed  
241 significantly between temperatures for females at 2 and 8 °C ( $p = 0.0004$ ) and HSI was higher in females  
242 than in juveniles at each temperature ( $p < 0.001$ ) (Table 2). Initial MSI was not different between  
243 temperatures (2-way ANOVA,  $F_{2, 182} = 2.46$ ,  $p > 0.08$ ) but was significantly influenced by developmental  
244 stage (2-way ANOVA,  $F_{2, 182} = 248.96$ ,  $p < 0.0001$ ) with MSI being lower in juveniles than in adults. Initial  
245 CSI only differed between temperatures for males with a significant difference between 2 and 8 °C ( $p =$   
246  $0.0003$ ) and between 5 and 8 °C ( $p = 0.0009$ ). However, at each temperature, initial CSI was significantly  
247 higher in juveniles than in adults ( $p < 0.0001$ ). Initial GSI for adult shrimp was significantly influenced by  
248 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  
249 in males at the different temperatures (Table 2).

250 At the end of the experiment, HSI was similar across temperatures and developmental stages (2-  
251 way ANOVA,  $p > 0.76$ ). Some differences were observed in final MSI and final CSI. However, no  
252 significant distinct pattern associated with either temperature or developmental stage was detected. Final  
253 GSI in males decreased with temperature (1-way ANOVA,  $F_{2,46} = 4.27$ ,  $p = 0.02$ ) with a significant  
254 difference between 2 and 8 °C. In females, final GSI was affected by temperature (1-way ANOVA,  $F_{2,34} =$   
255  $4.17$ ,  $p = 0.024$ ) with a significant difference between 2 and 5 °C ( $p = 0.018$ ) and between 5 and 8 °C ( $p =$   
256  $0.016$ ).

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

285

286

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

302         The present study indicates a pronounced effect of temperature on IP while  $MI_S$  changed little,  
303 indicating that the main influence of temperature on growth rate of *P. borealis* is through IP. Hence, the  
304 shortening of IP results in a faster growth at higher temperature. Hartnoll (1982) reported various examples  
305 of crustaceans in which an increase in temperature shortened IP and decreased or had no effect on CL  
306 increments per molt. Wainwright and Armstrong (1993) showed a declining probability of molt for mature  
307 Dungeness crab, *Cancer magister*, compared to juveniles. Temperature has been shown to strongly  
308 influence IP and to have a negligible influence on MI for *C. magister*. Moreover, higher temperature may  
309 result in faster growth even in cases when MI decreases with increasing temperature, if higher molt  
310 frequency compensates for reduced MI (Paglianti and Gherardi 2004). This lengthened IP duration with  
311 lower temperature may reflect the greater time needed for the accumulation of sufficient energy reserves for  
312 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<sub>s</sub> 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<sub>s</sub>. 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<sub>s</sub>. 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<sub>s</sub> 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

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

374         Apparent divergence in observed growth rate for age 2 and 3 shrimp in natural populations and  
375 predicted growth using IP and  $MI_s$  was examined by comparing predicted growth of juveniles in the  
376 present study to annual length increment of juvenile shrimp found at different bottom temperatures in West  
377 Greenland (Wieland 2005). In West Greenland, annual length increments for age 2 and 3 showed  
378 considerable variability and were not influenced by bottom temperature in the range of 1 to 5 °C.  
379 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  
380 year at age 3 (15-19 mm CL) (Wieland 2005). Predicted size increments for juveniles of the same sizes at 2  
381 °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  
382 CL per year for age 3. Thus, predicted increments for sizes below 14 mm CL may have been slightly  
383 underestimated in the present study. Comparable or higher size increments for juveniles of that size are  
384 only observed at 8 °C (5.2 to 5.7 mm CL per year). However, for larger juvenile sizes, a very good  
385 correspondence in increments per year is observed.

