



## Original Article

# Vertical distribution of snow crab (*Chionoecetes opilio*) pelagic stages in the Gulf of St. Lawrence (Canada) and effect of temperature on development and survival

Patrick Ouellet\* and Bernard Sainte-Marie

Institut Maurice-Lamontagne, Pêches et Océans Canada, 850 route de la Mer, Mont-Joli, QC G5H 3Z4, Canada

\*Corresponding author: tel: +1 418 725 4162; fax: +1 418 775 0546; e-mail: [patrick.ouellet@dfo-mpo.gc.ca](mailto:patrick.ouellet@dfo-mpo.gc.ca)

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Knowledge of the vertical distribution, thermal habitat, and growth of the larvae of the cold stenothermic snow crab (*Chionoecetes opilio*) is incomplete and inconsistent. This study explored aspects of the vertical distribution and development rate of larvae from eastern Canada. In the Gulf of St. Lawrence (GSL), during 2002, the mean vertical positions of the snow crab zoeae I and II larvae were recorded within and above the permanent thermocline and in close association with the depth of strong density discontinuities in the stratified water column. No statistically significant differences were detected between nighttime and daytime vertical positions. The water temperatures at the centre of the larvae distributions were 2–3 °C in late May in the colder northern GSL and 7–8 °C in June in the warmer southern GSL. Data from the literature and from a rearing experiment in 2014 were used to develop functions linking development and survival to water temperature. Assuming the snow crab larvae remain in the upper mixed layer until final metamorphosis, development may last 2.2–4 months depending on hatch time and location. Development would be prolonged by several weeks if premolt megalopae move into and reside in the deeper, colder waters as appears to be the case. A relative survival index suggests that optimum temperature for development is around 10.8 °C, 9.5 °C, and 8.7 °C for snow crab zoea I, zoea II, and megalopa, respectively. These results should contribute to modelling efforts that aim to evaluate the extent of larval drift and location of potential settlement areas, as well as the potential impact of climate change on snow crab in the North Atlantic.

**Keywords:** climate change, development, snow crab larvae, survival, vertical distribution, water temperature.

## Introduction

Brachyuran crab species may contribute importantly to the structuring and productivity of macrobenthic communities in coastal regions of the Northwest Atlantic (e.g. Boudreau and Worm, 2012; Hanson *et al.*, 2014). Notably, snow crab (*Chionoecetes opilio*, Oregoniidae, Majoidea) is a major benthic predator (e.g. Quijón and Snelgrove, 2005) and it supports one of Canada's foremost fisheries—in 2014, 3rd by landed volume at 96 103 t and 2nd by landed value at 533.7 M\$CAD (<http://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm>, accessed 12 November 2015). However, snow crab is one of the most cold adapted of marine commercial fishery resources in Canada (Foyle *et al.*, 1989)—with its earliest benthic instars apparently being the most stenothermic

of all life stages (Dionne *et al.*, 2003)—and as such is likely especially sensitive to global warming (Chabot *et al.*, 2013).

Climate change has already significantly impacted the upper layer of the ocean in the Northwest Atlantic—e.g. higher temperatures and increased mixed layer depth—and is expected to continue to do so (Chassé *et al.*, 2013; Lavoie *et al.*, 2013). Understanding the processes linking environmental changes to population abundance and distribution begins by identifying the current living environment of species or phases of the species' life cycle, in particular the thermal environment for early development and its variability, and the response of the organism to change or variations in temperature. The snow crab has a long pelagic larval phase consisting of three stages (zoea I, zoea II, and

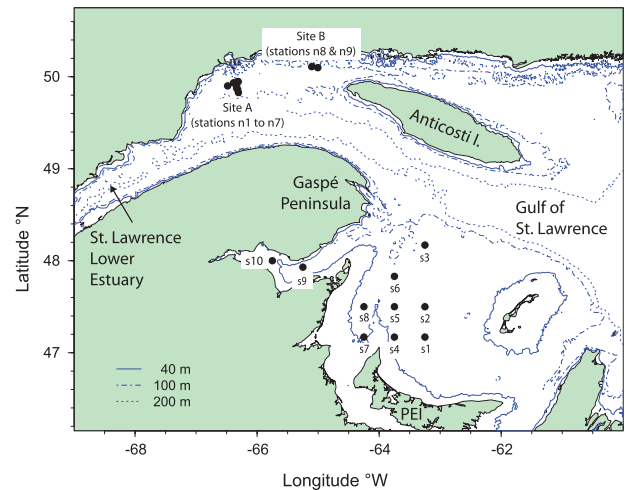
megalopa) lasting altogether up to 3 to 4 months or even more (Lanteigne, 1985; Lovrich *et al.*, 1995; Kon *et al.*, 2003). The snow crab larval phase plays a key role in many population dynamics processes such as dispersal, gene flow and population connectivity (Zheng and Kruse, 2000; Puebla *et al.*, 2008; Albrecht *et al.*, 2014), and ultimately recruitment (Parada *et al.*, 2010; Szuwalski and Punt, 2013; Émond *et al.*, 2015). Larval hatching in snow crab may be spread out over a period of up to 3 months (Kon *et al.*, 2003; Kuhn and Choi, 2011), centred on and peaking around mid-May in eastern Canada (Watson, 1969; Sainte-Marie, 1993; Conan *et al.*, 1996, and references therein). In previous studies, snow crab zoeae were found to be more abundant within the upper, warmer layer of the water column; however, for these stages there seems to be no clear or consistent pattern of diurnal vertical migration across regions or populations (e.g. Lanteigne, 1985; Incze *et al.*, 1987; Kon *et al.*, 2003). The megalopa (settlement stage) has rarely been well sampled, but it appears that it leaves the surface mixed layer and begins to move downward upon reaching the premolt stage (Kon *et al.*, 2003).

Better or region-specific information on snow crab larval behaviour, development and survival in relation to temperature is critical to understanding the impacts of climate change on the snow crab's potential to persist on current fishing grounds or to spread in the Arctic under warming, via larval production, survival and drift, and supply in the form of megalopae to traditional or new grounds offering suitable habitat for the cryptic early benthic instars (e.g. Parada *et al.*, 2010). Our study's first objective was to address gaps in the knowledge of vertical distribution and to identify the thermal habitat of the two zoeal stages of *C. opilio* in the strongly stratified water column of the Gulf of St. Lawrence (GSL), eastern Canada. A second objective was to study the effect of water temperature on development rate and survival of snow crab larval stages. A laboratory experiment was conducted to monitor development and survival of snow crab zoea I from a population in the GSL. These data were complemented by a thorough literature search for similar information to produce a comprehensive evaluation of the effect of temperature on *C. opilio* development rate and survival from zoea I to first benthic stage (C1). Specific information on conditions influencing larval drift and affecting development of snow crab pelagic stages will contribute to better biophysical modelling and understanding the vulnerability and response of snow crab populations in the GSL. The GSL is home to the earliest commercial snow crab fisheries in eastern Canada (FRCC, 2005) and is a well described and modelled physical environment, so its conditions should be representative of core habitat for snow crab in eastern Canada and probably elsewhere.

