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# Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland

**AnnDorte Burmeister · Bernard Sainte-Marie**

**Abstract** Geographic variation in size of male and female snow crabs (*Chionoecetes opilio*) was investigated along the west coast of Greenland to test the hypothesis that size at terminal molt (=adulthood) is temperature dependent. A total of 81,490 snow crabs were collected in small-mesh traps in Disko Bay (68–69°N) and six sites near Sisimiut (66–67°N) in May and June from 2000 to 2005. Average bottom temperature over the study period ranged from −0.8 to 3.2°C across the sampling sites. Mean carapace width was positively correlated with temperature in both sexes, a pattern often described as a converse Jame's cline. We infer that temperature per se is the causative factor and discount season length, food availability or density as ultimate causes of the cline. Temperature effects on body size of crabs apparently result from a change in the number of instars before terminal molt. This interpretation is supported by size frequency analysis showing that in general crabs were larger at instar in a colder than in a warmer site. We briefly discuss the implications of our findings for population reproductive potential and the effectiveness of a fixed legal size limit in protecting some adult males from exploitation at different temperature regimes.

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## Introduction

Bergmann's rule originally described the positive relationship between final body size of mammal species and latitude. This denomination was later extended to accommodate a similar supraspecific pattern in terrestrial ectotherms (Ray 1960; Ashton 2001) and an intraspecific pattern in both endo- and ectotherms whereby maximum size of individuals in populations increases with latitude, which Blackburn et al. (1999) proposed to rename as Jame's rule. As evidence accumulated that these patterns were widespread, laboratory experiments demonstrated that many terrestrial ectotherms matured at a larger size at colder temperatures, despite a reduction in growth and development rates, and this pattern was coined the developmental temperature-size rule (Atkinson and Sibly 1997). Temperature is thought to be the ultimate cause of the positive latitudinal (and altitudinal) clines in body size seen in many terrestrial ectotherms, but the debate continues about whether this phenotypic response is adaptive, e.g., for heat conservation or starvation resistance, or simply represents a byproduct of constraints on cell division that result in larger cells and hence larger individuals at cooler temperatures (Atkinson and Sibly 1997).

In contrast to the above, a smaller number of individual species or higher level taxa among terrestrial ectotherms exhibit a pattern of decreasing size with latitude (or

altitude) known as converse or inverse Bergmann/Jame's clines (Blanckenhorn and Demont 2004). The general consensus is that this phenotypic response is a season length effect and in arthropods specifically it may be more common in larger than in smaller species (Blanckenhorn and Demont 2004). Some taxa have apparently compensated the season length effect by evolving faster growth rates and show no change in size with latitude, a pattern called countergradient variation (Conover and Present 1990).

The marine environment is different from the terrestrial realm where direct or inverse Bergmann/Jame's clines were initially observed. Temperature in the sea is less variable across latitudinal or depth gradients and never descends much below 0°C; however, oxygen concentration generally decreases with increasing depth and decreasing latitude (i.e., increasing temperature). Season length is less likely to impact marine predatory ectotherms in the way or to the extent it does terrestrial ones because food may be accessible (although seasonally rarefied) and growth possible year-round irrespective of latitude. The highly diversified and widely distributed marine crustaceans may be a good group for testing the universality of factors controlling clines in body size (Chapelle and Peck 1999). Bergmann/Jame's clines have been demonstrated in some marine amphipods and crustacean decapods (Steele 1988; Sainte-Marie 1991; Poulin and Hamilton 1995; Timofeev 2001). Moreover, both Jame's cline and its converse exist in marine decapod crustaceans (e.g., Hines 1989; Contreras and Jaramillo 2003) and in the mole crab *Emerita brasiliensis* the pattern is divergent between the sexes (Defeo and Cardoso 2004) leading to a cline in sexual size dimorphism (SSD). However, this species is known for its complex and flexible life history, with alternative developmental pathways including neotenic males and possibly protandry (Delgado and Defeo 2006), which may confound spatial patterns of size at maturity. Latitudinal clines in body size of marine decapod crustaceans have most often been examined in only one sex (usually females) and/or at a limited number of sampling locales (sometimes only two).

