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## Contribution to the Symposium: 'Shellfish - Resources and Invaders of the North'

# Direction, ontogeny, and mechanism of the temperature-size rule operating in a large marine crab, *Chionoecetes opilio*

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The classic temperature-size rule (TSR) states that ectotherms mature smaller in warmer than in colder conditions; the reverse TSR is the opposite response. We combined field observations with laboratory experiments and published information to produce a synthesis of the response of snow crab (*Chionoecetes opilio*), a marine brachyuran with determinate growth, to temperature. Size at onset of physiological maturity and after terminal moult (TM) were positively related to temperature, thus indicating the reverse TSR. Moult increment varied little with temperature, but crabs were larger at instar in colder than in warmer water due to an initial difference in settlement size that propagated to higher instars, suggesting classic TSR during embryogenesis and larval development. The pattern of increasing TM size with temperature was caused by crabs moulting more times before TM in warmer than in colder water. Intermoult period (IP) declined exponentially with temperature, and lower instars were more temperature sensitive than higher instars. Temperature effects on IP were strong enough to explain changes in size and instar number at TM under a possible time-invariant maturation schedule. Skip moulting was observed in the smallest crabs reared in the laboratory and resulted in high mortality. The reverse TSR in snow crab seems to be adaptive to coping with ectotherm predation.

**Keywords:** development, growth, James' and Bergmann's clines, maturity, predation, snow crab, temperature-size rule

## Introduction

Climate change is modifying the development and growth rates of aquatic ectotherms, which are traits that contribute importantly to population productivity and ecosystem properties (Gardner *et al.*, 2011; Ohlberger, 2013). For example, size at maturity and maximum size are declining in many species, leading to reductions in per capita fecundity (Daufresne *et al.*, 2009). Changes in the size structure of populations, which may differ in magnitude depending on species' sensitivity to temperature and correlates such as food supply (Daufresne *et al.*, 2009; Gardner *et al.*, 2011), can alter trophic interactions and even lead to trophic cascades when top predators are involved (Ohlberger, 2013). Thus, understanding how and why the development and growth of aquatic ectotherms is affected by temperature is essential for predicting vulnerability, resilience, and opportunity for

indigenous and invasive species in face of climate change, including major fishery resources (Hollowed *et al.*, 2013; Kelley *et al.*, 2015).

The temperature-size rule (TSR) describes for ectotherms the phenotypic plasticity of development and growth observed in rearing experiments in response to natural temperature treatments and follows one of the two directions. In the classic TSR, ectotherms grow faster and mature at a smaller size with warming (Atkinson, 1995; Angilletta *et al.*, 2004; Kingsolver and Huey, 2008). Aquatic ectotherm species mostly conform to the classic TSR, but ≈10–15% of them follow the reverse TSR and grow faster but mature bigger with warming (Atkinson, 1995; Klok and Harrison, 2013). The classic TSR is often associated with macroecological patterns of increasing size with decreasing latitude at the supra- and intra-specific levels, coined Bergmann's and

James' clines respectively; the reverse TSR is associated with converse clines (Blackburn *et al.*, 1999; Kingsolver and Huey, 2008).

There appears to be no universal explanation for the classic and reverse TSR or for the associated James' clines; explanations may vary for example with habitat (terrestrial vs. aquatic) and phylogeny (Blackburn *et al.*, 1999; Walters and Hassall, 2006). Basically, intraspecific variability in body size reflects differences in cell number, cell size or a combination of both (James *et al.*, 1995; Arendt, 2007). Thus, the classic TSR could be an inevitable (non-adaptive) biophysical consequence of temperature and oxygen effects on cell physiology and size (e.g. van Voorhies, 1996). Alternatively, it may be an adaptive response to changes in temperature and/or correlates such as oxygen availability, food supply and intensity of ectotherm predation (Blackburn *et al.*, 1999; Forster *et al.*, 2012; Klok and Harrison, 2013). By contrast, the reverse TSR is thought to be only an adaptive response, most often to season length (Atkinson, 1995; Blanckenhorn and Demont, 2004). Walters and Hassall (2006) established a potential link between stenothermia and the reverse TSR, and Zuo *et al.* (2012) concluded that the reverse TSR should occur when it is "advantageous to develop in colder water, such as to behaviourally select cold microclimates to avoid predators or to prolong development owing to constraints of environmental seasonality".

The proximate cause of the TSR is an unequal response of development and growth to temperature: warming increases development and maturation (cell division and differentiation) rate more than it increases cell and body growth rate in the classic TSR; the opposite occurs in the reverse TSR (van der Have and de Jong, 1996; Forster and Hirst, 2012; Zuo *et al.*, 2012). Some species may conform throughout life to either TSR direction, with individuals being for example younger–smaller at every recognizable stage of development. In other species, the extent and direction of decoupling between development and growth may vary across life history stages/phases leading to complex patterns where classic TSR, reverse TSR or temperature "insensitivity" dominate at different times (Forster and Hirst, 2012; Aguilar-Alberola and Mesquita-Joanes, 2014; Horne *et al.*, 2019b).

The snow crab (*Chionoecetes opilio*) is a cold-stenothermic brachyuran that is widely distributed in shelf and bathyal habitats of the north Atlantic, north Pacific and lower Arctic Oceans at temperatures of  $-1.5$  to  $4-5^{\circ}\text{C}$  (Tremblay, 1997; Dawe and Colbourne, 2002; Alvsvåg *et al.*, 2009). The snow crab is an apex benthic invertebrate predator and a potent cannibal (Lovrich and Sainte-Marie, 1997; Divine *et al.*, 2017), as well as a valuable fisheries resource. This univoltine species exhibits strong sexual size/age dimorphism in favour of males, which can reach 152 mm in carapace width (CW) and 1.5 kg in body mass and live up to 18–20 years after settlement (Sainte-Marie *et al.*, 1992; Fonseca *et al.*, 2008). Snow crab has determinate growth and full development of secondary sexual characters occurs only at a terminal moult (TM) after which individuals cease to grow in body size and are called adults (hereafter, crabs not having terminally moulted are called subadults). Adult and fishery recruitment in snow crab may be cyclic over much of the species' distribution range and that variability—explained by intrinsic and extrinsic factors—has been factually sourced back to cohort strength of the larvae (Émond *et al.*, 2020) and earliest benthic instars (Ernst *et al.*, 2012; Émond *et al.*, 2015).

Snow crab appears to follow the reverse TSR. Adult females exhibit the converse James' cline in the Bering and adjacent Chukchi Seas, and this was attributed to temperature (Somerton,

1981; Paul *et al.*, 1997; Orensanz *et al.*, 2007). However, there was no latitudinal pattern in adult size of snow crab along west Greenland, but a strong positive relationship between site temperature and adult size existed in both sexes (Burmeister and Sainte-Marie, 2010). Dawe *et al.* (2012) found in eastern Canada a strong positive relationship between temperature and adult size of females, and a weaker one in males. Temperature is thus relevant to understanding snow crab population and commercial productivity because it contributes to determine size after TM (SaTM), which is consequential to reproductive output and yield per male recruit (Sainte-Marie *et al.*, 2008; Burmeister and Sainte-Marie, 2010; Dawe *et al.*, 2012).

Knowledge of the ontogeny and process of the reverse TSR and its contribution to variability in SaTM in snow crab is incomplete. Resolving instar structure and cohort progression is difficult for wild populations of most brachyurans (Hartnoll, 2015), yet this is key to understanding the process of TSR. Snow crab instar structure has been fully resolved in only some populations, and within those TM is distributed mainly over two consecutive instars in females and four in males (e.g. Alunno-Bruscia and Sainte-Marie, 1998; Comeau *et al.*, 1998). Differences in adult size between populations are thought to reflect changes in the number of moults before TM (Orensanz *et al.*, 2007; Burmeister and Sainte-Marie, 2010; Dawe *et al.*, 2012), rather than changes in moult increment (MI). This interpretation derives from the observation that size at instar of subadult snow crab is quite conservative within and across oceans (e.g. Comeau *et al.*, 1998; Orensanz *et al.*, 2007) and across many years within regions (Chabot *et al.*, 2008; Émond *et al.*, 2015). Conditioning of SaTM by temperature was proposed to occur during early benthic life (Orensanz *et al.*, 2007) or mainly in later benthic life up to TM (Dawe *et al.*, 2012). More specifically, Burmeister and Sainte-Marie (2010) posited that the size at onset of physiological (gonad) maturation (PM), which precedes TM, is also positively temperature-dependent and a key step in setting the minimum size (instar) for TM. These three last cited studies and Ernst *et al.* (2012) invoked time constraints on the triggering of TM, such that the number of moults before TM would depend primarily on the duration of previous subadult instars. AQ9

Data on snow crab intermoult period (IP) are sparse, especially with regard to early benthic instars. Seasonal sampling in the Gulf of St Lawrence (GSL) in eastern Canada during a very cold period [1991–1993, see Figure 35 in Galbraith *et al.* (2018)] revealed a pattern of moulting every 5–7 months from settlement until instar VI, after which IP lengthened to 1 year (Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998; Comeau *et al.*, 1998). However, field evidence of faster progression through these early instars exists (Ito, 1970; Robichaud *et al.*, 1989) but has not been attributed to temperature. A laboratory study found that temperature had a strong negative effect on IP of instars I–VII (Yamamoto *et al.*, 2015a). Subadults  $>45-50$  mm CW may sometimes skip an annual moult resulting in an instar duration of  $\approx 20-24$  months, about twice the IP of regular moulters (Benhalima *et al.*, 1998; Yamamoto *et al.*, 2018). Skip moulting may be a response to very cold water (Dawe *et al.*, 2012) or not (Comeau *et al.*, 1998).

This study used data from multiple sources to produce a comprehensive account of the effect of temperature on growth, maturation, and SaTM of snow crab. We tested the hypotheses that subadult size (and MI) at instar is conservative across a normal temperature range while IP is not and that PM and TM are

initiated at a smaller size and earlier instar in colder than in warmer water. We resolved CW at instar and CW at PM for subadults, and the CW range of adults, in wild populations of snow crab along a geographical temperature gradient in the St Lawrence marine system. Laboratory experiments and modelling determined temperature effects on MI and IP. Study results and literature were synthesized to evaluate how snow crab fits the TSR, consider the potential adaptive value of the thermal TM-size cline, and hypothesize about which life stages are most critical to the determination of SaTM.

## Material and methods

### Snow crab life history in the North GSL

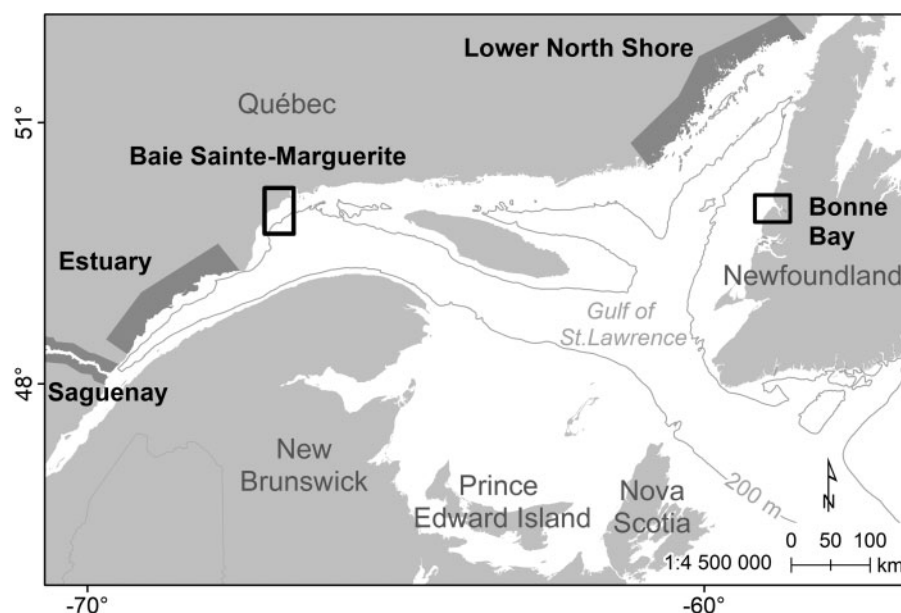
The complex life history of snow crab is well documented in the north GSL by studies in Baie Sainte-Marguerite (BSM) and Bonne Bay (Figure 1). There are six life phases: embryo, planktonic larvae, benthic sedentary (cryptic) juvenile, mobile juvenile, adolescent male or prepubescent-pubescent female, and adult (terminology from: Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998; Chabot *et al.*, 2008). The onset of PM defines prepuberty in females and adolescence in males (Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998). Instar VII is the last of the fully subadult instars, as some females may become adult at the next instar (Alunno-Bruscia and Sainte-Marie, 1998).