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

392         Temperature regimes reported for the different populations represent mean bottom temperatures  
393 encountered during annual surveys. These temperatures may differ from average ambient conditions to  
394 which northern shrimp are subjected, as they do not account for diurnal vertical migration, seasonal, spatial  
395 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

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

431

432

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550



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 25<sup>th</sup> and the 75<sup>th</sup> percentiles are represented. Whiskers below and above the  
554 box indicate the 10<sup>th</sup> and the 90<sup>th</sup> 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<sub>S</sub>) and in total mass (MI<sub>M</sub>) for juvenile, male and female  
557 northern shrimp *P. borealis* at 2, 5, and 8 °C. The median and the 25<sup>th</sup> and the 75<sup>th</sup> percentiles are  
558 represented. Whiskers below and above the box indicate the 10<sup>th</sup> and the 90<sup>th</sup> 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<sub>S</sub>) and in total mass (SGR<sub>M</sub>) for juvenile, male and  
561 female northern shrimp, *P. borealis* at 2, 5, and 8 °C. The median and the 25<sup>th</sup> and the 75<sup>th</sup> percentiles are  
562 represented. Whiskers below and above the box indicate the 10<sup>th</sup> and the 90<sup>th</sup> 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<sub>S</sub>) 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<sub>S</sub> 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