## Material and methods

### Field data: abundance and vertical distribution

Data on the abundance and vertical distribution of snow crab zoeae were obtained by analysing past zooplankton samples from the northern and southern GSL (Figure 1). In the northern GSL, vertically stratified sampling was conducted at two sites between 20 and 26 May 2002 (Figure 1). At each site, a 1 m<sup>2</sup> multi-net sampler (BIONESS, Sameoto *et al.*, 1980) was used to sample successive layers of variable thickness, 10 m strata for the first 50 m of depth and 25 or 50 m strata for the underlying waters, to cover thermally uniform strata over the entire water column (Ouellet and Allard, 2006). The stratified sampling was repeated every 3 h



**Figure 1.** Locations of the stations from which stratified zooplankton samples were analysed for estimation of abundance and vertical distribution of majoid crab zoea stages in the northern (Sites A and B, stations n1–n9) and southern (stations s1–s10) Gulf of St. Lawrence. Females for the larval rearing experiment were collected in the St. Lawrence Lower Estuary. PEI, Prince Edward Island.

for 72 h at site A and for 48 h at site B (Figure 1). Herein, four nighttime and three daytime stations, 7 stations, at site A and one nighttime and one daytime station, 2 stations, at site B were selected in order to document diurnal variability (Supplementary Table S1). At each station, the available maximum of 8 or 9 strata was examined to sort, identify, count and stage all majoid zoeae. In the southern GSL, samples were from a systematic grid of 65 stations sampled in June 2002 as part of a study to monitor Atlantic mackerel (*Scomber scombrus*) spawning activity (Grégoire *et al.*, 2013). Between 16 and 22 June 2002, the BIONESS was used for vertically stratified sampling, 5 m strata for the first 20 m of depth and 10 m strata from 20 m depth to near bottom, at 17 stations of the grid during an independent study on zooplankton. For our study, based on information on the distribution of snow crab zoeae in the southern GSL (K. Émond, Institut Maurice-Lamontagne, pers. comm.), ten stations including four daytime and four nighttime stations located on the western side of the southern GSL and two nighttime stations in Baie des Chaleurs (Figure 1) were selected for sorting, identifying, staging, and counting all majoid zoeae.

There are three known majoid species in the GSL, snow crab and the toad crabs *Hyas araneus* and *H. coarctatus* (Squires, 1990), whose zoeae I are notoriously difficult to distinguish. Identification and staging of majoid larvae were based on information from various sources (Roff *et al.*, 1984; Davidson and Chin, 1991; Korn *et al.*, 2010). Our ability to morphologically discriminate zoeae I from *Hyas* spp. and *C. opilio* was confirmed by microsatellite analysis (É. Parent, Institut Maurice-Lamontagne, pers. comm.). However, damaged majoid specimens often could not be identified to genus and zoea I and II larvae were sorted into three taxonomic groups: *C. opilio*, *Hyas* spp. and Majoidea spp. The larvae assigned to the Majoidea spp. group represented only 18.5% and 16.7% of all majoid larvae in the northern and southern GSL, respectively. The abundance of the Majoidea spp. group was highly correlated with that of *C. opilio* and *Hyas* spp.,

and since no other majoids are known to be present in the GSL, the damaged, unidentifiable majoid larvae were inferred to belong to *C. opilio* or *Hyas* spp. Therefore, a total abundance index for *C. opilio* and *Hyas* spp. zoea I and II larvae was estimated by assigning fractions of the Majoidea spp. zoeae in each sample to either one of the two taxa (and stages) based on their observed relative proportions in each sample. Here we report on the abundance and distribution of *C. opilio* only, although vertical distribution of *Hyas* spp. is shown in supplementary material.

The total number of snow crab larvae per station was estimated for each stage by summing counts from all depth strata and the stage abundance was expressed as number per square meter of water surface ( $N \cdot m^{-2}$ ). For analysis of vertical distribution, at each station the number of larvae per depth stratum was expressed as number per cubic meter ( $N \cdot m^{-3}$ ) based on the volume of water filtered by the net. The vertical position of the zoeae maximum abundance was obtained by calculating the weighted mean depth or centre of mass (CM) of the distribution, as:

$$Z_{CM} = \sum_{i=1}^n p_i z_i$$

where  $p_i$  is the proportion of zoeae in the  $i_{th}$  depth stratum,  $z_i$  is the median depth of the stratum and  $n$  is the number of strata at the station. The weighted mean temperature ( $^{\circ}C_{CM}$ ) was obtained by substituting the median depth by the median temperature of the stratum.

Temperature and density (sigma-t) data were available from a conductivity, temperature, depth (CTD) probe profile done at each station, allowing for the estimation of the stratification profile of the water column. For this purpose, the first 2 m at the surface were eliminated to avoid erroneous data sometimes caused by an insufficiently long adjustment period of the CTD probe from the ship deck to the water. Smooth continuous profiles of vertical differences were obtained by sliding a 5 m window over the sigma-t profile, already binned at 0.5 and 1 m for the southern and the northern GSL, respectively:

$$\Delta kg m^{-3} i = Sg_{t_i} - Sg_{t_{i+5}}, \text{ for } i = 3, \dots, N$$

where  $\Delta kg m^{-3} i$  is the difference in sigma-t between depth intervals and  $Sg_{t_i}$  is sigma-t at the  $i_{th}$  of  $N$  depth intervals. For each station the depth at maximum stratification is the depth at maximum  $\Delta kg m^{-3}$ .

### Snow crab zoea rearing experiment

Some previous studies have investigated the effects of water temperature on development of snow crab larvae, providing intermolt duration and survival of zoea I, zoea II, and megalopa at three or more temperatures (Kon, 1970; Lim *et al.*, 2001; Kogane *et al.*, 2005; Yamamoto *et al.*, 2014). However, to obtain data specific to GSL snow crab, females bearing soon-to-hatch embryos were captured in the St. Lawrence Lower Estuary (Figure 1) in mid-April 2014 to obtain larvae for a rearing experiment. Between 7 and 26 May 2014, five groups of newly hatched larvae were successfully reared to the zoea II stage, with each group representing a mixture of larvae hatched the same day from three to five females in different tanks. Larvae from different females were mixed to reduce potential “maternal effects” on the results. Eight 360-l tanks were set up to monitor development at eight

temperatures: 0, 3, 6, 9, 12, 15, 18, and 21 °C. The tanks were open water-baths and were used for incubating subgroups of 300 zoeae I each in closed 1.5 l jars. One subgroup from each larval group was incubated at each temperature. The larvae were fed manually each day with a per-litre ration of 1000 1-day old *Artemia* sp. nauplii enriched with EASY DHA Selco (INVE Aquaculture) and  $\approx 3.5 \times 10^5$  microalgae cells from a commercial concentrate (N-Rich®, Reed Mariculture, Inc). A continuous, gentle flow of compressed air ensured aeration and mixing of larvae and food. Each day, the live larvae were transferred to fresh water in a clean jar (e.g. Hamasaki *et al.*, 2007; Yamamoto *et al.*, 2014), counted and observed to detect molt events. Molting events were recorded and if possible a subsample of at least five live zoeae II was taken from each jar. Mortality was monitored daily; very high mortality was immediately recorded at 0, 3, and 21 °C, with no zoea I surviving to the zoea II stage. High mortality occurred during zoea II development in the subgroups at the remaining incubation temperatures, due to system failure, and we were unsuccessful at rearing zoeae II to the megalopa stage.