Snow crab zoeae emerge mainly in May, develop into megalopae, and settle and metamorphose into the first benthic instar in summer or fall (Lovrich *et al.*, 1995; Comeau *et al.*, 1998). In BSM, settlement occurs primarily below the core of the cold intermediate layer (CIL) (Dionne *et al.*, 2003; Ouellet and Sainte-Marie, 2018). The CIL is formed by winter cooling and convection and is isolated from the surface by spring warming and stratification; it persists through summer and fall beneath the warm surface mixed layer, although gradually its core temperature warms and its thickness erodes until the next winter (Galbraith *et al.*, 2018). Mobility of snow crab increases with size from instar

V on, and in BSM most mobile juveniles at greater depths are either cropped off by predation or relocate from below to above the core of the CIL (Lovrich *et al.*, 1995; Dionne *et al.*, 2003). As subadults further grow in size, they begin to perform annual (Lovrich *et al.*, 1995) or perhaps sporadic (Comeau *et al.*, 1998) cross-shelf migrations between shallow grounds (<30 m depth) in winter–spring and increasingly deep grounds in summer–fall, such that large adolescent males may move well beneath the core of the CIL (Lovrich *et al.*, 1995). In BSM, the shallow grounds are the primary areas for moulting of instars VII and higher, which occurs through winter or early spring depending on sex and size (Sainte-Marie and Hazel, 1992; Lovrich *et al.*, 1995).

### Size distribution and maturity of wild snow crab

Size distributions of wild snow crab were obtained from beam trawl surveys conducted by the Department of Fisheries and Oceans Canada in three regions in the north St Lawrence marine system: Estuary (EST), BSM, and Lower North Shore (LNS) (Figure 1). The surveys occurred from 1992 to 2013 in EST, from 1989 to 2013 in BSM, and from 1994 to 2014 in LNS, according to details and methods specified in Table 1. The three study regions are spread over 10° of longitude and 3° of latitude and subject to a temperature gradient. At depths relevant to benthic snow crab, the westernmost EST is consistently the warmest and the easternmost LNS is consistently the coldest of the three regions, with central BSM exhibiting intermediate temperature (Galbraith *et al.*, 2018). Mean  $\pm$  SD of August water temperature in EST, BSM, and LNS from 1992 to 2013 was, respectively,  $1.1 \pm 0.4$ ,  $0.9 \pm 0.4$ , and  $-0.5 \pm 0.3^\circ\text{C}$  at 100-m depth, and  $0.4 \pm 0.4$ ,  $0.0 \pm 0.4$ , and  $-0.7 \pm 0.3^\circ\text{C}$  at the shallower core (about 70-m depth) of the CIL. Annual minimum and maximum temperatures at these depths are reached around March and November, respectively, with water warming/cooling at a rate of about  $0.1^\circ\text{C}/\text{month}$  in between (P. Galbraith, Institut Maurice-



**Figure 1.** Map of the St Lawrence marine system showing the three study regions: Estuary, from dark-shaded coastline to  $\approx 260$  m depth; Baie Sainte-Marguerite (box on left) from coastline to  $\approx 200$  m depth; and Lower North Shore, from dark-shaded coastline to  $\approx 260$  m depth. The Saguenay Fjord and Bonne Bay (box on right) are also shown.



**Table 1.** Characteristics of beam trawl surveys conducted in the north St Lawrence marine system for snow crab.

Survey	Estuary/Lower North Shore	Baie Sainte-Marguerite
Years considered and frequency	1992–2002 (annually) and 2005–2013 (biannually)/ 1994, 1995, 1999, 2000, 2003, and 2004–2014 (biannually)	Annually from 1989 to 2013 (multiple surveys in some years)
Design	Fixed stations; random stations in early years of Estuary survey	Random depth-stratified stations
Duration and timing	≈3 weeks, usually between early July and mid- August	≈2 weeks, usually between late April and mid-May
Number of stations	≈40–90	≈12–24
Depth range of stations	≈30–260 m	≈10–200 m
Gear type	2.8-m beam trawl with 15- or 17-mm mesh codend	
Gear tow speed and duration	2.2–2.5 knots and 5–15 min	

Typical values are provided for duration and timing of surveys and for number and depth range of stations, which have varied across years due to ship availability, weather conditions, and specific sampling needs.

Lamontagne, pers. comm.). Substantial exchanges of benthic snow crab between these regions are unlikely because they are separated longitudinally by bottom features that act as barriers to crab movement (Sainte-Marie *et al.*, 2005) and their closest boundaries are at least 100 km apart.

Snow crabs captured during the surveys were sexed, measured in CW and examined for maturity status. Sex was determined from abdomen shape (triangular in males, oval to circular in females) except for the very smallest juveniles (instar I and most instar II) which were recorded as “sex undetermined”. CW of all crabs and chela (propodite) height (CH) of usually all males  $\geq 35$  mm CW in BSM and  $\geq 40$  mm CW in EST and LNS were measured to the nearest 0.01 or 0.1 mm with a vernier calliper, excluding spines when possible. As a rule, the right chela was measured and the left chela was used only when the right one was missing, damaged or incompletely regenerated. Females were easily classified as subadult when the abdomen was flat and narrow relative to the width of the cephalothorax sternites, and as adult when the abdomen was bulging and almost as wide as the sternites. Males  $< 35$  or  $< 40$  mm CW, depending on region, were by default recorded as subadult, whereas larger males were classified as subadult or adult using the CH to CW discriminant function of Sainte-Marie and Hazel (1992). However, in some BSM trawls with very high crab abundance, all crabs were measured in CW but the first author determined maturity of males  $> 60$ – $65$ -mm CW on the basis of visual examination with only ambiguous cases being measured in CH.

In 2010 (and 2011 in EST), subadult females and males from each region were examined for gonad development. Crabs were collected during Department of Fisheries and Oceans surveys and selected to cover the CW range of 9–12 to 50–62 mm in females and 8–12 to 50–71 mm in males. In the laboratory, crabs were sexed and measured in CW, in CH for males and in abdomen width (AW, across the middle of the fifth tergite) for females, and dissected to reveal internal organs. Females and males were designated as “physiologically immature” when gonads were not detected or were present as narrow translucent bands, females as “physiologically maturing” (PM) when ovaries were developing and progressing from white to bright orange with increasing CW (Alunno-Bruscia and Sainte-Marie, 1998), and males as “physiologically mature” (also PM) when vasa deferentia were opaque and white, reflecting the production of sperm and spermatophores (Watson, 1970; Comeau and Conan, 1992).

### Experimental effects of temperature on crab growth

Two rearing experiments were conducted at Institut Maurice-Lamontagne in 2007–2008 and 2008–2009 (hereafter called 2007 and 2008 experiments, respectively) to determine the effect of temperature on IP and MI of subadult crabs. The two experiments used crabs that were trawled in BSM on 5–7 May 2007 and 4–5 May 2008, respectively. Crabs were measured in CW and those near in size to instar III ( $\pm 7$ -mm CW) and instar VI ( $\pm 19$ -mm CW) were retained in 2007, but only instar VI crabs were retained in 2008. Assignment of crabs to instar was based on the comparison of individual CW against the modal (instar) size structure for BSM [Figure 1 in Lovrich *et al.* (1995)]. Instar III is in the middle position of instars I to V inferred to last about 6 months, and instar VI is the first instar inferred to last about 1 year in the north GSL (see above).

From times of capture to start of experiments 17–23 d later (or 35–37 d later in the case of one 2007 treatment, see below), crabs were held in flow-through tanks at natural photoperiod, temperature, and salinity (daily average and SD:  $1.2 \pm 0.3^\circ\text{C}$  and  $26.8 \pm 1.0\text{‰}$  in 2007,  $1.8 \pm 0.1^\circ\text{C}$  and  $26.1 \pm 0.4\text{‰}$  in 2008) and fed *ad libitum* twice weekly a mixture of minced capelin (*Mallotus villosus*) and northern shrimp (*Pandalus borealis*). During this time, crabs were further selected for experiments on the basis of being externally intact (no missing limbs, no apparent injuries, or scars) and were individually identified by using natural carapace markings and ornamentation (Gosselin *et al.*, 2007) and by gluing to the cephalothorax a visual implant tag (Northwest Marine Technology, Anacortes, WA, USA) on instar III crabs or a type FPN shellfish tag (Hallprint Fish Tags, Australia) on instar VI crabs. Groups of 7–11 crabs formed of equal or subequal numbers of females and males belonging to the same instar were randomly allocated to 60-l kreisel tanks or 50-l aquaria, which were the experimental replicates. The kreisel tanks were used for 1.5, 3.5, and  $4.5^\circ\text{C}$  treatments in 2007 (6 replicates each by instar, 10 instar III, or 7 instar VI crabs per replicate), and for 2.5 and  $5^\circ\text{C}$  treatments in 2008 (12 replicates each, 7 instar VI crabs per replicate). Temperature treatments were spread over 2 years (experiments) to ensure sufficiently high levels of replication considering the limited number of tanks, and replication was greater in 2008 to try to tease out sex and size effects. Kreisel tanks were connected by groups of 6 or 12 via individual water inlets and outlets to a 500-l head tank and cooling-heating unit. Circulating seawater was filtered and renewed at a rate of

≈15% volume/h, by inflow of fresh natural seawater to the head tank. The aquaria were used for 0°C treatments in 2007 (3 replicates of 8 instar VI crabs each; replicates of instar III crabs were also planned but the crabs died in the preparatory phase due to equipment malfunction) and 2008 (3 replicates of 11 instar VI crabs each). To achieve and maintain this low temperature, each aquarium was two-thirds immersed in an insulated larger tank filled with antifreeze. The antifreeze was cooled by a refrigeration coil and circulated (and if needed, heated) by a Haake Digital DC30 unit (Thermo Electron Corporation, Waltham, MA, USA), controlled by Honeywell or Johnson thermostats in the aquaria. Each flow-through aquarium was independently fed fresh natural seawater at a rate of ≈10–15% volume/h.

The first experiment was conducted from 28 May 2007 to 23 May 2008 (361 d), except for the 0°C treatment which ran from 11 June 2007 to 22 July 2008 (407 d). The second experiment occurred from 28 May 2008 to 10 June 2009 (378 d). The goal was to maintain experiments until each crab moulted twice, but this was not achieved with all crabs due to mortality or skip moulting (see Results). We did not pursue rearing further to minimize laboratory artefacts possibly arising from undiversified diet, temperature acclimation, and selective mortality. Both experiments were carried out with natural photoperiod. Crabs were fed capelin and shrimp (as above) *ad libitum* every other day, and tanks were cleaned twice weekly. Temperature, salinity, and crab moult or mortality events were recorded daily except some weekends. Realized temperature and salinity, and mean crab CW after first moult are shown in [Supplementary Tables S1 and S2](#).

When moulting occurred, the exuvium was retrieved, measured, and examined to confirm initial CW measurement and crab identity. Moulted crabs were immediately isolated within the tank/aquarium for 5–7 d until their exoskeleton hardened somewhat and then were examined for maturity status and measured in CW. No experimental crab terminally moulted. First-time moulters were identified again with a tag and returned to communal holding; second-time moulters were removed. The first moult to occur yielded information on partial IP for instars III and VI, as the date of the crab's previous (wild) moult was unknown, and on their MI to instars IV and VII, respectively. The second moult yielded information on complete IP of instars IV and VII and on MI to instar V and VIII, respectively. Note that IP strictly designates instar duration for regularly moulting crabs; skip moulters are excluded (see Results).

### Data analyses

Statistical analyses were done in R ([R Core Team, 2013](#)) or in Systat v13.1. Aggregated CW frequency distributions for subadult females and males were constructed for each region by binning all survey observations into 0.25-mm and 0.5-mm CW size classes for modal analyses and graphs, respectively. Crabs of undetermined sex were randomly assigned in equal numbers to female or male categories. Modes representing instars were resolved and mean and 95% confidence limits of CW at instar were computed for each sex and region using the R “finite mixture distribution model” package ([Macdonald and Du, 2012](#)). The model parameters allowed up to 1000 iterations. Goodness-of-fit of each model was verified visually and with the  $\chi^2$  statistic ( $p < 0.0001$  in all cases). Mean size at instar number  $i$  was used to estimate MI in nature [ $MI_i = (\text{mean } CW_i - \text{mean } CW_{i-1}) / \text{mean } CW_{i-1} \times 100$ ]. MIs common to both sexes and all regions were regressed against

instar number and compared by sex across regions by analysis of covariance (ANCOVA).

The CW at which 50% of subadult snow crabs were PM was estimated by sex for each region by fitting a logistic curve to the relationship of proportion maturing/mature by 0.25-mm CW size class (R packages stats and MASS; [Venables and Ripley, 2002](#)). Ratios of AW or CH to CW were plotted as a function of CW and fitted with a LOESS third order polynomial smoother, adjusted to the whole range of data.