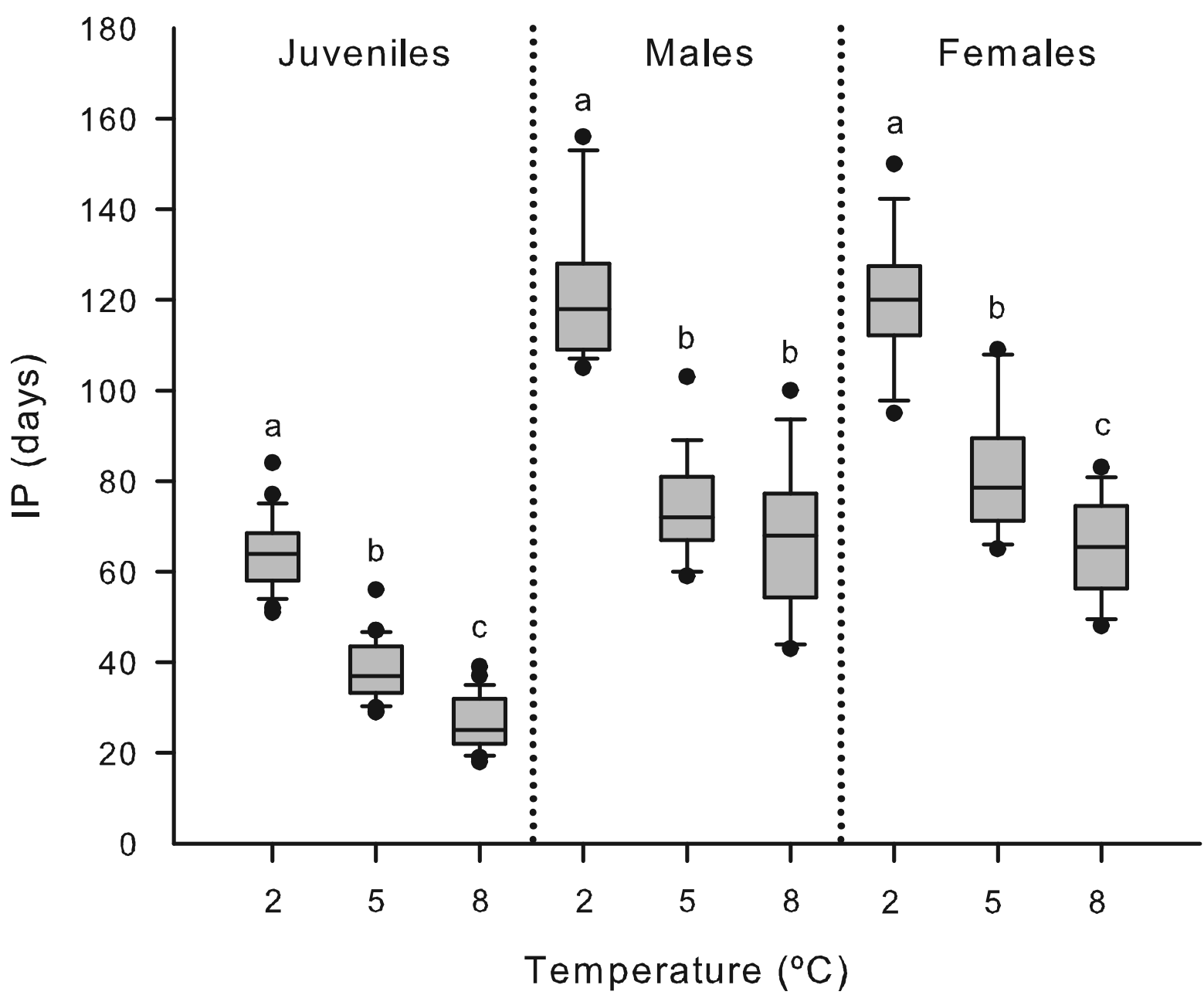


Figure 2