The snow crab (*Chionoecetes opilio* O. Fabricius; Brachyura, Majoidea) is widely distributed and extensively fished in the Japan, Okhotsk and Bering seas and in the Northwest Atlantic (Jadamec et al. 1999), and was recently found in the Barents Sea (Kuzmin et al. 1998; Alvsvag et al. 2009). The carnivorous snow crab mainly inhabits muddy or sandy mud grounds at depths from 30 to 1400 m, where bottom temperature ranges from −1.5 to 4°C year round (e.g., Squires 1990; Dawe and Colbourne 2002). Snow crab may be physiologically constrained to low temperatures, as its energy budget becomes negative above 4–5°C due to reduced feeding and rising metabolic costs (Foyle et al. 1989; Thompson and Hawryluk 1990). Despite its association with cold water, snow crab is considered to be an arctic-boreal species because it does not usually extend north of the Arctic Circle (Squires 1990), although exceptions exist in the Pacific and Atlantic (Paul et al. 1997; Burmeister 2002). The most northerly record for snow crab is from Greenland, where the species is distributed along the west coast from 60° to 74°N in both offshore and inshore (fjord) locations (Burmeister 2002).

Snow crab has a terminal moult, at which full development of secondary sexual characters in females (Ito and Kobayashi 1967) and males occurs (Conan and Comeau 1986); individuals are considered adult after this last moult. The final size after terminal moult is notoriously variable within and among populations of snow crab. Uncovering the factors that determine the onset of terminal moult is essential for managing snow crab (e.g., Bailey and Elner 1989; Comeau and Conan 1992; Sainte-Marie et al. 1995). Typically, terminal moult is reached by most females in one of two successive instars and by most males in one of 4–5 successive instars (Ito 1970; Kon 1980; Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998).

Investigations on snow crab and its congener the Tanner crab (*Chionoecetes bairdi*) in the Bering Sea found that mean size of adult females is inversely related to latitude and directly related to mean bottom temperature (Somerton 1981). Near-bottom temperature fields may guide the spatial distribution of various snow crab life history stages and size categories across the vast shelf domains of the Eastern Bering Sea during ontogenetic migration (Ernst et al. 2005). However, Orensanz et al. (2007) concluded that clinal variation in female adult size primarily reflected a phenotypic response to temperature that was controlled by a single reaction norm. A similar positive relationship between female adult size and temperature exists for snow crab in the northern Gulf of St. Lawrence (Sainte-Marie and Gilbert 1998) and it was proposed that size of adult males may also change with temperature (op. cit., Alunno-Bruscia and Sainte-Marie 1998). Temperature effects may be more difficult to discern in males because they are highly mobile and perform extensive annual mating runs (Lovrich et al. 1995), and because intense male-only fishing can truncate their size frequency distributions (Sainte-Marie and Gilbert 1998).

The Greenland coastal system of fjords and basins provides a very interesting opportunity for investigating the effects of latitude and temperature on size at terminal moult in snow crab. Fjord populations of snow crab in the benthic phase are partially or completely isolated from one another and from offshore populations by sills (Burmeister, unpublished tagging data). Here, we compare adult body size of snow crabs across seven localities along the west coast of Greenland and document a direct relationship between adult size and temperature in both sexes. We

develop predictive relationships for the temperature effect and contrast them between the sexes. A proximate mechanism of variability in adult size across localities is proposed. Finally, we conclude by briefly exploring some of the consequences of temperature-based variability of adult size for conservation of the snow crab resource in a climate change perspective.