For describing the CW distribution of adult females and males, we limited analyses to the period 1998–2013 for EST and BSM, and 1999–2014 for LNS (16-year span in all cases), so as to capture variability over two full recruitment cycles in each region. This was done because mean CW of adults oscillates through time as a function of cohort strength ([Sainte-Marie et al., 1996](#); [Ernst et al., 2012](#)), presumably independently of any temperature effect. For each sex, region and year, we determined the 1st, 5th, 50th, 95th, and 99th percentiles of CW distributions and then calculated by sex and region the mean and coefficient of variation (C.V.) of CW for the selected percentiles. The two lower and two upper percentiles of CW distributions were considered to be more robust indicators of limit sizes than minimum and maximum values, which can be due to reader error. For each sex, mean CW at median and 5th and 95th percentiles was compared across regions with the Kruskal–Wallis test.

In the rearing experiments, the statistical unit was the tank and so all tests were based on tank means. Scatterplots of individual MI and IP in relation to premoult CW were examined by instar and treatment, to determine whether or not to include CW as a covariate in analyses. The effect of temperature treatment on MI and IP was tested by analysis of variance (ANOVA) with type III sums of squares using the R package “car” ([Fox and Weisberg, 2011](#)). Normality was verified with the Shapiro–Wilk's test. Multiple comparisons were performed with Tukey's HSD in the R package “agricolae” ([de Mendiburu, 2014](#)). Models started with all possible interactions (factors temperature and sex, covariate CW) and were reduced by removing non-significant interactions and then non-significant factors or the covariate. For the 2007 experiment, instars were analysed separately when there were visually obvious differences in response variables.

### Modelling subadult IP

Many models exist for describing IP as a function of CW or body weight ([Chang et al., 2012](#)), but few are available for relating it to instar number. [Caddy \(2003\)](#) provided evidence that IP progresses geometrically to instar number ( $i$ ), increasing from an initial time interval ( $r$ ) by a constant proportion ( $a$ ) through successive instars following the equation:

$$IP_i = r \cdot a^i. \quad (1)$$

For modelling IP (days) by instar, data from the laboratory experiments were lightly censored based on the CW frequency distribution of BSM (see Results) to leave only crabs almost certainly belonging to instar III or VI prior to first laboratory moult, and the subsequent complete IP measured for these crabs at instar IV and VII was used. We also used first complete IPs of unsexed instar IV crabs recorded by [Gravel \(2002\)](#) in 0, 1.5, and 3°C treatments using the same equipment as us (see [Supplementary Text S1](#) and realized temperatures in [Supplementary Table S1](#)). To

quantify the effect of temperature on complete IP, considering differences between realized and target temperature, we used treatment interpolated mean temperature (Supplementary Table S1). A linear regression model, weighted by number of replicates, was fitted to the relation between the natural logarithm of mean IP and interpolated mean temperature by treatment for each of instar IV and VII. From the resulting regression equations, we predicted average IP at  $-1.5$ ,  $-1$ ,  $0$ ,  $1$ ,  $2$ ,  $3$ ,  $4$ , and  $5^\circ\text{C}$  for instars IV ( $i=4$ ) and VII ( $i=7$ ). Thus, based on (1), for each temperature, we obtained a two-equation system describing IP of instars IV and VII with each equation containing two knowns ( $IP_4$  for  $i=4$ ;  $IP_7$  for  $i=7$ ) and two unknowns ( $r$  and  $a$ ). To determine the unknowns, (1) was re-arranged as:

$$r = IP_i/a^i, \quad (2)$$

$$a = (IP_i/r)^{1/i}. \quad (3)$$

The value of  $r$  was resolved algebraically for each temperature as:

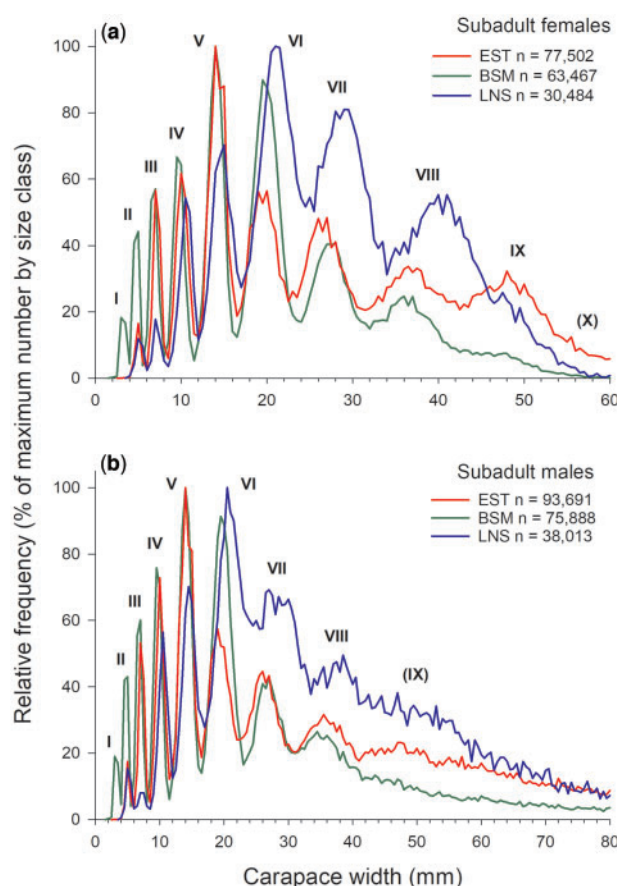
$$r = IP_4^{7/3}/IP_7^{4/3}, \quad (4)$$

and used in (3) to calculate the value of  $a$  for each temperature. With  $r$  and  $a$  resolved, we estimated IP for instars I, II, III, V, and VI at all of the above temperatures. We did not extrapolate to higher instars, which reportedly have a constant  $\approx 1$ -year IP. We semi-validated model results using the first complete IPs observed for instars IV, V, and VI at  $-1.4^\circ\text{C}$  by Gravel (2002) and reported for instars I, V, VI, and VII at various temperatures by Sainte-Marie and Lafrance (2002) and Yamamoto *et al.* (2015a, b).

## Results

### Size distribution and instar composition of subadults and adults in nature

A total of 379 045 subadult and 73 831 adult snow crab were measured in the three study regions (Figures 2 and 3). Subadult males could become much larger than subadult females, and both sexes grew to noticeably larger subadult sizes in EST than in BSM and LNS. Several modes representing instars were very evident in the CW frequency distributions of subadults (Figure 2). Instar I was captured in substantial numbers only in BSM, due to the survey occurring in spring before this stage had finished moulting to next instar [see Table 2 and Figure 6 in Sainte-Marie *et al.* (1995)]. In all regions and for both sexes, modes were sharply defined for instars I or II through VI and remained quite distinct up to instar VIII (Figure 2). Modes representing instars II to V overlapped considerably between the sexes and regions. An additional mode representing instar IX could be discerned in all regions, but more easily in females and most conspicuously in EST (where there was even a hint of female instar X). The CW frequency distributions of subadult females could be almost fully resolved into modes (Figure 2a), whereas for subadult males no modal structure could be detected visually in the tail-end of distributions extending from  $\approx 55$ – $60$  to over  $100$  mm CW (partially shown in Figure 2b). Modal analysis determined mean CW and 95% confidence limits (95% CI) for instars, from which MIs were calculated (Table 2). Mean CW at instar values were very close to previous estimates for the GSL, as shown for example for instars VII and VIII in Supplementary Table S3.

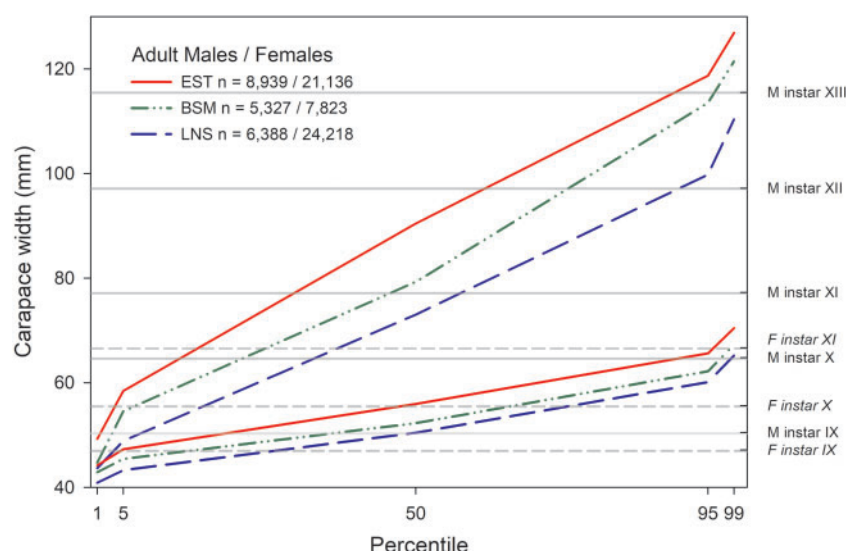


**Figure 2.** CW (mm) relative frequency distributions for subadult males (a) and females (b) of the snow crab (*Chionoecetes opilio*) in EST (1992–2013), BSM (1989–2013), and LNS (1994–2014) of the north St Lawrence marine system. Relative frequency is the percentage of maximum absolute frequency by 0.5-mm CW bin in each region. Roman numerals are the instar numbers (see Table 2 for mean CW at instar). Notice that distributions are truncated at 60-mm CW for females and 80-mm CW for males.

Small differences in mean CW at subadult instar were detected between the sexes and regions. Within regions, from instar V to VIII, mean CW at instar was less in males than in females, except for one case, and 8 out of 12 comparisons were significant based on the 95% CI around the mean (Table 2). The greatest difference between sexes in mean CW at instar, however, was only 1.0 mm representing 2.8% of the least of the two means (instar VIII, BSM). In both sexes, mean CW at instar was consistently larger in LNS compared to the two other regions, and the gap widened with increasing instar number (Table 2). However, for both sexes the largest difference in mean CW at instar between regions was only 3.5 mm representing 9.7% of the least of the two means (instar VIII females, between EST and LNS). In ANCOVA, considering both sexes separately, instar number (II–VI) had a negative effect on MI ( $p \leq 0.001$ ), but slopes and  $y$ -intercepts of the regressions did not differ among regions ( $p=0.306$ – $0.407$  and  $0.493$ – $0.681$ , respectively).

As adults, males expectedly reached larger sizes than females (Figure 3, Table 3). The average difference in mean CW at percentile between the sexes was much more pronounced for the 99th percentile (+51.9 mm in favour of males) than for the 1st





**Figure 3.** Mean CW (in mm) at 1st, 5th, 50th (median), 95th, and 99th percentiles of annual size distributions of adult male (three upper plots) and adult female (three lower plots) snow crab (*Chionoecetes opilio*) in EST (for the period 1998–2013), BSM (1998–2013), and LNS (1999–2014) of the north St Lawrence marine system. See Table 3 for numerical values of mean CW at percentile. For reference, mean CW of adult female instars IX–XI (F, horizontal grey dashed lines) and adult male instars IX–XIII (M, horizontal grey full lines) from Supplementary Table S3 are shown.

percentile (+3.2 mm) and was intermediate for the median (+28.0 mm) of CW distributions. Adult mean CW decreased from EST to LNS, in females by about 3–4 mm at the lower (1st and 5th) percentiles and 6–7 mm at the higher (95th and 99th) percentiles, and in males by about 5–10 mm at the lower percentiles and 16–19 mm at the higher percentiles (Table 3). Note that only a small minority of adult males from LNS exceeded the minimum legal harvest size of 95-mm CW (Figure 3). The difference among regions in mean CW at median, 5th and 95th percentile was significant for females (Kruskal–Wallis test,  $p \leq 0.032$ ) and males ( $p \leq 0.010$ ). Interannual variability in CW at percentile measured by the C.V. differed between the sexes, with average C.V. ranging across regions from 8.6 to 13.5% in males against 1.4 to 8.1% in females.

Individual modes could not confidently be resolved in the time-aggregated adult CW frequency distributions; however, we calculated mean CW at instar for adult females and males of instar IX and higher based on results of short-term (1–3 year) GSL studies (Supplementary Table S3). Again, CW at instar for adults was remarkably consistent across spatially and temporally independent studies. The mean CWs for adult instars, added to Figure 3, indicate that in each region adult females were a mixture of mainly 2 consecutive instars whereas adult males were a mixture of 4–5 consecutive instars, with the contribution of lower instars in the mixture distribution increasing from EST to LNS (and conversely for higher instars).

### Physiological maturation and sexual differentiation in nature

Snow crab became PM over a narrow CW range, as seen visually (Figure 4), and demonstrated by the very small 95% CI around the CW at 50% PM (Table 3). However, the maturity ogive was steeper in females than in males (Figure 4) and the CW at 50% PM was significantly smaller in females (22.3–25.9-mm CW)

than in males (37.2–41.2-mm CW) in the three regions (Table 3), the difference being 14.7 mm overall. Physiological maturation was initiated in some females as small as 20-mm CW and in some males as small as 32-mm CW. Note that gonads became apparent as narrow translucent bands at even smaller sizes in both sexes: 11–17-mm CW (instar IV–V) in females and 20–26-mm CW (instar VI–VII) in males.