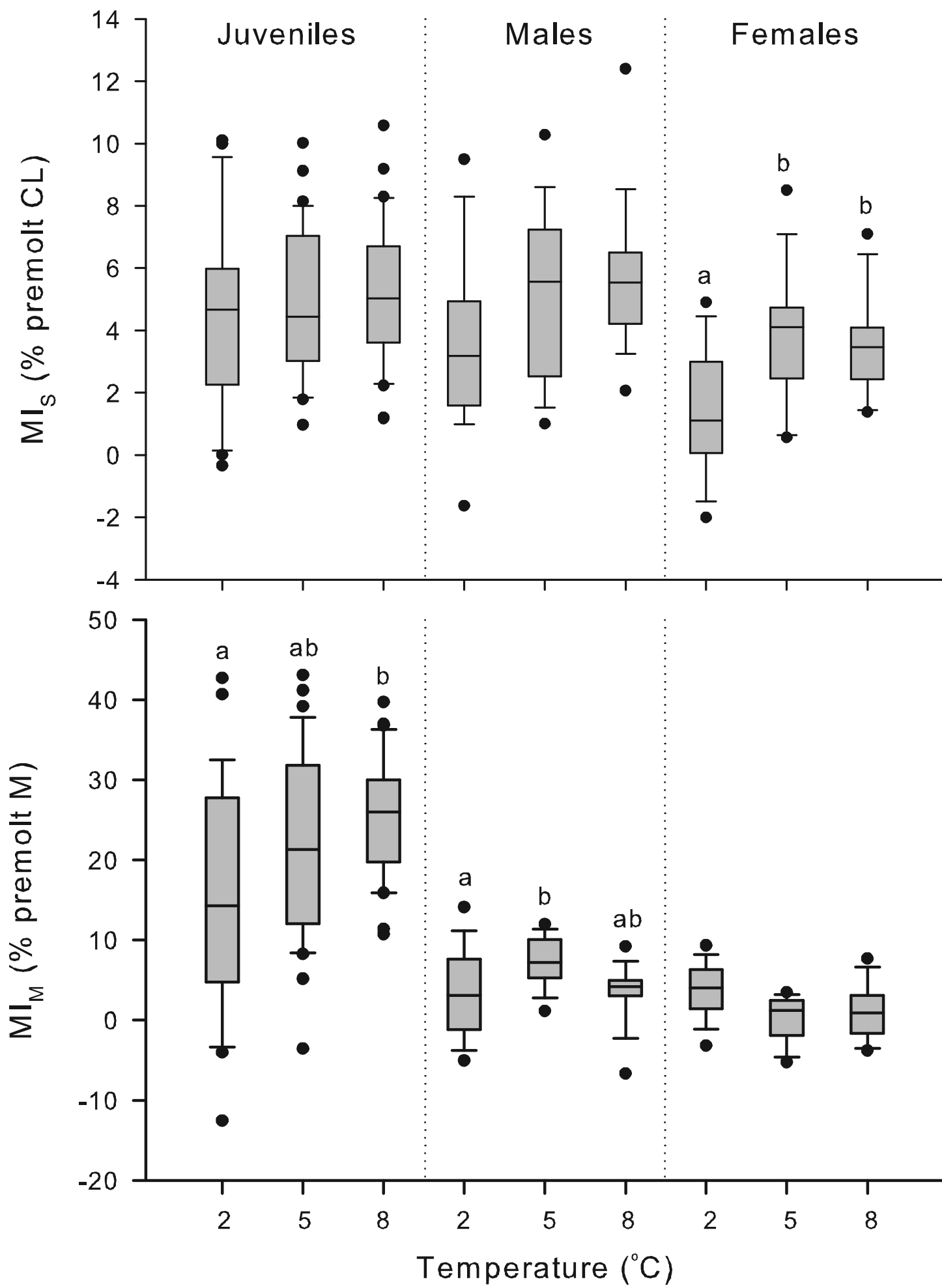


Figure 3