The first occurrence of a molt from zoea I to zoea II was recorded for each subgroup and the mean time (in days) to first occurrence of molting was estimated for each incubation temperature. Also, based on all available subgroups, a mean survival of zoea I up to that point was estimated at each temperature as the ratio of the number of larvae still alive at the occurrence of the first molt on the initial number of larvae in the jar. The time to first molting represents minimum intermolt duration ( $ID_{min}$ ) and was converted to mean intermolt duration ( $ID_{mean}$ ) using a relationship between  $ID_{min}$  and  $ID_{mean}$  that we developed from information on zoea I in Kon (1970) and Yamamoto *et al.* (2014):

$$ID_{mean} = 1.1201 \cdot ID_{min}; n = 11, r^2 = 0.999, F = 17\ 090.63, \\ P < 0.001$$

We derived a relative survival index by dividing mean survival at a given temperature by maximum mean survival over the range of temperatures tested in each study. Absolute survival may vary across studies due to different rearing techniques and feeds, but scaling mean survival at different temperatures to maximum survival in the same study and then combining the results from various studies, allows a much clearer resolution of the overall pattern of response to temperature. The collated information on snow crab larval development rate and survival allowed a comprehensive account of larval fate in relation to temperature.

### Snow crab morphometrics

Morphometric data were obtained from all or a maximum of 10 snow crab zoea I and zoea II larvae from each field sample, on subsamples of 10 newly hatched zoea I from each larval group reared in the laboratory, and on all live zoea II obtained at different temperatures in the laboratory. A snow crab zoea represents a complex tridimensional structure and larval “size” indices were estimated from two planes, a frontal and a side view (Figure 2). Following on previous works (Davidson and Chin, 1991; Pohle, 1991; Webb *et al.*, 2006), five measurements were selected, in frontal view: (i) cephalothorax width (CW) measured between outside edge of the eyes, (ii) full width (SW) measured from tip-to-tip of the two lateral spines, and (iii) total height (RDL) measured from the tip of the dorsal spine to the tip of the rostrum; in

side view: (iv) cephalothorax length (CL) measured from the posterior edge to the front of the cephalothorax below the dorsal spine, and (v) length of the posterior lateral spine (PLS) on the third abdominal segment. All measurements were obtained from digitalized images of larvae with software Image-Pro Premier v 9.1 and only data from undamaged larvae—all five measurements present—were retained for more robust analyses. Overall, for zoea I and II larvae there were relatively good correlations between CW and CL (Supplementary Table S2), suggesting that both measurements can be used as a reliable size index. Therefore, an estimate of the percent growth increase at first molt (%MI) was calculated for CW and CL as:  $\{(X_{II} - X_I)/X_I\} \times 100$ , where  $X_I$  and  $X_{II}$  are the mean measurements taken on all zoeae I and zoeae II, respectively, from each field region and from each group and subgroup from the laboratory experiment.

### Data analyses

For each region, the mean  $\pm$  1SD was estimated for daytime and nighttime total abundance of each larval stage. Welch's *t*-test, designed for unequal variances between groups, was used to test for significant differences between daytime and nighttime mean depth distributions of snow crab zoeae, and between morphometric measurements of zoeae I larvae in the northern and the southern GSL. A one-factor ANOVA and *a posteriori* multiple comparisons were conducted on the 2014 rearing experiment data to detect significant effects of incubation temperature on CL and CW %MI of snow crab larvae. Levene's test confirmed ( $P > 0.05$ ) homogeneity of variance among groups (incubation temperatures) for both CL and CW %MI.

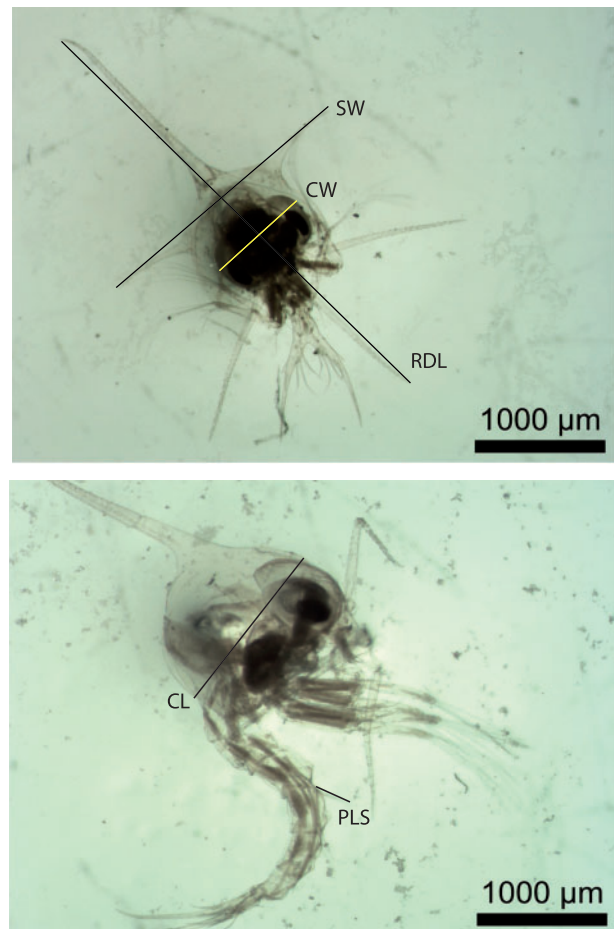
The estimated mean intermolt duration and relative survival index from the laboratory experiment were plotted along with similar data extracted from reviewed literature. Parameterizations of the relationship between water temperature and intermolt duration or survival in *C. opilio* zoeae I to megalopa stages were obtained by non-linear least squares curve fitting on the point distribution. All analyses and plots were produced within the R environment (R Core Team, 2017).

## Results

### Abundance and vertical distribution

In the northern GSL, only zoeae I were present at both sites during the May 2002 sampling. Snow crab mean abundance was  $17.7 \pm 14.9$  zoeae·m<sup>-2</sup> (Figure 3), and the larvae were more abundant at the westward Site A stations over the slope extending down into the Laurentian Channel ( $19.7 \pm 16.0$  zoeae·m<sup>-2</sup>) than at shallower stations at the eastward Site B ( $11.1 \pm 11.2$  zoeae·m<sup>-2</sup>) (Figure 3). At all stations, snow crab zoeae I were more abundant within the upper layer of the water column and there was no difference between daytime and nighttime mean depth distributions ( $Z_{CM}$ ) (Table 1 and Supplementary Figure S1).