In males, there was a clear and significant trend of decreasing CW at 50% PM from EST to LNS (Figure 4b, Table 3). In females, CW at 50% PM was also significantly smaller in LNS than in the two other regions; however, the CW at 50% PM was very similar between BSM and EST (Figure 4a, Table 3). Based on subadult instar CW (Table 2) and CW at 50% PM (Table 3), females that initiated ovary development were mostly smaller instar VII in EST and BSM, and mostly larger instar VI in LNS. Males became PM as larger instar VIII and to a lesser degree smaller instar IX in EST and probably also in BSM (although instar IX was not resolved there), and mostly as smaller instar VIII in LNS. Within each region, the number of moults needed to pass from CW at 50% PM to first percentile of adult CW distribution was two in females and one in males (based on Tables 2 and 3).

Differentiation of the abdomen and chelae of subadult females and males was initiated very soon in ontogeny. The female abdomen underwent strong positive allometric growth, reflected by a conspicuous progression of the AW: CW ratio from about 0.27 at 10 mm CW (instar IV) until a plateau of about 0.5 was reached at ≈45-mm CW (Supplementary Figure S1a). This transition occurred over four instars (V–VIII). In subadult males, there was allometric growth in chelae, but the relative change in CH was much more modest than that seen in female AW, from a CH: CW ratio of about 0.14 at 10-mm CW to about 0.16 at 55-mm CW (Supplementary Figure S1b). The development of the male chela was apparently more advanced at CW in LNS than in BSM and EST (Supplementary Figure S1b).



**Table 2.** Mean CW and 95% CIs at instar number (*i*) for female and male subadult snow crab (*Chionoecetes opilio*) in three regions of the north St Lawrence marine system: EST, BSM, and LNS.

Instar number	Females						Males					
	EST			BSM			LNS			EST		
	CW (95% CI)	MI	CW (95% CI)	MI	CW (95% CI)	MI	CW (95% CI)	MI	CW (95% CI)	MI	CW (95% CI)	MI
I	—	—	—	—	—	—	—	—	—	—	—	—
II	4.98 (4.95–5.01)	—	—	—	—	—	—	—	—	—	—	—
III	7.14 (7.13–7.16)	43.4	46.1	46.1	5.12 (5.06–5.18)	40.8	7.13 (7.10–7.15)	42.6	6.81 (6.79–6.82)	43.7	7.22 (7.12–7.32)	39.7
IV	10.10 (10.08–10.12)	41.5	42.5	42.5	10.54 (10.49–10.58)	46.2	10.03 (10.00–10.05)	40.7	9.72 (9.70–9.73)	42.7	10.56 (10.51–10.61)	46.3
V	14.19 (14.17–14.22)	40.5	44.9	44.9	14.70 (14.63–14.76)	39.5	14.11 (14.08–14.13)	40.7	14.00 (13.98–14.01)	44.0	14.57 (14.52–14.62)	38.0
VI	19.41 (19.36–19.47)	36.8	41.8	41.8	20.91 (20.80–21.01)	42.2	19.38 (19.33–19.42)	37.3	19.62 (19.59–19.65)	40.1	20.77 (20.70–20.84)	42.5
VII	26.38 (26.29–26.47)	35.9	37.5	37.5	28.66 (28.50–28.81)	37.1	26.34 (26.28–26.4)	35.9	26.95 (26.86–27.03)	37.4	28.72 (28.61–28.83)	38.3
VIII	36.15 (35.94–36.37)	37.0	32.6	32.6	39.66 (39.29–40.02)	38.4	35.75 (35.66–35.83)	35.7	35.20 (35.11–35.38)	30.6	39.08 (38.98–39.18)	36.1
IX	48.06 (47.78–48.34)	32.9	29.3	29.3	48.57 (47.28–49.86)	22.5	47.55 (47.46–47.63)	33.0	—	—	—	—
X	59.39 (58.86–59.91)	23.6	—	—	—	—	—	—	—	—	—	—

See text and Table 1 for survey years. MI is the percent increase in CW relative to premoult CW (calculated as the difference between CW<sub>i</sub> and CW<sub>i-1</sub>, divided by CW<sub>i-1</sub>, multiplied by 100). Regions are ordered from left to right by decreasing average temperature.

### Temperature effects on skip moulting, IP, and MI

Realized overall mean temperatures for tanks/aquaria in the 2007 and 2008 experiments were trendless in time and either on-target or off by no more than 0.17°C, except for the 0°C treatment which was colder by 0.38°C in 2007 and 0.53°C in 2008 (Supplementary Table S1). Salinity (Supplementary Table S1) was within normal range for snow crab in the GSL (26–33‰) and always well above the lower tolerance level of 21‰ (Hardy *et al.*, 1994).

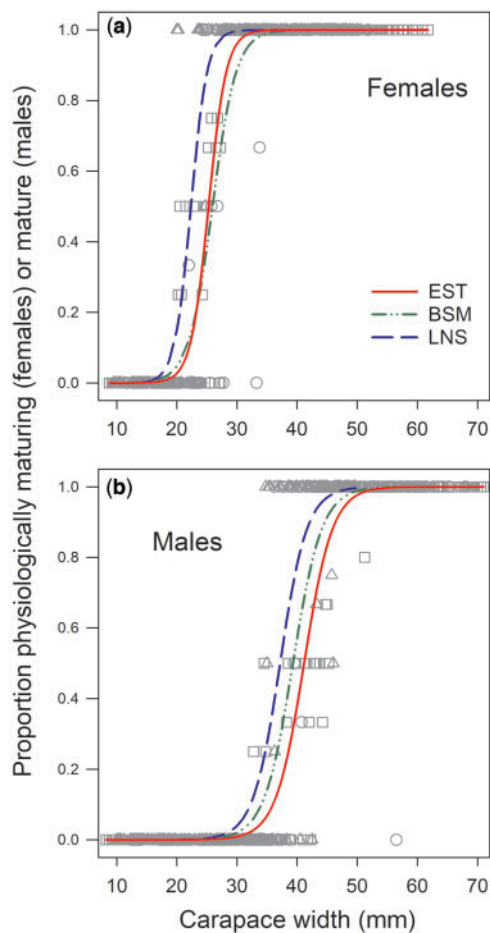
Skip moulting, defined loosely as not moulting twice during the course of experiments, occurred in 2007–2008 and 2008–2009 and its frequency was inversely related to treatment temperature (Supplementary Table S4). For instar III, the proportion of crabs that did not moult twice before dying or experiment's end increased from 21.7% at 4.5°C to 40.0% at 1.5°C. This trend was also apparent among instar III crabs that survived the experiment: 2.1% moulted only once or never at 4.5°C compared to 18.1% at 1.5°C. All surviving, never or once-moulted instar III crabs qualified as true skip moulters in having an elapsed time since last moult that was twice or more longer than the mean IP of instar IV crabs (see Figure 5a). For instar VI, the proportion of crabs not having moulted twice before dying or experiment's end also increased from 16.7% at 4.5°C to 37.5% at 0°C in 2007–2008 and, strikingly, from 44.1% at 5°C to 72.7% at 0°C in 2008–2009. The proportion of instar VI that survived but did not moult twice trended upward from 8.3% at 4.5°C to 15.4–20.0% at 0 and 1.5°C in 2007–2008, but there was no clear pattern in 2008–2009. Instar VI crabs that did not moult twice in the 2007 experiment were probably mostly true skip moulters, because regular moulting activity was synchronous within treatments (see small 95% CI around mean IP in Figure 5a) and had ceased in each treatment from 32 to 114 d before experiment's end. Thus, IPs for instar VII of the 2007 experiment are likely unbiased. However, the proportion of instar VI crabs that survived and moulted twice was conspicuously lower in 2008–2009 (treatment range: 65.6–70.8%) than in 2007–2008 (80.0–91.7%). Furthermore, the number of days elapsed between the last second moult and the 2008 experiment's end was 76 d at 2.5°C, but only 16 d at 5°C and 1 d at 0°C. Thus, in 2008–2009, although the tempo of second moulting in all temperature treatments had reduced considerably weeks before the end of the experiment, the incidence of skip moulting may be somewhat overestimated, and the IP somewhat underestimated for instar VII in the 0 and 5°C treatments.

Mortality was 19.1 and 29.4% overall in the 2007 and 2008 experiments, respectively, and was low to moderate (4.8–26.7%) in individual temperature treatments except at 0°C where it reached 45.8–60.6% (Supplementary Table S4). Skip moulters as loosely defined above, i.e. not moulted twice, represented 88.9 and 96.6% of all crabs that died in the 2007 and 2008 experiments, respectively. Combined results from the two experiments show that “skip moulters” deaths were due in almost equal proportions to crabs that never moulted (47.8% of 113 crabs) or that moulted only once (52.2%). For those crabs that never moulted, death occurred mostly within ≈10 weeks before or after the median time of either the first or second moulting event of individual treatments. For those crabs that moulted only once, 33.9% died at first moulting, 18.6% died soon (4–18 d) after first moult, and 47.5% died from ≈11 weeks before to ≈4 weeks after the median time of the second moulting event.

**Table 3.** Mean CW (in mm) and corresponding instar number (I) at 50% physiological maturity (PM50) during 2010–2011, and mean of regional CW at the first, middle and last instar of the 1980s–2010s, BSM (1980–2010), EST (1980–2010) and LNS (1980–2010) (*Chionoecetes opilio*) in three

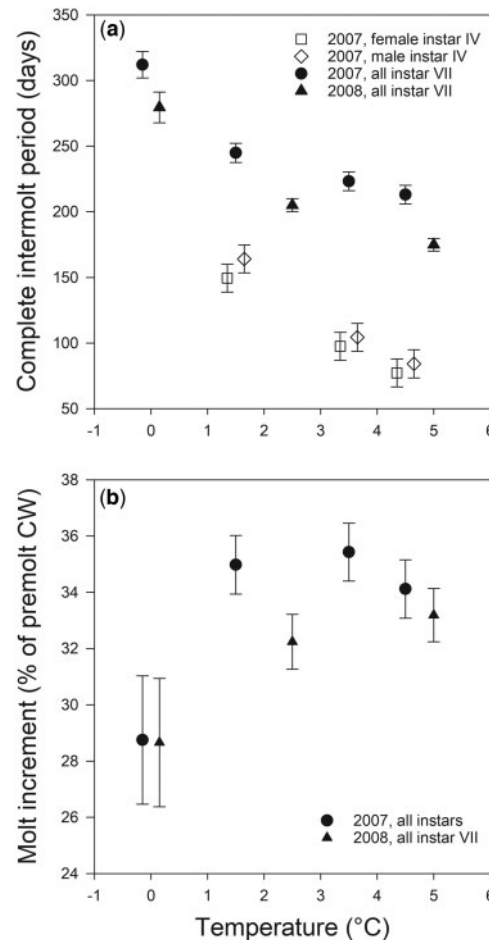
Trait	Females			Males		
	EST	BSM	LNS	EST	BSM	LNS
CW <sub>PM50</sub>	25.26 (24.00–26.52)	25.90 (24.30–27.51)	22.33 (20.78–23.98)	41.16 (39.52–42.81)	39.52 (37.32–41.31)	37.17 (35.50–38.83)
I <sub>PM50</sub>	VII	VII	VI	VIII→IX	VIII→IX	VIII
CW <sub>AD1</sub>	44.19 (43.31–45.08)	42.87 (40.75–44.99)	40.87 (40.53–41.21)	49.26 (44.31–54.21)	44.74 (41.49–47.99)	43.67 (41.25–46.09)
CW <sub>AD5</sub>	47.28 (46.17–48.38)	45.41 (43.11–47.71)	43.25 (42.91–43.60)	58.42 (52.93–63.92)	54.53 (51.92–57.15)	48.89 (45.37–52.41)
CW <sub>AD50</sub>	55.93 (55.07–56.79)	52.25 (49.99–54.51)	50.43 (49.90–50.96)	90.45 (84.90–96.00)	79.27 (73.57–84.97)	73.00 (68.17–77.83)
CW <sub>AD95</sub>	65.63 (64.97–66.29)	62.19 (59.90–64.47)	60.11 (59.22–61.00)	118.72 (116.39–121.06)	113.55 (109.19–117.91)	99.83 (95.56–104.11)
CW <sub>AD99</sub>	70.45 (69.54–71.35)	67.24 (64.45–70.03)	65.20 (63.94–66.45)	126.92 (125.37–128.47)	121.45 (117.45–125.45)	110.34 (105.72–114.96)

Regions are ordered from left to right by decreasing average temperature. 95% confidence limits of CW are shown in parentheses.