## Materials and methods

### Study sites

The study sites on the west coast of Greenland (Fig. 1) are Disko Bay (69°14′N, 53°19′W), four fjords near Sisimiut (Amerloq 66°54′N, 53°22′W; Ikertooq 66°45′N, 53°33′W; Kangerluarsuk 66°41′N, 53°21′W; Itilleq 66°32′N, 53°25′W), an area off the mouth of the fjords called Uden for Fjorden Inden for Basis linien (UF, 66°49′N, 53°49′W) and Holsteinsborg Depth (66°38′N, 54°13′W). The deep, silty bottoms account for most if not all of snow crab habitat in the fjords, because their steep sides offer comparatively little surface area and usually are composed of bedrock, which is less hospitable to snow crab.

The topography of Disko Bay is very complex; a system of banks and trenches combined with a maximum sill depth of 300 m at its mouth partially limit exchange of bottom water with offshore areas. The upper water layer in Disko Bay is influenced by atmospheric conditions so that winter convection extends to ≈150 m depth in cold years when and where the Bay is covered by ice. The bottom water layer consists of a mixture of water of Polar and Atlantic

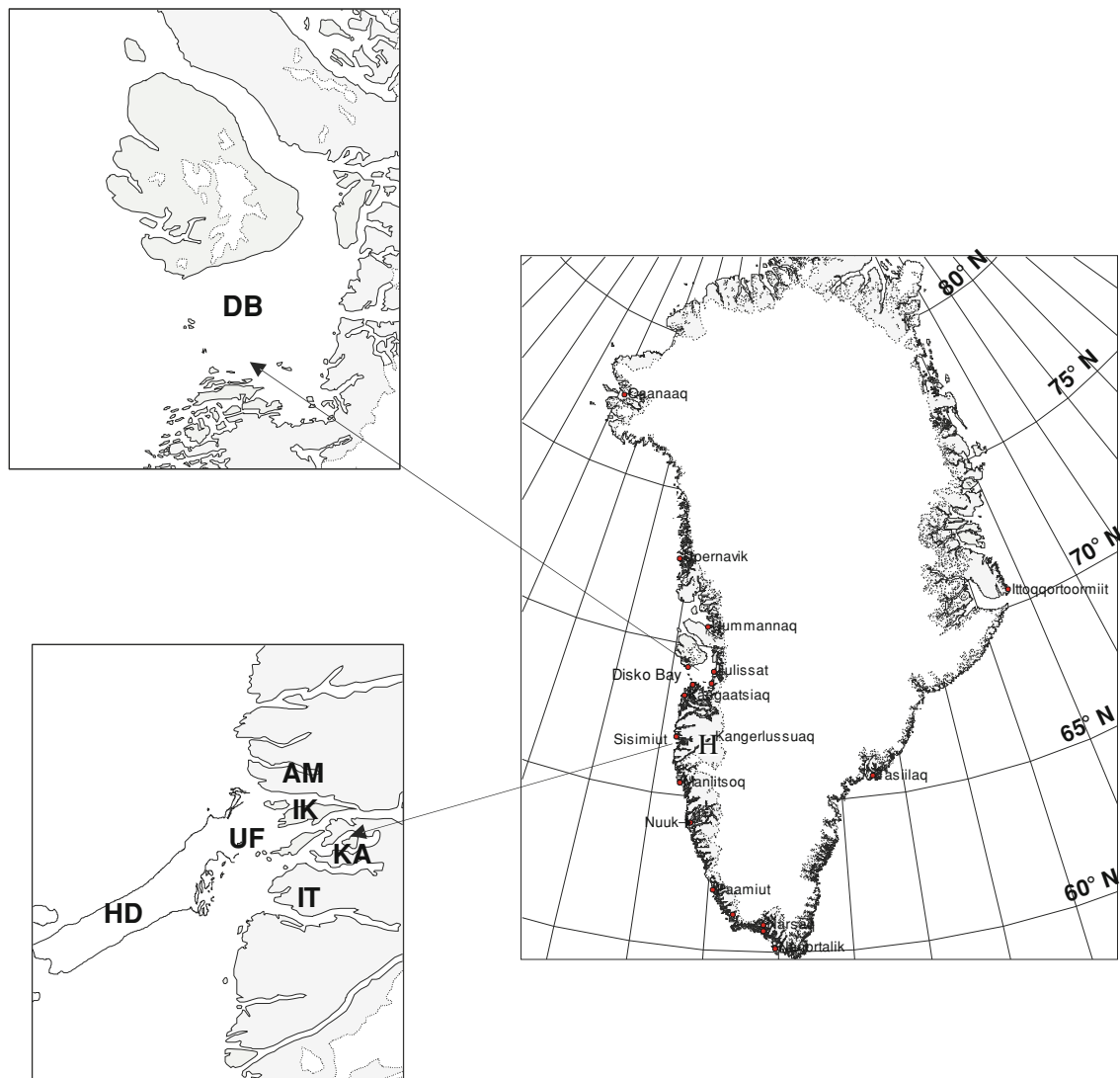

**Fig. 1** Location of sampling sites in Greenland: Disko Bay (DB); fjords near Sisimiut are Amerloq (AM), Ikertooq (IK), Kangerluarsuk (KA), Itilleq (IT); inshore area outside the fjords (UF) and Holsteinsborg Dyb (HD)

origin that is renewed once a year during fall and early winter due to increased flow of the west Greenland current (Buch 1990/2000).

The fjords south of Sisimiut are of two different types. Amerloq and Ikertooq have a deep sill at 150–180 m, whereas Kangerluarsuk has a shallow sill at 50 m and Itilleq an intermediate sill at $\approx 100$ m. The hydrographical conditions in the fjords are to a large extent determined by freshwater runoff from land, more saline water inflow near the bottom at the mouth of the fjord, and winter cooling and convection. None of the fjords is directly connected to the ice sheet (Ribergaard 2007). The depth of the fjord sill greatly affects temperature and salinity conditions. Fjords with a deep sill allow penetration of warm, salty Irminger and sub-Atlantic water, which remains denser than Coastal Polar Water, thereby