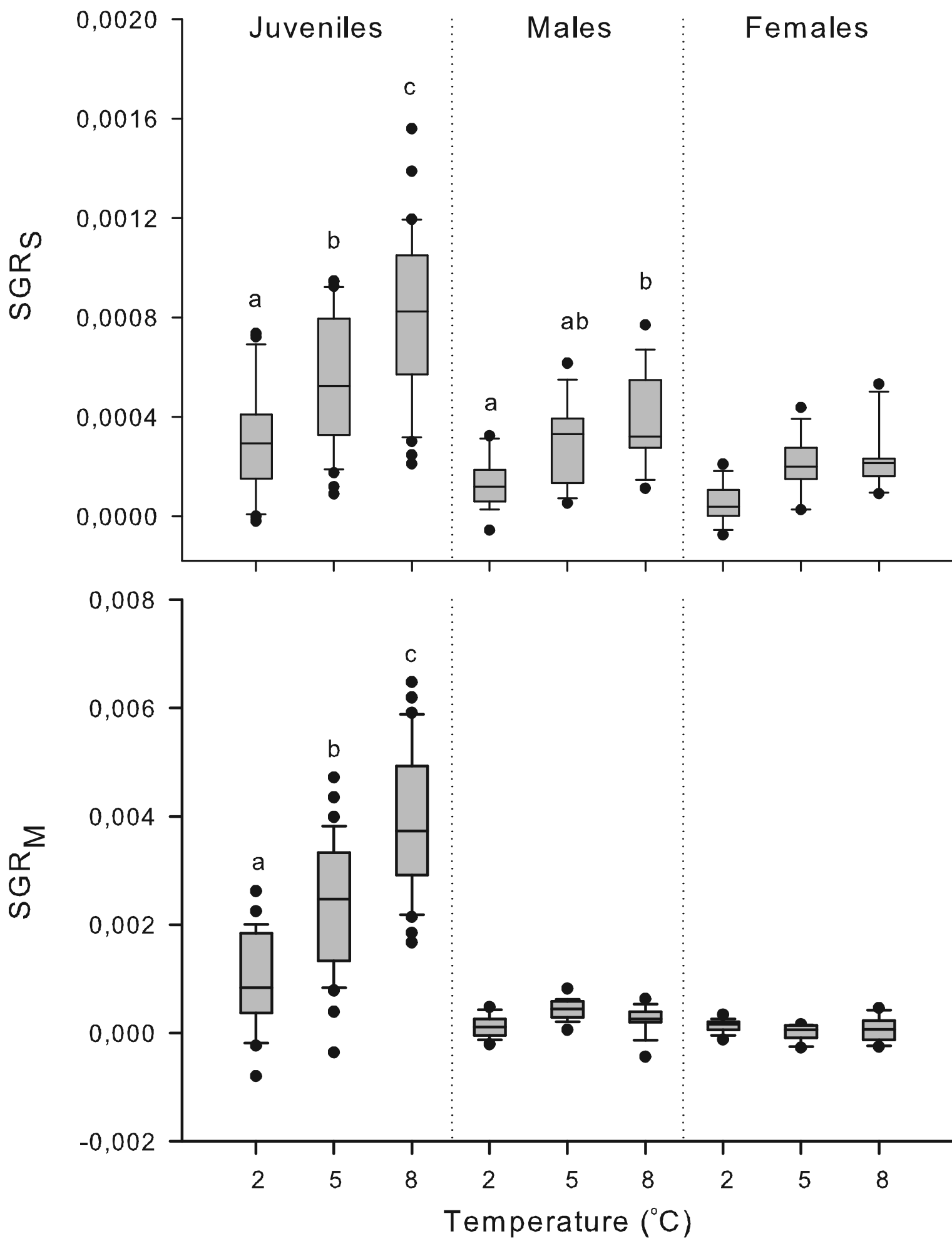


Figure 4

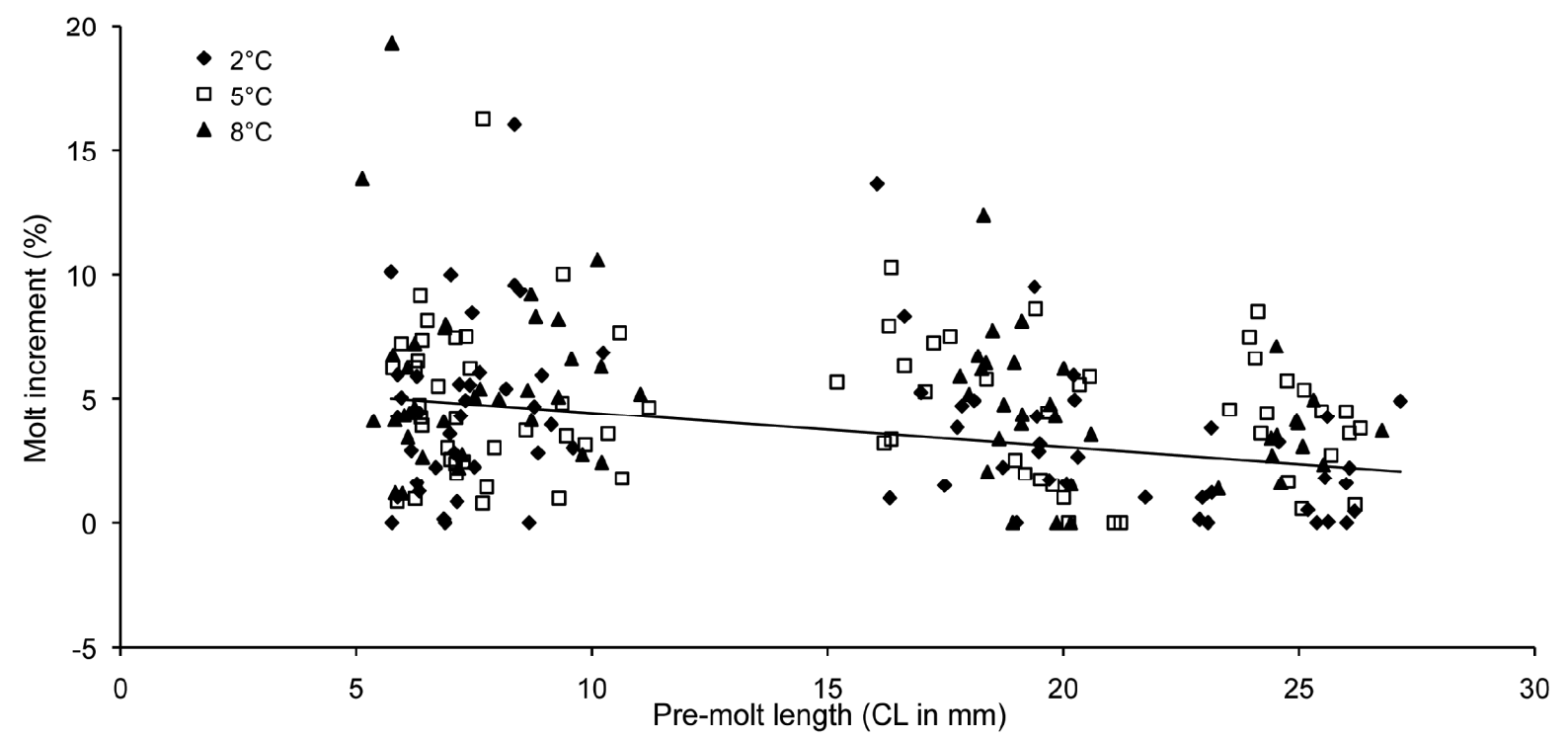