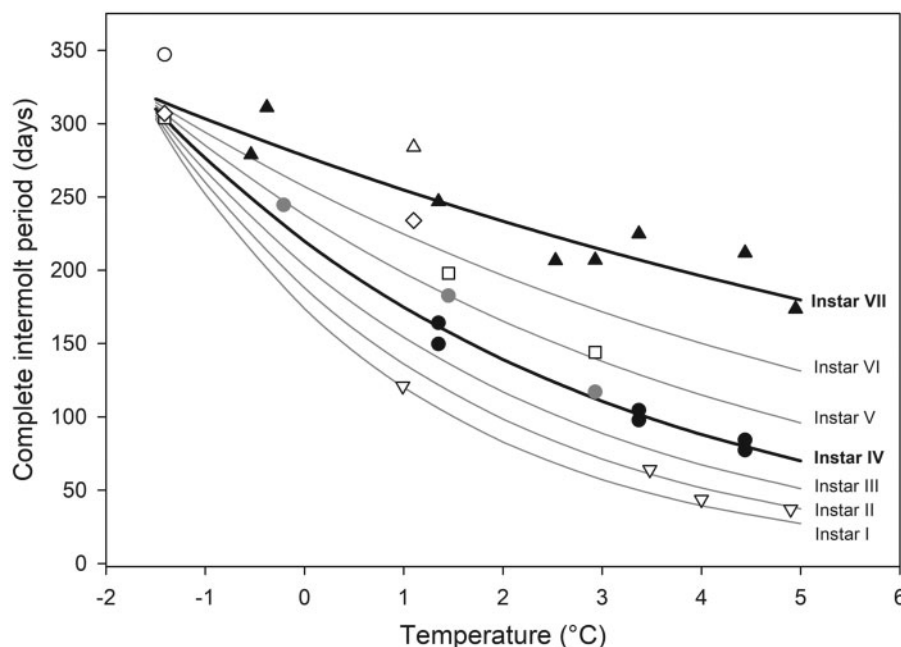
**Figure 4.** Proportion of physiologically maturing females (a) and mature males (b) among subadult snow crab (*Chionoecetes opilio*) as a function of CW (mm) in EST (square; 2010–2011), BSM (circle; 2010), and LNS (triangle; 2010) of the north St Lawrence marine system. The CW at 50% physiological maturity based on logistic regressions (shown) is in Table 3. Observations are binned by 0.25-mm CW classes, with 1–7 crabs per size class.

Table 4 summarizes the ANOVA results for IP and MI during the 2007 and 2008 experiments. Sex was a significant factor only for IP, in three out of six cases, with females consistently having shorter IPs than males at any given temperature/instar. Mean CW



**Figure 5.** Mean ( $\pm 95\%$  CI) moult increment (a) and complete intermoult period (b) of instar IV and VII snow crab (*Chionoecetes opilio*) in temperature treatments of the 2007 and 2008 laboratory experiments. Within experiments, instars are grouped or separated according to factors having significant effects (see Material and methods and Table 4). Note that data points for the 0°C treatment and for females and males of instar IV are staggered for readability.

was influential on mean IP and MI, but only of higher instars likely due to the fact that the range of replicate mean CW within treatments was greater for instars VI and VII than for instars III and IV (Supplementary Table S2).



**Figure 6.** Observed or modelled complete intermolt periods for snow crab (*Chionoecetes opilio*) of instars I–VII as a function of rearing temperature. Bold black lines are weighted linear regressions (see text) based on results of experiments conducted in this study (full black symbols) or by Gravel (2002, full grey symbols) for instar IV (circle) and instar VII (upright triangle). Regular grey lines are modelled (see text). Open symbols represent instar I (upside-down triangle) from Sainte-Marie and Lafrance (2002) and Yamamoto *et al.* (2015a), and instars IV (circle), V (square), VI (diamond), and VII (upright triangle) from Gravel (2002) and/or Yamamoto *et al.* (2015b).

Considering the first moult in the 2007 experiment, partial IP was shorter for instar III than for instar VI at any given temperature treatment, and for both instars it declined significantly with increasing temperature (Table 4). For instar III, the sex-adjusted mean partial IP declined progressively from 40.0 d at 1.5°C to 20.6 d at 4.5°C in females and from 46.8 d at 1.5°C to 32.4 d at 4.5°C in males ( $\pm 9.9$  d 95% CI on all means), a 39% average decrease. The mean partial IP of instar VI, adjusted for CW, declined progressively from 113.4  $\pm$  39.1 d at 0°C, 72.6  $\pm$  28.2 d at 1.5°C, and down to 40.4  $\pm$  27.5 d at 4.5°C, representing a 64% decrease overall. In 2008, by contrast, temperature had no significant effect on partial IP of instar VI (Table 4), although durations for females and males were shortest (average 84 d) at the maximum temperature of 5°C. The first MI was independent of temperature for instar III and instar VI in 2007 and for instar VI in 2008 (Table 4). Instar III had a larger MI (range of treatment means: 40.0–42.2%) than instar VI in 2007 (32.3–34.1%) and 2008 (27.2–29.7%). These laboratory first MIs were similar to MIs in nature for instar III (Table 3: average for females and males across regions = 42.4%) but were noticeably smaller than MIs in nature for instar VI (Table 3: 40.1%).

Considering the second moult cycle, which occurred completely in the laboratory, temperature was the only factor in both experiments that almost always (one exception) had an effect on IP and MI (Table 4). Sex was a significant factor only in the duration of instar IV crabs (Table 4, 2007 experiment), with males having IPs 7.0–9.7% longer than those of females depending on temperature treatment. Mean CW had a significant and positive effect on mean IP of instar VII in both experiments and a significant and negative effect on MI of instar VII in the 2008 experiment (Table 4).

The effect of temperature treatment on complete IP, once adjusted for any other significant factor, was overall very strong but more pronounced in instar IV than instar VII (Figure 5a). The mean complete IP for instar IV in the 2007 experiment declined from 149.6 d in females and 164.4 d in males at 1.5°C–77.3 d in females and 84.2 d in males at 4.5°C, an average decrease of 49%. The mean complete IP of instar VII in 2007 decreased from 312.1 d at 0°C, to 245.0 d at 1.5°C and continued down to 213.1 d at 4.5°C, representing a 31.7% change from 0°C but only a 13.0% change from 1.5°C. In the 2008 experiment, the mean complete IP decreased by 37.4% from 0°C (279.5 d) to 5°C (174.9 d).

The effect of temperature treatment on the MI through a complete moult cycle, once adjusted for the effect of any other significant factor, was rather weak but consistent across experiments and the two instars (Figure 5b): MI was significantly less at 0°C (28.4–28.7%) than at the warmer treatments (32.4–35.4%). These laboratory MIs were smaller than the corresponding MIs in nature, but more so for instar IV (Table 3: average for females and males across regions = 43.1%) than for instar VII (37.0%).

The weighted linear regression of adjusted mean complete IP (days) on interpolated mean temperature (iT, °C), including observations of Gravel (2002), was significant for the two instars considered:

$$\begin{aligned} \text{Instar IV : } IP &= 219.8634 \cdot e^{(-0.2376 \cdot iT)}; p < 0.001, \\ \text{Instar VII : } IP &= 277.9872 \cdot e^{(-0.0872 \cdot iT)}; p = 0.001. \end{aligned}$$

The regressions are shown in Figure 6, where the negative slope coefficient between IP and temperature is obviously much steeper for instar IV than for instar VII, indicating greater temperature sensitivity of the former.

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Direction, ontogeny and mechanism

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**Table 4.** Reduced ANOVA models on snow crab (*Chionoecetes opilio*) IP (days) and moult increment (%) by instar transition (III–IV, IV–V, VI–VII, and VII–VIII) in the 2007 and 2008 laboratory experiments, with temperature as the experimental treatment and CW and sex as potential factors.

Dependent variable and source of variation	Experiment and ANOVA statistics					
	2007			2008		
	df	F	p	df	F	p
Intermoult period						
Partial moult cycle, instar III–IV						
Temperature	2	6.74	0.004	–	–	–
Sex	1	4.69	0.038	–	–	–
Residuals	32	–	–	–	–	–
Complete moult cycle, instar IV–V						
Temperature	2	119.31	<0.001	–	–	–
Sex	1	5.12	0.031	–	–	–
Residuals	32	–	–	–	–	–
Partial moult cycle, instar VI–VII						
Temperature	3	3.76	0.019	2	1.57	0.217
Sex	–	–	–	1	10.62	0.002
CW	1	5.36	0.026	–	–	–
Residuals	37	–	–	50	–	–
Complete moult cycle, instar VII–VIII						
Temperature	3	98.50	<0.001	2	149.13	<0.001
CW	1	25.26	<0.001	1	4.42	0.041
Residuals	37	–	–	46	–	–
Moult increment						
Partial moult cycle, instar III–IV						
Temperature	2	1.81	0.179	–	–	–
Residuals	33	–	–	–	–	–
Partial moult cycle, instar VI–VII						
Temperature	3	0.78	0.512	2	2.55	0.088
Residuals	38	–	–	51	–	–
Complete moult cycle		Instar IV–V and VII–VIII			Instar VII to VIII	
Temperature	3	10.00	<0.001	2	6.92	0.002
CW	–	–	–	1	16.46	<0.001
Residuals	73	–	–	45	–	–

Wild crabs were introduced into the experiment at instar III or VI and allowed to moult once (partial moult cycle and IP, as date of previous moult was unknown) and then a second time (complete moult cycle and IP). Instars were analysed separately except when visual scrutiny of data revealed no difference between instars in the response of dependent variable to treatment. All analyses are based on replicate mean response values.

The modelled relationships between IP and temperature for instars I, II, III, V, and VI are also shown in Figure 6. All instars converged to similarly long IPs of about 310–320 d at  $-1.5^{\circ}\text{C}$ , the slope of the relationship between IP and temperature decreasing progressively from instars I to VII. Model predictions were consistent with temperature-specific IPs for various instars reported in other studies (Figure 6). Based on the model, the average time required for females and males to pass through the sedentary (cryptic) life phase (instars I–IV) in the absence of skip moulting would be as fast as 568 d (1.6 year) at  $1.1^{\circ}\text{C}$  and as slow as 910 d (2.5 year) at  $-0.5^{\circ}\text{C}$ , which represent, respectively, the warmest and coldest August mean temperatures at 100-m depth in our study regions. Hypothetically, development through the sedentary phase could be as brief as 246 d (0.7 year) at  $4^{\circ}\text{C}$  and as long as 1226 d (3.4 years) at  $-1.5^{\circ}\text{C}$ , a fivefold difference.

## Discussion

The TSR and related literature provide a framework for exploring the variability in ectotherm maturation and final size in relation to temperature and environmental correlates. To date, TSR studies on aquatic crustaceans have considered mostly small species,

e.g. copepods and isopods (Atkinson, 1995; Forster and Hirst, 2012; Manyak-Davis *et al.*, 2013). However, the toad crabs *Hyas araneus* and *Hyas coarctatus*—which like the snow crab belong to the family Oregoniidae—and the green crab *Carcinus maenas* are exceptions by their greater size, and have been described cursorily as conforming to the classic TSR in benthic life (Forster and Hirst, 2012; Kelley *et al.*, 2015). In contrast, snow crab conforms to the reverse TSR: growth outpaces maturation with warming (Forster and Hirst, 2012; Zuo *et al.*, 2012) as evidenced herein by the increasing size at PM and TM along a positive temperature gradient in the north St Lawrence marine system. We consider below the staging, size patterns, mechanisms and adaptive value of thermal TM size plasticity in snow crab, briefly addressing the implications in context of climate change.

## Setting the stage for TM

The TM is likely to be energetically more demanding than a non-TM and more so in female than in male snow crab (Dawe *et al.*, 2012). Females fully mature their oocytes just before and become competent to mate and spawn only after, TM. Female functional maturity also requires that the vaginae, spermathecae, and



oviducts be fully developed (Lanteigne *et al.*, 1996) and that major anatomical and morphometric changes occur in the abdomen at TM to accommodate the egg clutch. The energetic challenge that TM poses to females is met by initiating PM sooner in ontogeny than males, by spreading PM over at least two prepubescent instars, and by a conspicuous reduction in the ultimate MI (this study; Alunno-Bruscia and Sainte-Marie, 1998). Male investment in gonads and secondary sexual characters seems comparatively modest to that of females, and male functional maturity is achieved before TM (Sainte-Marie *et al.*, 2008). The male strategy of maturing physiologically and functionally before TM is associated with a subtle but likely energetically meaningful reduction in CW/instar-specific MI and slightly longer IP at instar compared to females (this study; for MI also see Miller and Watson, 1976). The lower cost of male TM may explain why males can transition from onset of PM to adulthood in just one moult (this study) and why there is generally no substantial difference in MI between non-terminal and terminal male moults (Hoenig *et al.*, 1994; Sainte-Marie *et al.*, 1995; Comeau *et al.*, 1998; Yamamoto *et al.*, 2018).