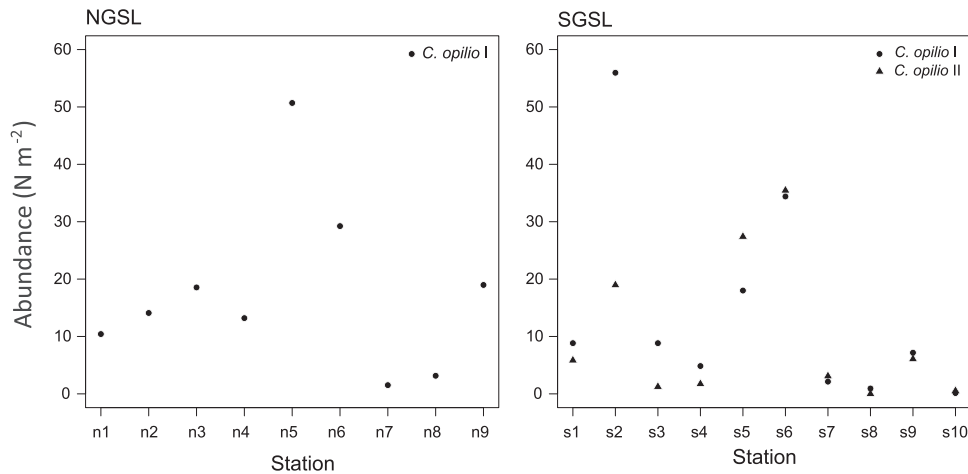
In the southern GSL, both zoeal stages but no megalopae of snow crab were present during the June 2002 sampling and mean total abundance was  $14.1 \pm 17.9$  and  $10.0 \pm 12.7$  zoeae·m<sup>-2</sup> for zoeae I and zoeae II, respectively. Overall, zoeae II represented 41.5% of total snow crab larvae. Snow crab zoeae I and II were generally more abundant at the deeper stations s1 to s6, north of Prince Edward Island, than at the shallower stations s7 and s8 and the Baie des Chaleurs stations s9 and s10 (Figure 3). As was the case for the northern GSL, all zoeae (both stages) were more abundant in the upper layer of the water column. There was a



**Figure 2.** Photograph of a *C. opilio* zoea I larva showing the five morphological variables used to characterize larval size. Frontal view: (i) distance between outside edge of the eyes, cephalothorax width (CW), (ii) distance between the tips of the two lateral spines, full width (SW), and (iii) distance from the tip of the dorsal spine to the tip of the rostrum, total height (RDL). Side view: (iv) from the posterior edge to the front of the cephalothorax below the dorsal spine, cephalothorax length (CL), and (v) the length of the posterior lateral spine (PLS) on the third abdominal segment.

tendency for snow crab zoeal stages in the southern GSL to be shallower at night than in the day, but only for zoea I was the difference between the mean daytime and nighttime  $Z_{CM}$  statistically significant (Table 1; Supplementary Figure S2). However, since different stations were sampled at different times of the day, it is not possible to separate the effects of location and time of day on the  $Z_{CM}$  in the southern GSL.

In both regions, at the time of the surveys the water column was strongly thermally and density stratified (Supplementary Figure S3). In the northern GSL, in May 2002, strong density gradients were observed at about 10 m below the surface (Figure 4). Mean  $\pm$  1SD  $Z_{CM}$  of snow crab zoea I was closely associated to the sub-surface pycnocline and within the warmer portion of the water column (Figure 4). Nonetheless, the mean water temperature at the mean zoea I  $Z_{CM}$  depth was only  $2.8 \pm 0.9^\circ\text{C}$ . In the southern GSL, in June 2002, the mean zoea  $Z_{CM}$  of all snow crab larval stages remained above or at the level of the maximum sub-surface density gradient and within the warmer upper layer of the



**Figure 3.** Total abundance of *C. opilio* zoea I and II larvae at the selected stations in the northern Gulf of St. Lawrence (NGSL) in May 2002 and in the southern Gulf of St. Lawrence (SGSL) in June in 2002. See Figure 1 for station locations.

**Table 1.** Summary of *t*-tests performed between daytime and nighttime depth at centre of mass (CM) of snow crab zoeae I or II distribution in the water column of the northern and southern GSL sampled in 2002.

Taxon	Mean $\pm$ 1SD depth CM (m)		Welch's <i>t</i>	df	<i>P</i>
	Day	Night			
northern GSL					
<i>C. opilio</i> I	10.99 $\pm$ 5.02	10.95 $\pm$ 2.83	0.016	4.5	0.987
southern GSL*					
<i>C. opilio</i> I	18.43 $\pm$ 8.01	7.47 $\pm$ 5.82	2.375	6.9	0.049
<i>C. opilio</i> II	21.14 $\pm$ 13.46	11.44 $\pm$ 5.15	1.482	5.3	0.194

\*In the southern GSL, at station s8 (night) only one snow crab zoea I was caught in the deepest stratum and that station was excluded from the comparison.

water column (Figure 4). The mean water temperature at the mean  $Z_{CM}$  depth was  $7.7 \pm 2.9^\circ\text{C}$  and  $7.6 \pm 1.9^\circ\text{C}$  for snow crab zoea I and zoea II, respectively.

### Snow crab larvae size in the northern and southern GSL

Comparison of snow crab zoea I from the northern and southern GSL revealed significant differences in mean CL, SW and PLS (Figure 5 and Table 2). Mean CL and SW were larger for northern GSL than for southern GSL zoea I, whereas mean PLS was larger for southern GSL than for northern GSL zoea I (Table 2). Examination of the size frequency distributions also showed wider ranges for all zoea I measurements in the southern GSL zoea I compared to the northern GSL (Figure 5, also see SD values in Table 2).

### Water temperature and development and survival of snow crab larvae

Water temperature had a strong effect on the time to first molt and on the relative survival index of snow crab zoea I in our experiment as in previous studies (Figures 6 and 7). Our minimum zoea I intermolt duration (=time to first molt) converted to mean zoea I intermolt duration (see Material and Methods) fell nicely within the narrow scatter of published values for this larval