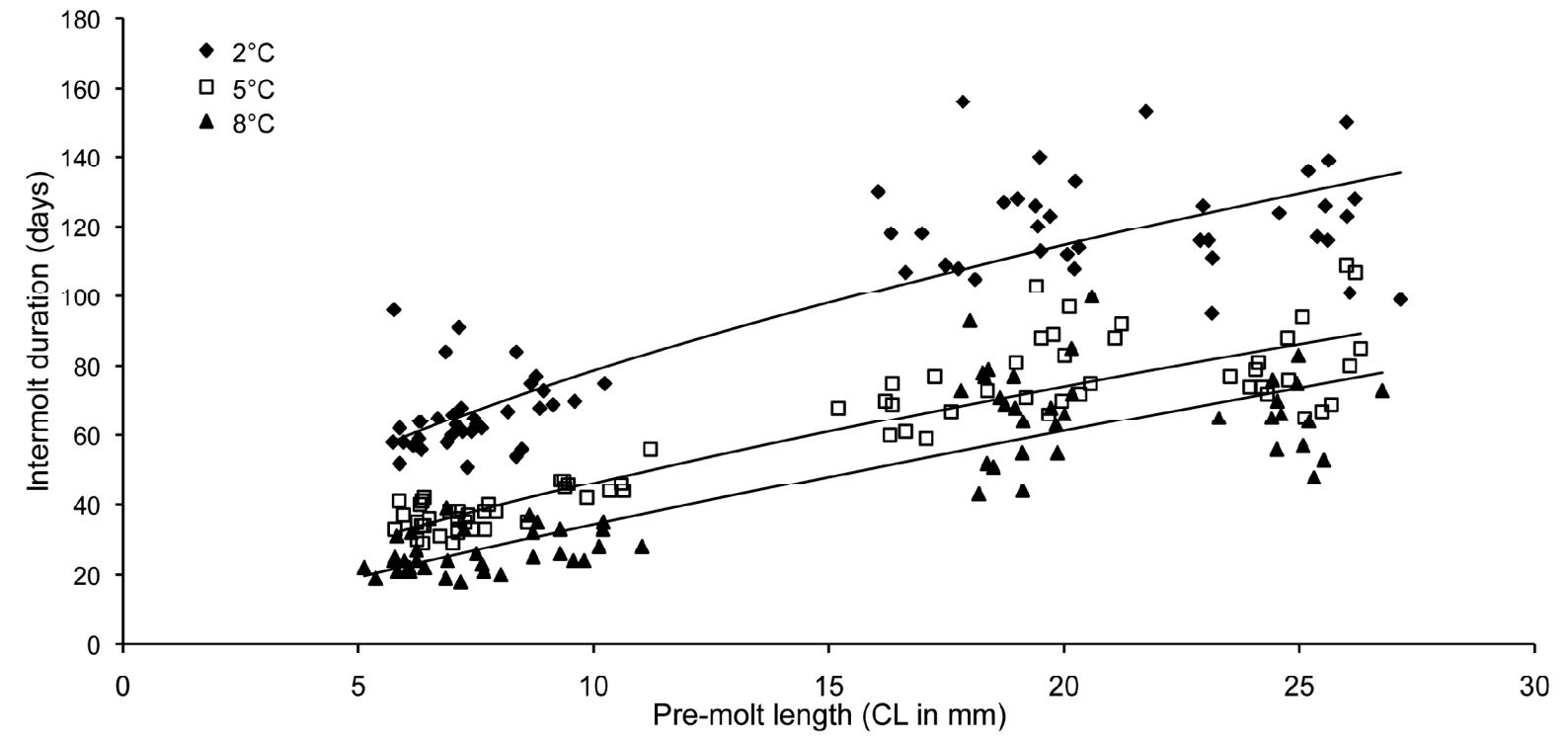