### Geographic-thermal patterns of size

The CW distributions of adult females in this study are considered to be unbiased because even very small females can easily be recognized and large ones are not harvested (although they may be subject to incidental fishing mortality). In the case of males, however, some smaller adults probably went undetected due to the arbitrary 35- or 40-mm lower CW cut-offs for the examination of maturity, and indirect and direct fishing mortality on large adults may be high. Thus, male adult CW may be slightly overestimated at lower percentiles of the CW distribution and it is certainly underestimated at higher percentiles compared to what it would be in unfished populations.

Still, this study demonstrated a clear geographic gradient of increasing SaTM from east (cold) to west (warm) in the north St Lawrence system in both female and male snow crab. This cline can be extended further westward into the Saguenay Fjord (Figure 1), which is warmer than EST by  $\approx 1^\circ\text{C}$  and has very large adult females (mean CW: 76 mm) and males (118 mm) (Sainte-Marie *et al.*, 1992; Sainte-Marie and Gilbert, 1998). This longitudinal TM-size cline likely reflects mainly or only phenotypic plasticity, as there is considerable potential for genetic connectivity among regions through the snow crab's long larval phase (Ouellet and Sainte-Marie, 2018) and no evidence of population genetic differentiation throughout Atlantic Canada (Puebla *et al.*, 2008). A positive thermal reaction norm (reverse TSR) can explain this longitudinal cline of snow crab SaTM, as well as the warmer-bigger geographic patterns of females in the eastern Bering Sea (Orensanz *et al.*, 2007) and of females and males along west Greenland (Burmeister and Sainte-Marie, 2010).

Furthermore, in this study, the size at PM of both sexes followed the same geographic pattern as SaTM, indicating that the reverse TSR was also operating early in snow crab ontogeny. This is not surprising, since PM is a prerequisite for TM to occur. The scope for geographical (and temporal) variability in size at PM is greater than seen in this study: male PM occurred at 20–30 mm CW in the very cold waters of the Chukchi Sea (Paul *et al.*, 1997) and historically at 50–65 mm CW in the south GSL following warmer than usual conditions (Watson, 1970; Sainte-Marie and Gilbert, 1998).

Snow crab were larger in LNS than in the other two regions at every instar, and this most likely reflects a difference in size at settlement. The 0.2–0.4-mm difference in mean CW at instar II between regions is sufficient when projected by average MI at instar to explain the  $\leq 3.5$ -mm CW differences between regions observed at instar VIII. The LNS may be partly provisioned with snow crab larvae originating through the Belle-Isle Strait from along the very cold Labrador coast. Snow crab zoea I were larger in northern (colder) than in southern (warmer) areas of Bering-Chukchi Seas and GSL, presumably due to maternal effects related to temperature during oogenesis and/or embryo incubation (Landeira *et al.*, 2017; Ouellet and Sainte-Marie, 2018). The snow crab zoea II also was, and the megalopa tended to be, larger in the north than in the south Bering-Chukchi Seas and this could be due to maternal carry-over effects and/or to better larval feeding conditions (Landeira *et al.*, 2017). In addition, the greater size of megalopa and instar I crabs in cold water could be a direct effect of larval development temperature (Anger, 1984; Webb *et al.*, 2006; Weiss *et al.*, 2010). Thus, the snow crab's embryo and larval phases seem to conform to the classic TSR. Interestingly, Burmeister and Sainte-Marie (2010) concluded that snow crab were bigger at instar in the coldest compared to the warmest of west Greenland sites, and such a relationship is also supported by the relatively large size of presumptive instars IV–VII in the northernmost part of the Bering Sea [Figure 6 in Kolts *et al.* (2015)]. Thus, the reverse TSR for PM and TM occurs in spite of snow crab being larger at instar in colder than in warmer water.

### Mechanisms of changing size at TM

This study provides additional support for the interpretation that change in SaTM with temperature occurs by a progressive and directional shift in the distribution of crabs among consecutive adult instars, leading eventually to symmetrical loss of one or more lower adult instars and gain of one of more higher adult instars with warming, and vice versa with cooling (Orensanz *et al.*, 2007; Burmeister and Sainte-Marie, 2010). The number of instar losses and gains will reflect the magnitude of temperature change, but throughout this process the range of 2 major adult instars in females and 4–5 in males (with a minor instar possibly flanking on either side) remains rather constant. This is directly supported herein by the geographic-temperature cline in SaTM, which was observable at every selected percentile of adult CW distribution, as in Burmeister and Sainte-Marie (2010), and by the parallel temperature-specific female TM vs. CW ogives in Dawe *et al.* (2012). The conservative mean CW at instar of subadults and invariance of MI at instars II–VI across our three study regions confirm the importance of number of moults for determining SaTM. Our laboratory experiments also showed that the MI of subadult crabs was largely temperature independent, being similar for instars IV and VII across mean interpolated temperatures of 1.3–5.0°C and declining only weakly for instar VII at  $-0.4$  and  $-0.5^\circ\text{C}$ , possibly due to different holding conditions for the coldest treatment. Similarly, Yamamoto *et al.* (2015a) found that MI of unsexed snow crab (3–22 mm premoult CW) did not differ between rearing temperatures of 1 and 3°C and increased only slightly at 5°C.

Time appears to be the other key component of change in snow crab SaTM with temperature. Ernst *et al.* (2012) provided evidence for the uniformity of age-at-TM of female snow crab across the latitudinal (temperature) cline of SaTM in the eastern

Bering Sea. They showed that recruitment pulses synchronously produced adult females of larger mean CW (and higher instar composition) at lower compared to higher latitudes. To be clear, this does not imply that all females are of the same age-at-TM, only that the first transition from subadult to adult in a cohort is relatively time invariant and that remaining prepubescent females from that cohort subsequently distribute themselves annually to consecutive higher instars, such that age-at-TM of any given female (in the absence of skip moulting) scales to instar number (Orensanz *et al.*, 2007). Thus, moulting tempo prior to the time of first transition to TM would determine the minimum and maximum instar number for female (and male) TM as proposed previously (Orensanz *et al.*, 2007; Burmeister and Sainte-Marie, 2010).

Temperature is a major source of variability in moulting tempo for snow crab early benthic instars through its very strong negative effect on IP, as demonstrated by Yamamoto *et al.* (2015a) and this study. However, unlike Yamamoto *et al.* (2015a), we found that IP was progressively less sensitive to temperature with increasing instar number and projected that it converged towards a similar value for all instars at the coldest temperature ( $-1.5^{\circ}\text{C}$ ). A probable explanation for this difference is that the negative exponential response of IP to temperature was better resolved in our study through the inclusion of temperature treatments ranging between  $-0.5$  and  $1^{\circ}\text{C}$ , in the steepest part of the response curve. A negative exponential response of IP to temperature, and of declining slope with increasing instar number, may be general among crabs (e.g. Anger, 1984). Most interestingly, like snow crab, the related and slightly warmer stenothermic Tanner crab *Chionoecetes bairdi* also appears to follow the reverse TSR in benthic life (e.g. Somerton, 1981) and its IP is much more sensitive to temperature than its MI (Ryer *et al.*, 2016). Other sources of variability in IP of snow crab early benthic instars, which may or not be correlated with temperature, include density-dependent cannibalism risk and competition for food, which lengthen IP at constant temperature (Sainte-Marie and Lafrance, 2002). The temperature sensitivity of the moulting rate of early snow crab instars in this study is more than enough to explain the upward or downward shifts in instar numbers at adulthood needed to account for documented geographic/temperature variability of SaTM under the time-invariant hypothesis for TM schedules. This process operates on all females and males, thus ensuring that sexual size dimorphism—which is itself a sexually selected trait—is to some extent constrained along temperature or geographical gradients (Horne *et al.*, 2019a).

The present study implies that the moult leading to onset of PM has a pivotal role in the subsequent life history of snow crab, a role that has not been widely examined/recognized in the brachyuran literature (Hartnoll, 2015) but may be common to many species. Indeed, change in minimum CW/instar at TM in snow crab must be staged by a prior change in CW/instar at PM, considering the energetic and developmental constraints on TM discussed above. The steep PM ogives of both sexes (this study; for males, also see: Watson, 1970; Comeau and Conan, 1992) can indicate that the transition from juvenile to prepubescent/adolescent is triggered by an age threshold, on the condition that growth rate through the early instars is quite uniform among individuals within cohorts and/or that mortality rate of stragglers is high. The narrow 95% CI on IP and MI and low survival of skip moulters in this study provides evidence for both premises. Alternatively, a temperature-dependent size threshold (CW or

mass) could determine the onset of PM (e.g. Ghosh *et al.*, 2013). Note that a shift in the CW/instar at PM can by itself bring about some change in SaTM, because the negative inflexion in the relation of postmoult to premoult CW (Hiatt diagram) associated with PM (Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998) is advanced to a smaller size or delayed to a larger size with effects on mean CW of subsequent instars (see Supplementary Text S2 for a brief discussion of modal/instar structure of larger subadult and adult crabs).

Sedentary juvenile snow crab may be more important than mobile juveniles for the determination of CW/instar at PM and first transition to TM. Indeed, sedentary instars I–IV are much more temperature sensitive for IP and have little/no capability for behavioural thermoregulation compared to later instars. In the north GSL, the late-fall or winter migrations of mobile snow crab (>instar V) into shallow waters for moulting create exposure to extreme cold ( $-1.8^{\circ}\text{C}$ ) through winter and potential exposure to warmth ( $4-5^{\circ}\text{C}$ ) in the spring when the mixed surface layer begins to form (Lovrich *et al.*, 1995). The timing of movement to and from the shallow waters and choice of depth (temperature) distribution during the summer–fall may allow mobile crabs to modulate their moult schedule and energetic condition (Dutil *et al.*, 2010). Partial IP was highly temperature sensitive in Dutil *et al.* (2010) and this study, such that even short-term (3–6 months) changes in temperature can impact moult timing and synchrony but—it is noteworthy—not probability of TM (Dutil *et al.*, 2010; Sainte-Marie *et al.*, 2010). Seasonal moulting migrations are rather well documented in the north GSL (Sainte-Marie and Hazel, 1992), and there is some evidence that they occur more generally throughout Atlantic Canada (Bouchard *et al.*, 1986; Mullowney *et al.*, 2018). Winter exposure to extreme cold may explain why instar VII lasts about 12 months in the north GSL (e.g. Sainte-Marie *et al.*, 1995; Comeau *et al.*, 1998) compared to only 7–10 months at constant  $0-2^{\circ}\text{C}$  in our laboratory experiments.

How snow crab of a cohort distribute themselves over the range of instar options for TM set by the thermal reaction norm may depend on factors that are not directly related to temperature and/or on temperature effects in later benthic life (see Skip moulting below). For females, Alunno-Bruscia and Sainte-Marie (1998) found that the probability of early (smaller) TM was greater for larger than for smaller females belonging to the same instar (cohort). For males, Elner and Beninger (1995) proposed that mating success or failure in adolescence could modify the TM schedule, by either promoting immediate TM or delaying it to a later instar (also see Comeau *et al.*, 1998). Modulation of size-maturity schedules through these or other density-dependent processes is likely to be more evident in males because TM is spread out over a greater number of instars compared to females. In this respect, interannual variability in SaTM was less for females than for males (this study; Burmeister and Sainte-Marie, 2010) and TM vs. CW ogives were steep and regular in females whereas they were rather gentle and irregularly shaped in males (Dawe *et al.*, 2012). The foregoing does not preclude the possibility that some heterogeneity of individual snow crab SaTM reflects genetic variation within populations (e.g. Orensanz *et al.*, 2007).

### Skip moulting

Skip moulting was observed even in the smallest snow crab instar (III) reared in our laboratory experiments and could exceed two

IPs. So far, skip moulting was reported to be negligible in snow crab smaller than 45–50 mm CW (Dawe *et al.*, 2012; Murphy, 2019), i.e. instar VIII and lower. Identification of skip moulters in nature is based on shell condition, with subadults having new shells (unabraded and without epibionts) assumed to be regular moulters and those having intermediate or old shells (variably abraded and populated by epibionts) assumed to be skip moulters. Lack of detection of small skip moulters in nature could be due to their generally higher moulting frequency and lesser mobility which do not favour extensive shell abrasion. Furthermore, fouling organisms may avoid settling on snow crab early benthic instars due to their more frequent moulting and small size (i.e. they are an ephemeral and exiguous substrate), and indeed the prevalence of epibionts does decrease with host size in other marine arthropods (Key *et al.*, 1996; Dvoretsky and Dvoretsky, 2009).