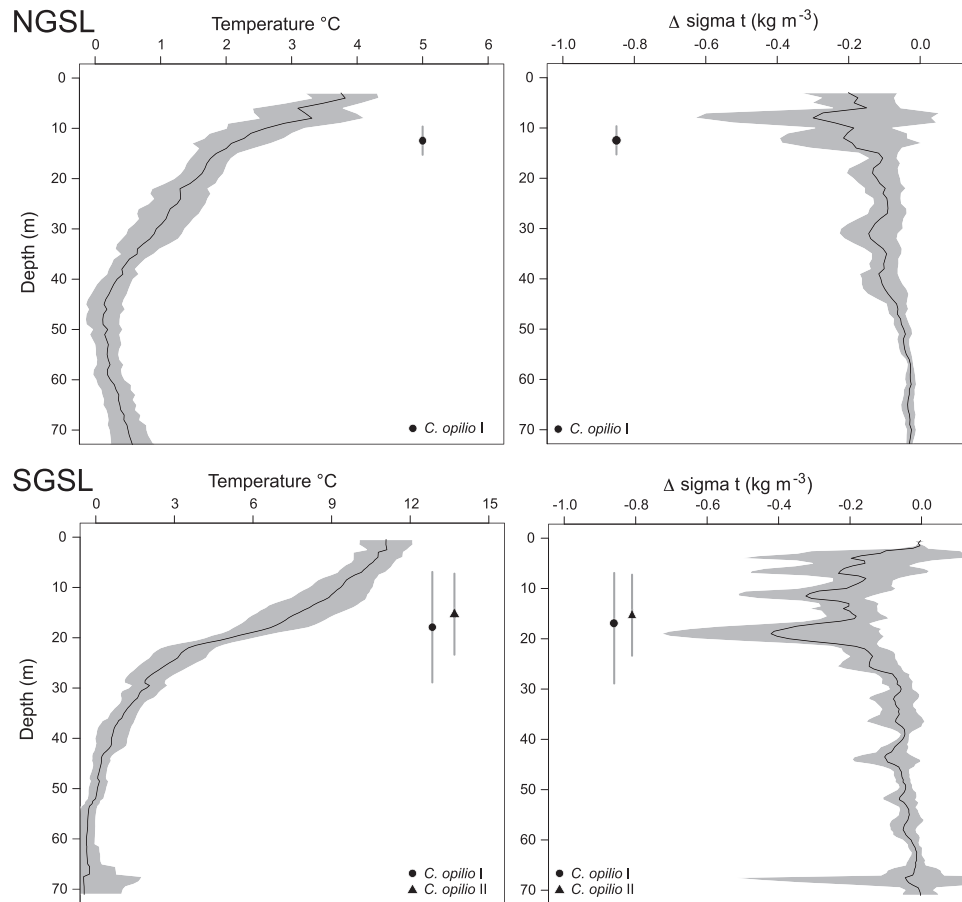
stage, as did our relative survival index (Figure 7). Estimated mean intermolt duration of the zoea I stage decreased exponentially with increasing temperature, from about 82 days in the northern GSL to about 35 days in the southern GSL at the respective zoea I mean  $Z_{CM}$  temperatures of  $2.8$  and  $7.8^\circ\text{C}$ . Based on the published literature (Figure 7), the duration of the zoea II stage at the same temperatures—84 and 36 days, respectively—was almost identical to that of the zoea I stage. On the other hand, the duration of the megalopa stage would be about 4 days shorter (80 days) than the projected duration of each of the zoeal stages at the lower temperature but 6 days longer (42 days) at the warmer temperature. The duration of each larval stage, when expressed in accumulated degree-days, also decreased with increasing temperature (e.g. for zoea I, see Figure 6).

The relative survival indices were a dome-shaped function of temperature for all larval stages (Figure 7). Maximum absolute survival measured in the underlying studies ranged from 11 to 98% for the zoea I, 60 to 83% for the zoea II, and 29 to 100% for the megalopa. For both the zoea I and zoea II stages, relative survival was more variable among studies at the lower than at the higher tested temperatures. From the relationships, the temperature at the maximum relative survival (i.e. maximum of the estimated curve) was  $10.8^\circ\text{C}$ ,  $9.5^\circ\text{C}$ , and  $8.7^\circ\text{C}$  for the zoea I, zoea II, and megalopa, respectively. Overall, the megalopa appears to be more cold-tolerant and warm-averse than the zoeae I and II in both development rate and survival index.

In the laboratory, temperature had a significant effect on the percent size increment at the molt (%MI) from zoea I to zoea II (Table 3). The mean %MI was smaller in CL than in CW but, overall, it peaked at  $12$ – $15^\circ\text{C}$  and declined moderately at colder temperatures and more sharply at  $18^\circ\text{C}$  (Figure 8). In the field, estimation of %MI was possible only for the southern GSL in June 2002. Calculations based on mean size of snow crab zoea I and II for all stations showed that %MI was also less in CL (55.5%) than in CW (60.8%) in the field, although both values were somewhat greater than those measured in the laboratory.

### Discussion

This study revealed detailed information on the abundance and vertical distribution of the first two zoeal stages of snow crab in a strongly stratified water column, and an assessment of the effect



**Figure 4.** Relationships between the density stratification (solid line = mean delta sigma-t; shaded area = 95% confidence intervals) and temperature profiles (solid line = mean temperature; shaded area = 95% confidence intervals) and the mean  $\pm$  1SD depth (center of mass:  $Z_{CM}$ ) of *C. opilio* zoea I and zoea II larvae in the northern and southern Gulf of St. Lawrence (NGSL and SGSL, respectively) in 2002.

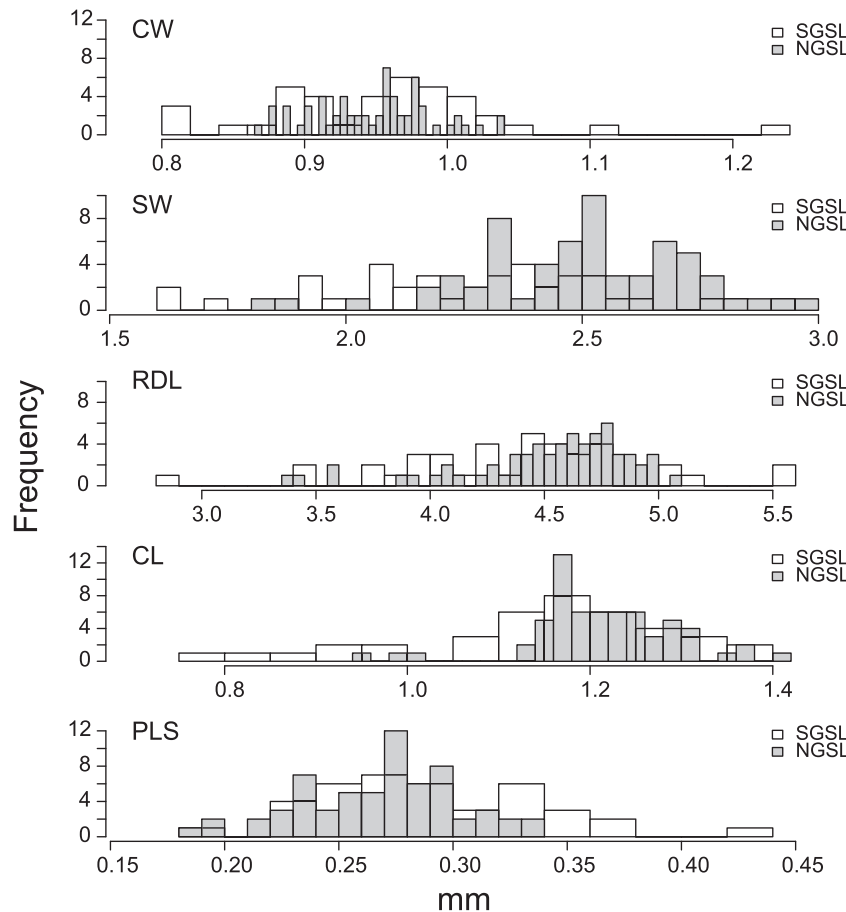
of water temperature on development time and survival of snow crab larvae. These results should be useful in particular to any modelling effort aiming to evaluate the extent of larval drift, location of potential settlement areas (megalopa distribution) and estimation of connectivity among snow crab population units, as has been done for example in American lobster *Homarus americanus* (Quinn *et al.*, in press), as well as the potential impact of climate change on snow crab in the North Atlantic and elsewhere.