Figure 5

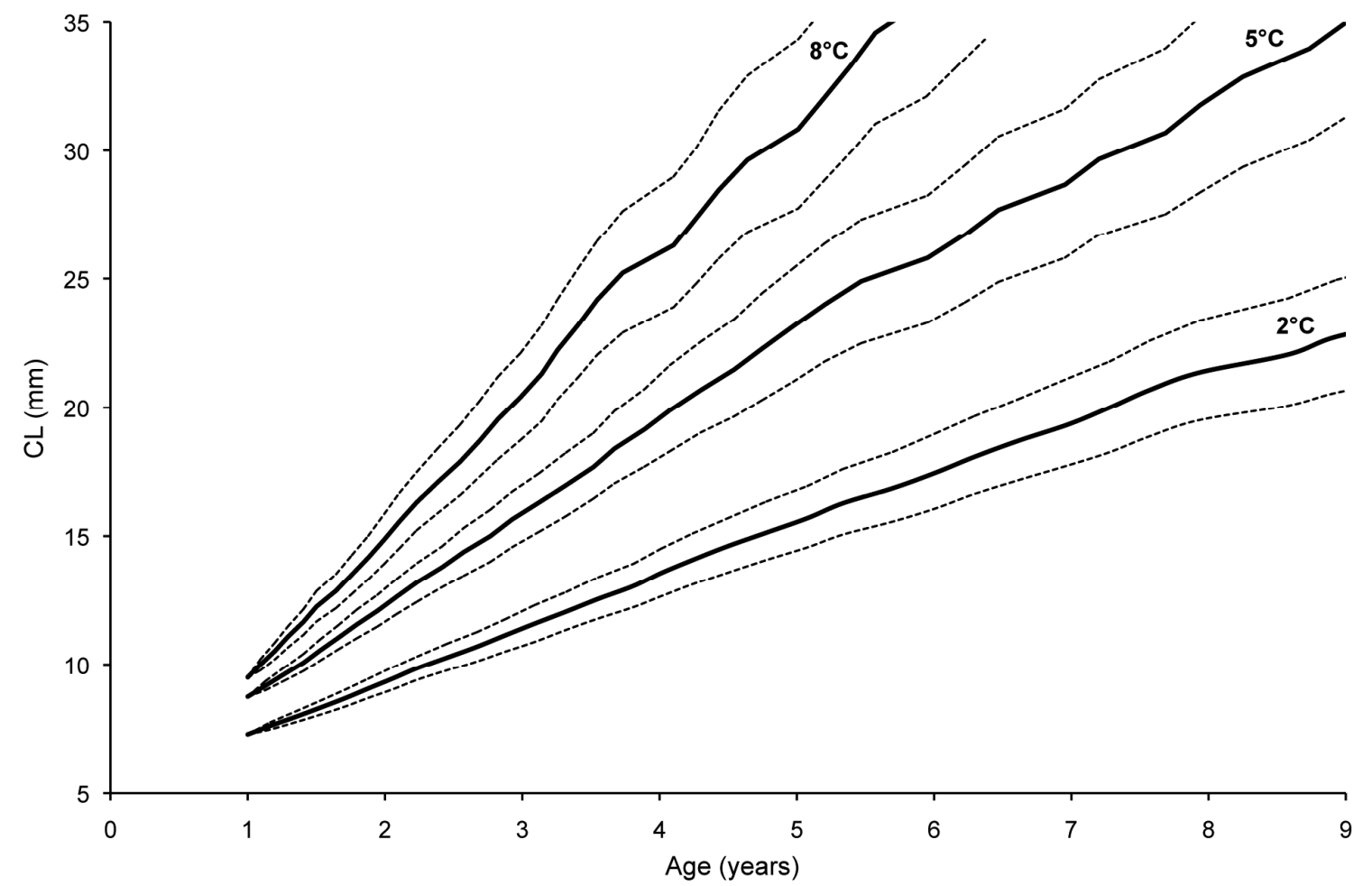


Figure 6

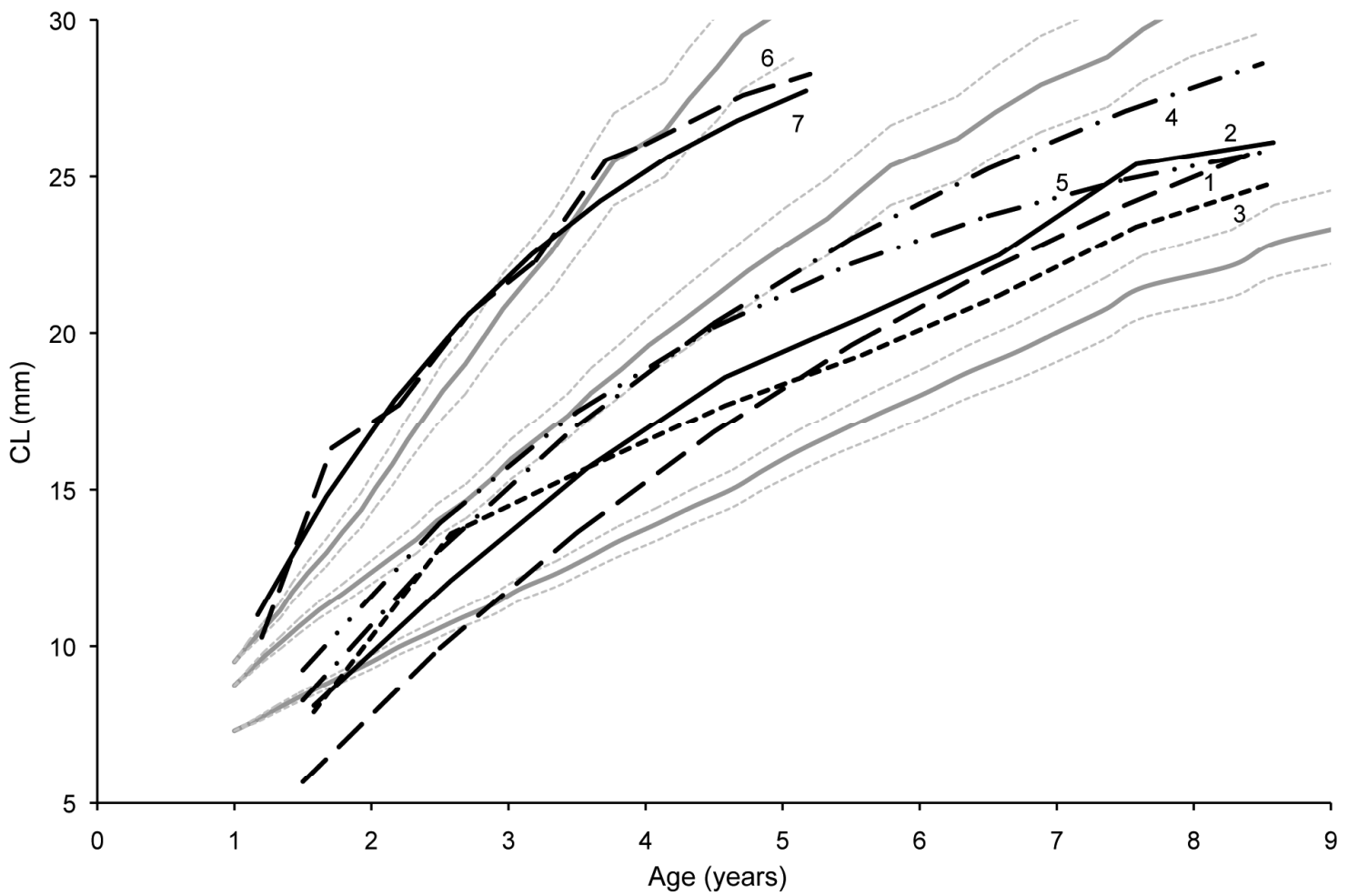


Table 1. Size ( $CL_i$ ) and mass ( $M_i$ ) of juveniles, males and females at the beginning of the intermolt period. Mean values, SD, range of values, and number of samples in parenthesis are presented. For both  $CL_i$  and  $M_i$ , no significant differences were observed ( $p > 0.05$ ) between temperatures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

Temperature		2°C	5°C	8°C
<b>Juvenile</b>	$CL_i$ (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
<b>Male</b>	$CL_i$ (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
<b>Female</b>	$CL_i$ (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:  $\text{Log}(M) = -3.103 + 2.882 \text{Log}(CL)$ ,  $n = 146$ ,  $r^2 = 0.94$ .

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



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
<b>2°C</b>	0.579	1.305	0.86	<0.0001	58	62	111	130
<b>5°C</b>	0.675	0.989	0.89	<0.0001	61	36	71	86
<b>8°C</b>	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 ( $CL_1$ ) 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 $r^2$
<b>Log IP</b>						
Intercept	1.2961	0.0289	13.91	< 0.0001		
Log $CL_1$	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
<b><math>MI_s</math></b>						
Intercept	5.0458	0.5646	79.87	< 0.0001		
$CL_1$	-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 <sup>1</sup>	1990-1993	1-2°C	Skuladottir et al. (2005)
Davis Strait <sup>2</sup>	1978-1986	1-4°C	Parsons et al. (1989)
Hopedale Channel <sup>3</sup>	1981-1987	2-4°C	Parsons et al. (1989)
Flemish Cap <sup>4</sup>	1993-1999	3.2°C	Skuladottir et al. (2005)
Iceland <sup>5</sup>	1981-1989	4.5°C	Skuladottir et al. (2005)
Gullmarsfjorden <sup>6</sup>	1980-1985	4-6°C	Bergstrom (1992)
Gulf of Maine <sup>7</sup>	1969-1986- 1990-1991	5.5-6.5°C	Clark et al. (2000)