preventing winter convection of bottom water (Ribergaard and Buch 2003). In contrast, fjords with a shallow sill are mostly filled with colder Coastal Polar Water and exhibit more homogeneous temperature and salinity properties with depth throughout the year, in particular during the winter, when convection fully mixes and cools the whole water column (Mads Hvid Ribergaard, DMI, Denmark, personal communication).

## Sampling

Snow crab was sampled in Disko Bay in late May from 2000 to 2005, and in the four fjords, UF and Holsteinsborg Dyb during June from 2000 to 2005. Crabs were collected with Japanese traps, fitted with either coarse (140-mm stretched mesh) or fine (42-mm stretched mesh) netting, during regular surveys by the Greenland Institute of Natural Resources. Traps were each baited with four squid, *Illex argentinus*, and soaked for 24 h on average over a range of depths (Table 1). Bottom temperature was measured using Starmon-mini underwater temperature recorders (Star-Oddi Marine Device Manufacturing, Iceland)

attached to traps. Salinity measurements came from oceanographic investigations conducted in 2000–2006 by the Danish Meteorological Institute (Ribergaard and Buch 2003; Ribergaard 2007). Additionally, a 3-m beam trawl with 17-mm stretched mesh in the codend was used to collect snow crab in Kangerluarsuk and a neighboring cold fjord, Eqaluit Paarliit.

Crabs were sorted by sex and ascribed a shell condition (SC) following criteria in Fonseca et al. (2008). Various linear measurements were taken on crabs with a vernier calliper to the nearest 0.01 mm: carapace width (CW) of females and males, abdomen width (AW) across the fifth pleonite for females, and chela height excluding spines for males (CH). Females were categorized as preadult (includes immature, prepubescent and pubescent females, see Alunno-Bruscia and Sainte-Marie 1998) or adult (=terminally moulted) based on the shape and width of the abdomen relative to CW. Adult females were further divided into two categories: primiparous had a clean soft (SC1) or a clean hard (SC2) shell and no mating scars on their legs; multiparous had an intermediate (SC3), dirty hard (SC4) or dirty soft (SC5) shell and mating scars.