### Snow crab larvae vertical distribution and surrounding temperature

The two zoeal stages of snow crab were distributed mainly in the upper mixed layer of the water column, where the water was warmest and presumably where phytoplankton concentrations support the energy needs of the morphologically similar zoea I of *Chionoecetes* and *Hyas* species (Incze and Paul, 1983; Meyer-Harms and Harms, 1993). The mean center of the distribution of zoeae of snow crab was found within the thermocline close to the depth of a strong density discontinuity in the water column. Our sampling was limited to short periods in early spring, but seasonal (ontogenetic) changes in the vertical distribution of snow crab zoeae have been shown for a region of the northeastern GSL by Conan *et al.* (1996). However, their observation that snow crab zoeae were centered on  $\approx 15$  m depth in spring, around 50 m

depth in early summer and back to  $\approx 15$  m depth in late summer may suggest that the larvae were responding to occasional turbulent mixing (winds) or to changes in the thickness of the upper mixed layer during the season. Some snow crab zoeae can be found in deeper water, below the thermocline (e.g. Lanteigne, 1985; this study—Supplementary Figures S1 and S2), but there are no convincing data to support the idea of large, behaviourally driven vertical movements (i.e. migration) across the thermocline or throughout the water column. Therefore, the current information available indicates that snow crab larval stages most likely remain in the upper mixed layer of the water column for development, at least until the megalopa stage. Moreover, considering that the density of snow crab zoeae is much greater than the density of the surrounding water (Yamamoto *et al.*, 2015), active and presumably costly behaviour must be involved to maintain their position in the upper layer to stay within favourable (temperature and feeding) conditions for development.

There was some suggestion for the southern GSL that the snow crab zoeae may have moved higher in the water column within the upper mixed layer at night. The relatively coarse upper layer depth strata sampled, 5-m for the first 20 m in south GSL and 10-m for the first 50 m in northern GSL, may have limited our capacity to detect statistically significant fine scale vertical movement within the mixed layer. For snow crab zoeae, similar observations of limited or no diel vertical movements have been reported



**Figure 5.** Frequency distributions of five morphometric measurements of *C. opilio* zoea I from the northern and southern GSL. Frontal view: CW = cephalothorax width, SW = full width, RDL = total height. Side view: CL = cephalothorax length, PLS = length of the posterior lateral spine on the third abdominal segment. See Figure 2.

**Table 2.** Mean and standard deviation of morphometric measurements\* on snow crab zoea I and statistical comparisons between the northern and southern GSL sampled in 2002.

Variable	NGSL (mm)	SGSL (mm)	Welch's <i>t</i>	<i>df</i>	<i>P</i>
CW	0.948 ± 0.040	0.967 ± 0.089	-1.333	53.7	0.188
SW	2.495 ± 0.226	2.292 ± 0.298	3.774	73.7	0.003
RDL	4.512 ± 0.379	4.396 ± 0.532	1.235	70.3	0.221
CL	1.212 ± 0.081	1.161 ± 0.143	2.158	60.5	0.035
PLS	0.268 ± 0.034	0.295 ± 0.048	-3.179	70.8	0.002

\*CW, cephalothorax width; SW, full width; RDL, total height; CL, cephalothorax length; PLS, posterior lateral spine length.

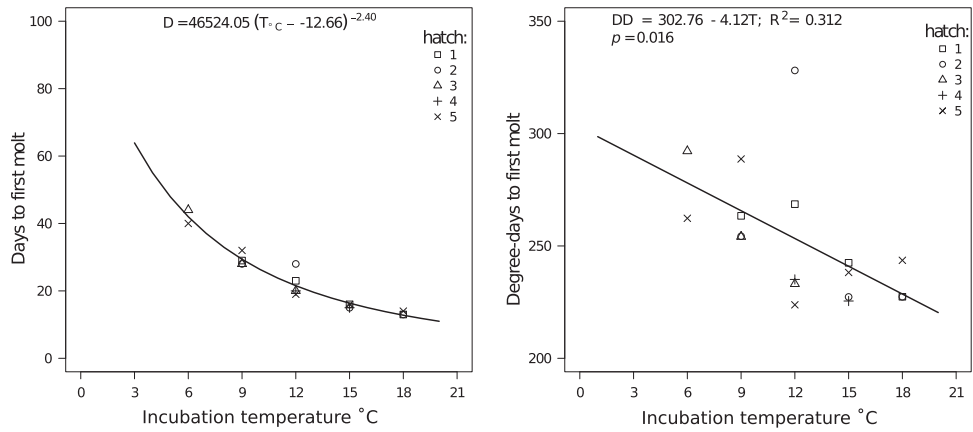
before (Incze *et al.*, 1987; Ouellet and Lefaivre, 1994). However, Kon *et al.* (2003) documented large shifts in the day-night vertical distribution of snow crab zoea II in the Japan Sea, but still within the upper mixed layer which in that case was >150 m thick. Also, Roff *et al.* (1986) reported greater abundance of snow crab zoeae near the surface at night compared to day on the Scotian Shelf (Canada) and interpreted this to indicate diel vertical migration.

Given the strong thermal stratification of the GSL beginning in early spring (Galbraith *et al.*, 2016), the vertical position of the larvae also defines the temperature conditions for their development and growth. Snow crab larvae were concentrated at