The frequency of skip moulting declined with increasing temperature in our study as reported by Dawe *et al.* (2012) for larger snow crab. However, skip moulting was clearly not an inevitable outcome of cold temperature only, as it did not occur in all crabs even in our coldest temperature treatment. Skip moulting has been linked to poor physiological condition and the non-uniform skip moulting response of crabs to cold temperature in experiments probably reflects pre-treatment (individual historical) differences in condition (Dutil *et al.*, 2010). High density and competition for food may depress physiological condition of subordinate crabs (Dutil *et al.*, 2009; Dawe *et al.*, 2012), and it may be more difficult for these crabs to improve their condition in cold than in warm water due to reduced metabolism (Dutil *et al.*, 2010). We suggest that temperature and density-dependent effects on incidence of skip moulting may be partially or completely confounded because cold temperature also promotes abundance of larvae, settler (Émond *et al.* 2015, 2020), and subadult snow crab (Boudreau *et al.*, 2011; Marcello *et al.*, 2012; Szuwalski and Punt, 2013).

Skip moulting cannot be the fundamental mechanism for the reverse TSR and geographic-thermal size clines of snow crab, because it (contrary to IP) is not strictly related to temperature and does not operate uniformly on all population members (see above). Furthermore, the incidence of skip moulting can vary from year to year and/or from one marine basin to another independently of temperature (Comeau *et al.*, 1998; Murphy, 2019). Skip moulting can, however, potentially modify the distribution of crabs among the TM instar options set by the thermal reaction norm, with a general expectation that skip moulting should result in a decrease in SaTM (for males: Dawe *et al.*, 2012; for both sexes: Murphy, 2019). To what extent this is actually the case is unclear because survival of skip moulters is uncertain (Murphy, 2019). In our experiments, small skip moulters suffered high mortality and this was also deduced to be the case for large skip moulters in a wild population (Comeau *et al.*, 1998). Snow crab recruitment cycles lead to very different average crab condition through successive cohorts, such that the fate of skip moulters may vary interannually as they are more or less able to achieve a threshold condition for moulting and postmoult survival (Dutil *et al.*, 2009, 2010).

### Adaptive value of reverse TSR and some implications in context of climate change

The reverse TSR in snow crab is not an adaptation to season length, as has been held for some other ectotherms (Atkinson,

1995; Blanckenhorn and Demont, 2004). Snow crab can perform vital benthic life history functions—development, growth and reproduction—in the coldest marine conditions (Orensanz *et al.*, 2007; Burmeister and Sainte-Marie, 2008). We propose as suggested by Zuo *et al.* (2012) that the reverse TSR in benthic snow crab is an adaptation to cope with ectotherm predation, the intensity of which scales positively to temperature (Atkinson, 1995). For snow crab, major sources of ectotherm predation can be groundfish, most notably Atlantic cod *Gadus morhua* or Pacific cod *G. macrocephala* (Chabot *et al.*, 2008; Burgos *et al.*, 2013), and cannibalism (Lovrich and Sainte-Marie, 1997; Divine *et al.*, 2017). Considering Atlantic Canada, on one hand, cold water may reduce the rate of intra- and inter-specific ectothermic predation, impose some spatial separation between the cryophilic snow crab and cod which is a warmer-water species (Lafrance *et al.*, 2005), and provide snow crab with more habitat that reduces density-dependent interactions (food competition and cannibalism). On the other hand, “warm” water may challenge snow crab with increased ectothermic predation and density-dependent interactions (through habitat contraction), which may at least partially be offset by increased reproductive output (Sainte-Marie *et al.*, 2008) and by growing quickly (Ryer *et al.*, 2016) to a size refuge ( $\approx 50$  mm CW) from cannibalism (Dutil *et al.*, 1997; Lovrich and Sainte-Marie, 1997) and cod predation (Chabot *et al.*, 2008). Seasonal inshore migration in the north GSL to very cold water also largely puts snow crab out of reach of cod and larger cannibals at moulting, when the size refuge does not protect against predation due to shell softness (Lovrich and Sainte-Marie, 1997; Chabot *et al.*, 2008).

This study has many potential implications for understanding the impact of climate change on snow crab productivity. Importantly, and provided early juvenile habitat is defined, it may become possible to predict several years in advance the direction and amplitude of temperature-induced change in the TM schedule. This capability should be heightened by a better understanding of factors that modulate the reverse TSR in snow crab, such as density-dependent mating success and skip moulting. While increasing snow crab size and reproductive output with warming may provide resilience to climate change, this pattern is potentially a liability in face of commercial harvest under a fixed minimum legal size (MLS). Indeed, the proportion of males reaching MLS will increase with warming just as female sperm demand grows due to increasing clutch fecundity and reproductive tempo. Adaptive management will be needed to limit the risk of sperm limitation, by adjusting MLS or exploitation rate at a fixed MLS to ensure sperm supply (Sainte-Marie *et al.*, 2008).

### Conclusion

Snow crab follows the reverse TSR in benthic life resulting in a warmer-bigger pattern of size at PM and TM and possibly follows the classic TSR through embryogenesis and larval development resulting in a colder-bigger pattern of larval and settlement size. Temperature has little influence on MI during benthic life, so thermal variability in SaTM is due mostly to a change in the number of moults. Minimum and maximum CW/instar at TM may be symmetrically fixed before or at onset of PM. Temperature has a very strong negative exponential effect on IP, of decreasing slope with increasing instar number. Thus, under the strict or loose hypothesis of time-invariant onset of TM, temperature likely controls the range of possible CWs/instars via IP. The reality of this time-invariant hypothesis for TM, and



eventually for PM, is an important outstanding issue to resolve. Another key issue is what factors trigger TM within the range of instar options set by temperature. The reverse TSR during snow crab benthic life may be adaptive to cope with ectothermic predation and has important implications for conservation of this major marine resource, which will be considered in a later study.

### Supplementary data

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

### Data availability

Experimental data will be shared without undue reservation on reasonable request by qualified researchers. Survey data may also be shared, but this requires permission of multiple parties within Fisheries and Oceans Canada. All enquiries should be addressed

[AQ10] to the corresponding author.

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### References

- Aguilar-Alberola, J. A., and Mesquita-Joanes, F. 2014. Breaking the temperature-size rule: thermal effects on growth, development and fecundity of a crustacean from temporary waters. *Journal of Thermal Biology*, 42: 15–24.
- Alunno-Bruscia, M., and Sainte-Marie, B. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 459–477.
- Alvsvåg, J., Agnalt, A.-L., and Jørstad, K. E. 2009. Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. *Biological Invasions*, 11: 587–595.
- Anger, K. 1984. Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda, Majidae) reared in the laboratory. *Marine Ecology Progress Series*, 19: 115–123.
- Angilletta, M. J., Steury, T. D., and Sears, M. W. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44: 498–509.
- Arendt, J. 2007. Ecological correlates of body size in relation to cell size and cell number: patterns in flies, fish, fruits and foliage. *Biological Reviews*, 82: 241–256.
- Atkinson, D. 1995. Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *Journal of Thermal Biology*, 20: 61–74.
- Benhalima, K., Moriyasu, M., and Hébert, M. 1998. A technique for identifying the early-premolt stage in the male snow crab *Chionoecetes opilio* (Brachyura: Majidae) in Baie des Chaleurs, southern Gulf of St. Lawrence. *Canadian Journal of Zoology*, 76: 609–617.
- Blackburn, T. M., Gaston, K. J., and Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, 5: 165–174.
- Blanckenhorn, W. U., and Demont, M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology*, 44: 413–424.
- Bouchard, R., Brêthes, J. F., Desrosiers, G., and Bailey, R. F. J. 1986. Changes in size distribution of snow crabs (*Chionoecetes opilio*) in the southwestern Gulf of St. Lawrence. *Journal of Northwest Atlantic Fishery Science*, 7: 67–75.
- Boudreau, S. A., Anderson, S. C., and Worm, B. 2011. Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean. *Marine Ecology Progress Series*, 429: 169–183.
- Burgos, J., Ernst, B., Armstrong, D., and Orensanz, J. M. 2013. Fluctuations in range and abundance of snow crab (*Chionoecetes opilio*) from the eastern Bering Sea: what role for Pacific cod (*Gadus macrocephalus*) predation? *Bulletin of Marine Science*, 89: 57–81.
- Burmeister, A. D., and Sainte-Marie, B. 2010. Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland. *Polar Biology*, 33: 775–788.
- Caddy, J. F. 2003. Scaling elapsed time: an alternative approach to modelling crustacean moulting schedules? *Fisheries Research*, 63: 73–84.
- Chabot, D., Sainte-Marie, B., Briand, K., and Hanson, M. H. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. *Marine Ecology Progress Series*, 363: 227–240.
- Chang, Y. J., Sun, C. L., Chen, Y., and Yeh, S. Z. 2012. Modelling the growth of crustacean species. *Reviews in Fish Biology and Fisheries*, 22: 157–187.
- Comeau, M., and Conan, G. Y. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2460–2468.
- Comeau, M., Conan, G. Y., Maynou, F., Robichaud, G., Therriault, J.-C., and Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 262–279.
- Daufresne, M., Lengfellner, K., and Sommer, U. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 12788–12793.
- Dawe, E. G., and et Colbourne, E. B. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador Shelf. In *Crabs in Cold Water Regions: Biology, Management, and Economics*, Alaska Sea Grant College Program Report No. 02-01, pp. 577–594. Ed. by A. J. Paul, E. G. Dawe, R. Elner, G. S. Jamieson, G. H. Kruse, R. S. Otto, and B. Sainte-Marie University of Alaska Fairbanks, Fairbanks, AK.
- Dawe, E. G., Mullowney, D. R., Moriyasu, M., and Wade, E. 2012. Effects of temperature on size-at-terminal molt and molting frequency in snow crab *Chionoecetes opilio* from two Canadian Atlantic ecosystems. *Marine Ecology Progress Series*, 469: 279–296.
- de Mendiburu, F. 2014. agricolae: statistical procedures for agricultural research. R package version 1.1-7. <http://CRAN.R-project.org/package=agricolae>. [AQ12]
- Dionne, M., Sainte-Marie, B., Bourget, E., and Gilbert, D. 2003. Distribution and habitat selection of early benthic stages of snow crab, *Chionoecetes opilio*. *Marine Ecology Progress Series*, 259: 117–128.
- Divine, L. M., Bluhm, B. A., Mueter, F. J., and Iken, K. 2017. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using