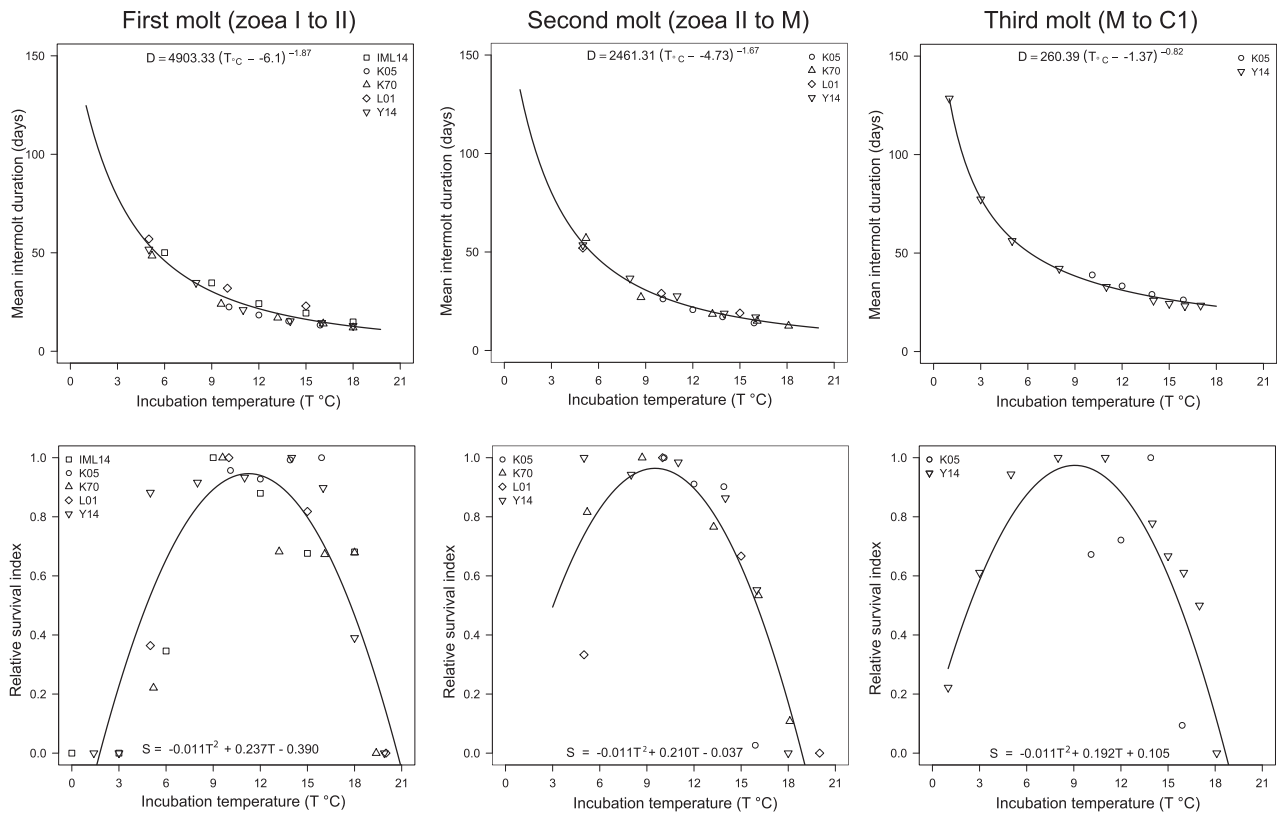
temperatures between 2 and 3°C in the northern GSL in late May 2002 and between 7 and 8°C in the southern GSL in June 2002. However, we had limited capacity to detect fine scale vertical movement of larvae (see above) and thus corresponding changes in the actual water temperature for development. Additionally, the northern GSL was not fully stratified at the time of the May survey (and much less so than the southern GSL), thus zoea I larvae had less scope for vertical movement within waters in the preferred/optimal temperature range, as evidenced by the very small variance about mean center of distribution compared to the southern GSL. Nevertheless, in the northern GSL, the actual temperature with which larvae were associated might be somewhere on the order of 0.5°C warmer than what we estimated.

### Effect of water temperature on snow crab larvae development and size

Data obtained from the 2014 rearing experiment fitted well within the range of values extracted from our literature review to produce general functions linking snow crab larval intermolt duration to temperature. Moreover, development times for a given snow crab larval stage in other studies with only one or two constant rearing temperatures align closely with results from the more comprehensive studies reviewed herein. For example, Charmantier and Charmantier-Daures (1995) reported that



**Figure 6.** Relationships between incubation temperature (T) and time in days (D) (left) and accumulated degree-days (DD) (right) for the occurrence of the first molt from zoea I to zoea II of *C. opilio*. The parameters of the Belehrádek equation,  $D = a(T - \alpha)^{-b}$ , were estimated using data from five hatches between 7 and 21 May 2014.

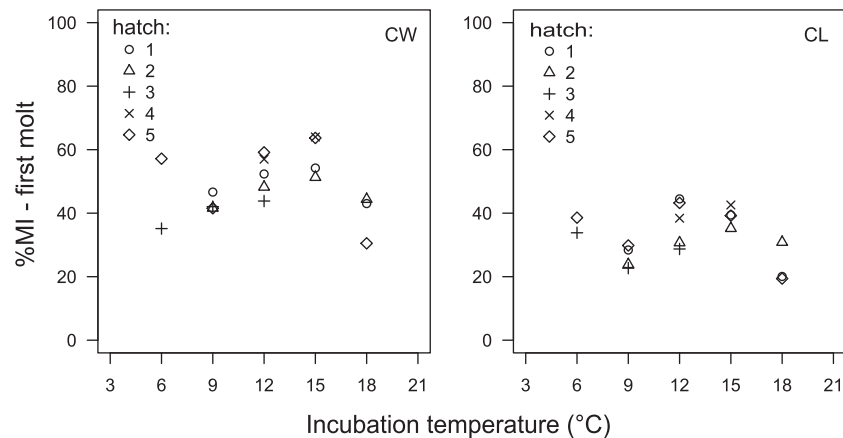


**Figure 7.** Relationships between water temperature (T) and mean intermolt duration (in days, D) and the relative survival (S) index of *C. opilio* crab zoea I, zoea II and megalopa stages. IML14 = Our 2014 experiment; K05 = Kogane *et al.* (2005); K70 = Kon *et al.* (1970); L01 = Lim *et al.* (2001); Y14 = Yamamoto *et al.* (2014).

development of zoea I to zoea II was slower at 9.5 °C (24–38 days) compared to 14 °C (15 days) and Pohle (1991) reported development times of 30 days for zoea I and 30.5 days for zoea II at 9 °C. The strong coherence of larval intermolt durations for snow crab populations in the north Pacific and north Atlantic, revealed herein, reinforces the view that snow crab life history schedules are extremely conservative (e.g. Orensanz *et al.*, 2007).

The regressions for larval development on temperature were nearly identical for both zoeal stages, whereas development of the megalopa was progressively slower than that of zoeae as temperature increased from 4 °C to 17 °C. Zoeae development was projected to be noticeably slower than that observed for megalopae at temperatures <4 °C, although it should be noted that actual data for zoeae at temperatures <4 °C are lacking. Nonetheless, the





**Figure 8.** Relationships between incubation temperature and percent size increment in carapace width (CW) and carapace length (CL) at the molt from zoea I to zoea II (%MI) in *C. opilio* larvae from five hatches between 7 and 21 May 2014.

**Table 3.** One-factor ANOVA on the effect of incubation temperature on snow crab zoeae percent increment in carapace length (CL) and carapace width (CW) at the molt from zoea I to zoea II during the 2014 rearing experiment, and multiple comparisons (*t*-tests) for significant differences between incubation temperatures.

Factors	DF	SS	Mean SS	F	P
CW:					
T (°C)	4	821.6	205.4	3.72	0.034
Residuals	12	661.9	55.2		
CL:					
T (°C)	4	634.7	158.7	6.47	0.005
Residuals	12	294.3	24.5		
P values of multiple comparisons—Holm-Bonferroni correction					
T (°C)		CW		CL	
6–9		1.000		0.189	
6–12		1.000		1.000	
6–15		0.584		1.000	
6–18		1.000		0.108	
9–12		0.655		0.142	
9–15		0.116		0.028	
9–18		1.000		1.000	
12–15		1.000		1.000	
12–18		0.354		0.070	

megalopa, in contrast to the zoeae, appears to be better suited for development in cold than in warm waters.

The duration of the larval phase in situ can be estimated from the modelled development times and local temperature conditions. The summer water column in the GSL consists of three distinct strata: surface layer, cold intermediate layer (CIL), and deeper water layer. Following retreat of winter sea ice, vernal warming and freshwater runoff create the warm surface water and stratification in summer. Typically, surface temperatures are cold (< 2°C) in April–May, but they warm subsequently and the mixed layer thickness (depth of 1°C isotherm) increases to reach maximum values (~15°C and ~50 m, GSL wide average) in early to mid-August (Galbraith *et al.*, 2016). However, surface temperatures are not evenly distributed around the GSL and there exists a persistent temperature gradient from the warm southern GSL to the cold northern GSL and especially its northeast region

(Galbraith *et al.*, 2016). Based on historical records of mixed layer temperature through time and the larval development regressions herein, snow crab pelagic development (zoeae and megalopa stages) is expected to last between 99 and 125 days (3.2–4 months) for larvae hatching around May 1 in the northern regions. Snow crab larvae hatching very early in the southern GSL, around April 1, could also take up to 4 months to complete development, whereas larvae hatching there in early June could complete the pelagic phase in as little as about 70 days (2.2 months). Our results support those estimates; however, in late June 2002 the majority of snow crab larvae were stage I in the southern GSL and no megalopa was found suggesting that emergence in that year occurred mainly in mid to late May.

The preceding estimates of larval phase duration are optimistic because they assume that all larval stages remain in the surface mixed layer through development from hatch to metamorphosis and settlement. However, the megalopa is thought to initiate its transition from the upper mixed layer to the demersal/benthic habitat sometime during the premolt stage (Kon *et al.*, 2003), which starts at about one-third of total megalopa development time (Yamamoto *et al.*, 2015). In the GSL, a permanent transition of the premolt megalopa to the cold waters of the CIL, at around –1 to 2°C, would extend the time to metamorphosis into C1 by several weeks relative to the above total estimates. For example, in the northern GSL, a larva emerging on May 15 and moving down from the surface mixed layer to water at 1°C as a premolt megalopa would not settle and metamorphose into C1 until the end of October. This is consistent with northern GSL observations reported in Lovrich *et al.* (1995) that megalopae were present in the near-bottom (suprabenthic) layer in October and that C1 density was null in late August and significantly greater (61.5% more) in mid-December than in late October of the same year, indicating that settlement continued through the late fall. Judging from distribution patterns of C1 crabs in the northwest GSL, it is possible that the megalopae avoid the coldest, core part of the CIL (Dionne *et al.*, 2003) – where temperatures are often at or below 0°C and development would be excessively slow – by remaining above it or moving below it where waters are slightly warmer. Although megalopae have often been assumed to settle soon after dropping out of the surface mixed layer (e.g. Lanteigne, 1985), we infer that they in fact drift in intermediate or near-bottom layers for a longer time than they drift in

the surface layer. This is important to consider when modelling drift and settlement patterns because the current fields in the surface, intermediate and near-bottom layers may be very different.

Interestingly, the snow crab zoea I were larger in the northern (colder) than in the southern (warmer) GSL. This could reflect differences in embryo size linked to thermal variability of maternal habitat for ovary development and/or egg incubation (e.g. Takeda *et al.*, 1992; Webb *et al.*, 2006) across localities of the GSL system. Landeira *et al.* (2017) also found that body size of snow crab zoea I increased from south to north in the Bering and Chukchi Seas and was negatively correlated to bottom temperature, and suggested the cause to be maternal effects and embryo incubation temperature. In turn, in this study, the greater variability of morphometric measurements for zoea I in the southern GSL can suggest larval supply from the northern GSL, mainly via the Gaspé Current flowing eastward along the Gaspé Peninsula, and mixing with locally originating southern GSL larvae. This is consistent with the fact that longer development times for larvae hatching in the colder northern GSL are conducive to greater dispersal. On the other hand, the relatively equal proportions of snow crab zoea I and II in the southern GSL in June can suggest again that the main hatch occurred there from mid- to late May and that many larvae remained within the survey area until the second stage.

The laboratory experiment of 2014 also provided the first data on the effect of temperature on relative growth at molt for snow crab larvae, albeit limited to the first molt. Few hatches performed well at 6°C, but there was much more consistency in the results among cohorts and better growth from 9 to 15°C, followed by a sharp decline at 18°C. The molt increment for CL and CW estimated for the southern GSL is consistent with molting at temperatures above 9°C such as were recorded at the mean depth of the zoea I at many stations.

### Vulnerability of snow crab larvae to ocean warming

The relative survival index suggests that the optimum temperature for development of snow crab larvae is probably around 11°C at the zoea I stage, but that it progressively decreases for each of the two following stages. The megalopa's optimum temperature for development seems to be around 9°C, suggesting again that this last larval stage is more cold-adapted than the previous stages. This conclusion was also stated by Yamamoto *et al.* (2017), who used a thermodynamic model to derive optimum temperatures for larval development of snow crab of about 9.1°C for the zoea I, 8.8°C for the zoea II and 6.9°C for the megalopa; these are about 1–2°C colder than our values. The relationships for relative survival reported herein were tight and appear robust for temperatures over ≈9°C, but below this threshold temperature there was much more variability in relative survival and therefore uncertainty about the real survival potential. Maintaining optimal rearing conditions (e.g. food and water quality) in small containers over the very long development times at low temperatures is a challenge and the high variability in survival may reflect differences between studies in the success at providing those optimal conditions at low temperatures. Whereas physiological stress due to an imbalance between oxygen demand and delivery (Storch *et al.*, 2009; Pörtner, 2010) may be fatal at higher temperatures irrespective of rearing conditions, at low temperatures the variability in relative survival among studies

suggests that other factors such as food abundance and quality could to some extent offset or attenuate physiological stress. For example, it is known that starvation resistance of a variety of crab larvae increases less quickly than development time as temperature declines (Anger *et al.*, 1981; Anger, 2001) suggesting the importance of an abundant, high-quality food supply for survival at low temperatures. There is indeed an inconsistency between the optimum temperature for megalopa development and survival based on laboratory studies (herein; Yamamoto *et al.*, 2014, 2017) and the temperature actually occupied by the megalopa after the early premolt stage.

From the mid-1990s to date, there is evidence of a trend of earlier spring warming, record high late summer sea surface temperatures and later fall cooling in the GSL (Galbraith *et al.*, 2016), conditions that could already have impacted the survival of snow crab zoeal stages. Indeed, sea surface temperature averaged over the months of June, July, and August has warmed by about 1.4°C on average in the northern GSL over the period 1986–2012, reaching about 12.5°C, and this was inferred to have had a negative effect on the abundance of C1 and C2 crabs owing to a reduction of larval survival and settlement (Émond *et al.*, 2015). Conditions in the southern GSL are even warmer. Adaptation by snow crab populations to these warming conditions might be possible to some extent, by earlier larval release and/or larval positioning in deeper, colder waters at or below the thermocline. However, such “strategies” may incur nutritional costs if the larvae can no longer exploit prime food sources due to a temporal mismatch with spring plankton bloom or a spatial mismatch with depth of peak plankton productivity.

### Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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