- stomach contents and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotopes. Deep-Sea Research II, 135: 124–136.
- Dutil, J.-D., Dion, C., Gamache, L., Larocque, R., and Ouellet, J.-F. 2010. Ration and temperature effects on the condition of male adolescent molter and skip molter snow crab. Journal of Shellfish Research, 29: 1025–1033.
- Dutil, J.-D., Larocque, R., Valois, S., Mayrand, É., and Sainte-Marie, B. 2009. Spatial, annual and seasonal patterns in the condition and muscle size of snow crab. Marine Biology, 156: 1903–1916.
- Dutil, J.-D., Munro, J., and Pêloquin, M. 1997. Laboratory study of the influence of prey size on vulnerability to cannibalism in snow crab (*Chionoecetes opilio* O. Fabricius, 1780). Journal of Experimental Marine Biology and Ecology, 212: 81–94.
- Dvoretsky, A. G., and Dvoretsky, V. G. 2009. Fouling community of the red king crab, *Paralithodes camtschaticus* (Tilesius 1815), in a subarctic fjord of the Barents Sea. Polar Biology, 32: 1047–1054.
- Elner, R. W., and Beninger, P. G. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: physiological pathways and behavioral plasticity. Journal of Experimental Marine Biology and Ecology, 193: 93–112.
- Émond, K., Sainte-Marie, B., and Bêty, J. 2020. Long-term trends and drivers of larval phenology and abundance of dominant brachyuran crabs in the Gulf of St. Lawrence (Canada). Fisheries Oceanography, 29: 185–200.
- Émond, K., Sainte-Marie, B., Galbraith, P. S., and Bêty, J. 2015. Top-down vs. bottom-up drivers of recruitment in a key marine invertebrate: investigating early life stages of snow crab. ICES Journal of Marine Science, 72: 1336–1348.
- Ernst, B., Armstrong, D. A., Burgos, J., and Orensanz, J. M. 2012. Life history schedule and periodic recruitment of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences, 69: 532–550.
- Fonseca, D. B., Sainte-Marie, B., and Hazel, F. 2008. Longevity and change in shell condition of adult male snow crab inferred from dactyl wear and mark-recapture data. Transactions of the American Fisheries Society, 137: 1029–1043.
- Forster, J., and Hirst, A. G. 2012. The temperature-size rule emerges from ontogenetic differences between growth and development rates. Functional Ecology, 26: 483–492.
- Forster, J., Hirst, A. G., and Atkinson, D. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences of the United States of America, 109: 19310–19314.
- Fox, J., and Weisberg, S. 2011. An {R} Companion to Applied Regression, 2nd edn. Sage, Thousand Oaks, CA.
- Galbraith, P. S., Chassé, J., Caverhill, C., Nicot, P., Gilbert, D., Lefavre, D., and Lafleur, C. 2018. Physical oceanographic conditions in the Gulf of St. Lawrence during 2017. DFO Canadian Science Advisory Secretariat Research Document 2018/050. 80 pp.
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. 2011. Declining body size: a third universal response to warming? Trends in Ecology and Evolution, 26: 285–291.
- Ghosh, S. M., Testa, N. D., and Shingleton, A. W. 2013. Temperature-size rule is mediated by thermal plasticity of critical size in *Drosophila melanogaster*. Proceedings of the Royal Society B, 280: 20130174.
- Gosselin, T., Sainte-Marie, B., and Sévigny, J.-M. 2007. Individual identification of decapod crustaceans II: natural and genetic markers in snow crab (*Chionoecetes opilio*). Journal of Crustacean Biology, 27: 399–403.
- Gravel, K. 2002. Bilan énergétique des juvéniles du crabe des neiges, *Chionoecetes opilio*, à différentes températures. MSc thesis, Université du Québec à Rimouski, Rimouski, Québec. 121 pp.
- Hardy, D., Munro, J., and Dutil, J.-D. 1994. Temperature and salinity tolerance of the soft-shell and hard-shell male snow crab, *Chionoecetes opilio*. Aquaculture, 122: 249–265.
- Hartnoll, R. G. 2015. Postlarval life histories of Brachyura. In Treatise on Zoology—Anatomy, Taxonomy, Biology. The Crustacea. Decapoda: Brachyura, 9C-1, pp. 375–416. Ed. by P. Castro, P. J. F. Davie, D. Guinot, F. R. Schram, and J. C. von Vaupel Klein. Brill, Leiden, The Netherlands.
- Hoenig, J. M., Dawe, E. G., and O’Keefe, P. G. 1994. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). Journal of Crustacean Biology, 14: 273–279.
- Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G. *et al.* 2013. Projected impacts of climate change on marine fish and fisheries. ICES Journal of Marine Science, 70: 1023–1037.
- Horne, C. R., Hirst, A. G., and Atkinson, D. 2019a. A synthesis of major environmental-body size clines of the sexes within arthropod species. Oecologia, 190: 343–353.
- Horne, C. R., Hirst, A. G., Atkinson, D., Almeda, R., and Kiørboe, T. 2019b. Rapid shifts in the thermal sensitivity of growth but not development rate causes temperature–size response variability during ontogeny in arthropods. Oikos, 128: 823–835.
- Ito, K. 1970. Ecological studies on the edible crab, *Chionoecetes opilio* O. Fabricius in the Japan Sea. III. Age and growth as estimated on the basis of the seasonal changes in the carapace width frequencies and carapace hardness. Bulletin of the Japan Sea Regional Fisheries Research Laboratory, 22: 81–116.
- James, A. C., Azevedo, R. B. R., and Partridge, L. 1995. Cellular basis and developmental timing in a size cline of *Drosophila melanogaster*. Genetics, 140: 659–666.
- Kelley, A. L., de Rivera, C. E., Grosholz, E. D., Ruiz, G. M., Yamada, S. B., and Gillespie, G. 2015. Thermogeographic variation in body size of *Carcinus maenas*, the European green crab. Marine Biology, 162: 1625–1635.
- Key, M. M., Jeffries, M. B., Voris, H. K., and Yang, C. M. 1996. Epizoic bryozoans, horseshoe crabs, and other mobile benthic substrates. Bulletin of Marine Science, 58: 368–384.
- Kingsolver, J. G., and Huey, R. B. 2008. Size, temperature, and fitness: three rules. Evolutionary Ecology Research, 10: 251–268.
- Klok, C. J., and Harrison, J. F. 2013. The temperature size rule in arthropods: independent of macro-environmental variables but size dependent. Integrative and Comparative Biology, 53: 557–570.
- Kolts, J. M., Lovvorn, J. R., North, C. A., and Janout, M. A. 2015. Oceanographic and demographic mechanisms affecting population structure of snow crabs in the northern Bering Sea. Marine Ecology Progress Series, 518: 193–208.
- Lafrance, P., Castonguay, M., Chabot, D., and Audet, C. 2005. Ontogenetic changes in temperature preference of Atlantic cod. Journal of Fish Biology, 66: 553–567.
- Landeira, J. M., Matsuno, K., Yamaguchi, A., Hirawake, T., and Kikuchi, T. 2017. Abundance, development stage, and size of decapod larvae through the Bering and Chukchi Seas during summer. Polar Biology, 40: 1805–1819.
- Lanteigne, C., Beninger, P. G., and Gionet, C. 1996. Ontogeny of female primary sexual characters in the majid crabs *Chionoecetes opilio* and *Hyas coarctatus*. Journal of Crustacean Biology, 16: 501–514.
- Lovrich, G. A., Sainte-Marie, B., and Smith, B. D. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Canadian Journal of Zoology, 73: 1712–1726.
- Lovrich, G. A., and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (Brachyura: Majidae), and its potential importance to recruitment. Journal of Experimental Marine Biology and Ecology, 211: 225–245.
- Macdonald, P. D. M., and Du, J. 2012. Mixdist: finite mixture distribution models. R package version 0.5-4. <http://CRAN.R-project.org/package=mixdist>.

- Marcello, L. A., Mueter, F. J., Dawe, E. G., and Moriyasu, M. 2012. Effects of temperature and gadid predation on snow crab recruitment: comparisons between the Bering Sea and Atlantic Canada. *Marine Ecology Progress Series*, 469: 249–261.
- Manyak-Davis, A., Bell, T. M., and Sotka, E. E. 2013. The relative importance of predation risk and water temperature in maintaining Bergmann's rule in a marine ectotherm. *The American Naturalist*, 182: 347–358.
- Miller, R. J., and Watson, J. 1976. Growth per molt and limb regeneration in the spider crab, *Chionoecetes opilio*. *Journal of the Fisheries Research Board of Canada*, 33: 1644–1649.
- Muldowney, D., Morris, C., Dawe, E., Zagorsky, Y., and Goryanina, S. 2018. Dynamics of snow crab (*Chionoecetes opilio*) movement and migration along the Newfoundland and Labrador and Eastern Barents Sea continental shelves. *Reviews in Fish Biology and Fisheries*, 28: 435–459.
- Murphy, J. T. 2019. Patterns and implications of skip-molting for the Eastern Bering Sea snow and Tanner crab (*Chionoecetes opilio* and *C. bairdi*). *Fisheries Research*, 210: 63–70.
- Ohlberger, J. 2013. Climate warming and ectotherm body size—from individual physiology to community ecology. *Functional Ecology*, 27: 991–1001.
- Orensanz, J. M., Ernst, B., and Armstrong, D. A. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. *Journal of Crustacean Biology*, 27: 576–591.
- Ouellet, P., and Sainte-Marie, B. 2018. Vertical distribution of snow crab (*Chionoecetes opilio*) pelagic stages in the Gulf of St. Lawrence (Canada) and effect of temperature on development and survival. *ICES Journal of Marine Science*, 75: 773–784.
- Paul, J. M., Paul, A. J., and Barber, W. E. 1997. Reproductive biology and distribution of the snow crab from the northeastern Chukchi Sea. *American Fisheries Society Symposium*, 19: 287–294.
- Puebla, O., Sévigny, J.-M., Sainte-Marie, B., Brêthes, J.-C., Burmeister, A., Dawe, E. G., and Moriyasu, M. 2008. Population genetic structure of the snow crab (*Chionoecetes opilio*) at the Northwest Atlantic scale. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 425–436.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robichaud, D. A., Bailey, R. F. J., and Elner, R. W. 1989. Growth and distribution of snow crab, *Chionoecetes opilio*, in the southeastern Gulf of St. Lawrence. *Journal of Shellfish Research*, 8: 13–23.
- Ryer, C. H., Ottmar, M., Spencer, M., Anderson, J. D., and Cooper, D. 2016. Temperature-dependent growth of early juvenile southern Tanner crab *Chionoecetes bairdi*: implications for cold pool effects and climate change in the southeastern Bering Sea. *Journal of Shellfish Research*, 35: 259–267.
- Sainte-Marie, B., Dionne, H., and Alarie, M.-C. 2010. Temperature and age dependent fertile period in female snow crab (*Chionoecetes opilio*) at the maturity molt. *In* *Biology and Management of Exploited Crab Populations under Climate Change*, Alaska Sea Grant College Program Report No. 10-01, pp. 217–235. Ed. by G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby. University of Alaska Fairbanks, Fairbanks, AK.
- Sainte-Marie, B., Dufour, R., Bourassa, L., Chabot, D., Dionne, M., Gilbert, D., Rondeau, A. *et al.* 2005. Critères et proposition pour une définition des unités de production du crabe des neiges (*Chionoecetes opilio*) dans l'estuaire et le nord du golfe du Saint-Laurent. *Canadian Science Advisory Secretariat Research Document*, 2005/059. 20 pp.
- Sainte-Marie, B., and Gilbert, D. 1998. Possible effects of change in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence. *Canadian Stock Assessment Secretariat Research Document*, 98/38. 19 pp.
- Sainte-Marie, B., Gosselin, T., Sévigny, J.-M., and Urbani, N. 2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. *Bulletin of Marine Science*, 83: 131–161.
- Sainte-Marie, B., and Hazel, F. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 1282–1293.
- Sainte-Marie, B., and Lafrance, M. 2002. Growth and survival of recently settled snow crab *Chionoecetes opilio* in relation to intra- and intercohort competition and cannibalism: a laboratory study. *Marine Ecology Progress Series*, 244: 191–203.
- Sainte-Marie, B., Lapointe, V., Archambault, D., and Dufour, R. 1992. Distribution spatiale et structure de taille du crabe des neiges, *Chionoecetes opilio* (O. Fabricius), dans le fjord du Saguenay. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, 2156. 12 pp.
- Sainte-Marie, B., Raymond, S., and Brêthes, J.-C. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae). *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 903–924.
- Sainte-Marie, B., Sévigny, J.-M., Smith, B. D., and Lovrich, G. A. 1996. Recruitment variability in snow crab *Chionoecetes opilio*: pattern, possible causes, and implications for fishery management. *In* *High Latitude Crabs: Biology, Management, and Economics*, Alaska Sea Grant College Program Report No. 96-02, pp. 451–478. University of Alaska Fairbanks, Fairbanks, AK.
- Somerton, D. A. 1981. Regional variation in the size of maturity of two species of Tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 163–174.
- Szuwalski, C., and Punt, A. E. 2013. Regime shifts and recruitment dynamics of snow crab, *Chionoecetes opilio*, in the eastern Bering Sea. *Fisheries Oceanography*, 22: 345–354.
- Tremblay, J. M. 1997. Snow crab (*Chionoecetes opilio*) distribution limits and abundance trends on the Scotian Shelf. *Journal of Northwest Atlantic Fishery Science*, 21: 7–22.
- van der Have, T. M., and de Jong, G. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. *Journal of Theoretical Biology*, 183: 329–340.
- van Voorhies, W. A. 1996. Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution*, 50: 1259–1264.
- Venables, W. N., and Ripley, B. D. 2002. *Modern Applied Statistics with S*. 4th edn. Springer, New-York.
- Walters, R. J., and Hassall, M. 2006. The temperature-size rule in ectotherms: may a general explanation exist after all? *The American Naturalist*, 167: 510–523.
- Watson, J. 1970. Maturity, mating, and egg laying in the crab, *Chionoecetes opilio*. *Journal of the Fisheries Research Board of Canada*, 27: 1607–1616.
- Webb, J. B., Eckert, G. L., Shirley, T. C., and Tamone, S. L. 2006. Changes in zoeae of the snow crab, *Chionoecetes opilio*, with variation in incubation temperature. *Journal of Experimental Marine Biology and Ecology*, 339: 96–103.
- Weiss, M., Thatje, S., and Heilmayer, O. 2010. Temperature effects on zoeal morphometric traits and intraspecific variability in the hairy crab *Cancer setosus* across latitude. *Helgolander Marine Research*, 64: 125–133.
- Yamamoto, T., Yamada, T., Kinoshita, T., Ueda, Y., Fujimoto, H., Yamasaki, A., and Hamasaki, K. 2015a. Effects of temperature on growth of juvenile snow crabs, *Chionoecetes opilio*, in the laboratory. *Journal of Crustacean Biology*, 35: 140–148.
- Yamamoto, T., Yamada, T., Kinoshita, T., Ueda, Y., Fujimoto, H., Yamasaki, A., and Hamasaki, K. 2015b. Growth and moulting of

- wild-born immature snow crabs, *Chionoecetes opilio* (Fabricius, 1788) (Decapoda, Majoidea), in the laboratory. *Crustaceana*, 88: 911–922.
- Yamamoto, T., Yamada, T., Kinoshita, T., Ueda, Y., Yamasaki, A., and Hamasaki, K. 2018. Moulting and growth in earlier and later moulters of adolescent male snow crabs (*Chionoecetes opilio*) (Brachyura: Majoidea) under laboratory conditions. *Invertebrate Reproduction and Development*, 62: 49–55.
- Zuo, W., Moses, M. E., West, G. B., Hou, C., and Brown, J. H. 2012. A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society B*, 279: 1840–1846.

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