## Data analysis

Maturity of males was determined a posteriori on the basis of chela allometry (Conan and Comeau 1986). Following the terminology and size limits of Sainte-Marie et al. (1995), all males <35 mm CW were considered to be immature and males ≥35 mm CW with small chelae relative to carapace were considered to be adolescent, whereas males ≥35 mm CW with relatively large chelae were adult (=terminally moulted). Discrimination of adolescent and adult males was done by a new, assumption-free method based on simple trigonometry and minimization procedures (Burmeister, in preparation) and results were cross-checked using Somerton's (1980) classic method.

**Table 1** Depths for trap deployment, average temperature and catch rate (number of crabs per trap haul) of male and female adult snow crabs at sampling sites along the west coast of Greenland over the period 2000–2005

| Sampling sites | Trap hauls | Temperature (°C) | Depth (m) | | Mean ± SD per trap | |
| | ♂ (♀) | Mean ± SD | Mean ± SD | Range | ♂ | ♀ |
|---|---|---|---|---|---|---|
| Disko Bay (DB) | 1,608 (168) | 2.8 ± 0.6 | 353 ± 120 | 44–707 | 7.4 ± 5.0 | 17.8 ± 13.4 |
| Amerloq (AM) | 408 (68) | 1.9 ± 0.5 | 353 ± 138 | 160–620 | 7.9 ± 7.3 | 38.6 ± 65.2 |
| Ikertooq (IK) | 600 (100) | 1.6 ± 0.7 | 240 ± 76 | 90–424 | 8.1 ± 6.4 | 23.7 ± 53.9 |
| Kangerluarsuk (KA) | 360 (60) | −0.2 ± 0.4 | 228 ± 48 | 139–314 | 11.0 ± 5.0 | 43.1 ± 42.5 |
| Itilleq (IT) | 420 (70) | 0.5 ± 0.6 | 357 ± 83 | 192–476 | 10.0 ± 4.7 | 15.1 ± 18.5 |
| Area at mouth of fjords (UF) | 888 (148) | 1.8 ± 07 | 211 ± 87 | 66–421 | 7.3 ± 11.2 | 15.1 ± 29.7 |
| Holsteinsborg Dyb (HD) | 1,008 (168) | 2.6 ± 0.4 | 315 ± 64 | 199–420 | 3.8 ± 4.0 | 5.7 ± 12.7 |

Number of trap hauls used for calculating catch rate is shown: all traps for males, only small-mesh traps for females

SD standard deviation

We described temperature and salinity at a given site as the annual mean of all measurements in a given year or as the overall mean, standard deviation (SD) and coefficient of variation (CV) of annual means. We compared catch rate (i.e., number of crabs per trap haul), as a rough index of population density, for adult males and adult females across sites by ANOVA. For females, Levene's test indicated heterogeneity of variances ($P < 0.001$) so we performed a Welch ANOVA (Sokal and Rolf 1995). Catch rates were based on all small- and large-mesh trap hauls for males, but only on small-mesh trap hauls for females. For each site and year, we described size of crabs by year using the median and expressed extremes as the 1% (Q1%) and 99% (Q99%) quantiles of CW distributions of adult females and males. CW median, Q1% and Q99% are based on data from all traps for males and only small-mesh traps for females. Quantiles were used instead of the actual minimum and maximum values as a check against measurement and classification errors. To summarize size data, we calculated the mean, SD and CV of annual median values of CW by site. We examined SSD using the Lovich and Gibbons (1992) index:

$$1 - \frac{(\overline{\text{median CW}})_{\text{males}}}{(\overline{\text{median CW}})_{\text{females}}}.$$

Least squares (Model I) linear regression was used to test for relationships between the mean of median CW or SSD and overall mean temperature by site, and between CW Q1% or Q99% and CW median across sites and years. Simple linear regression analysis was also performed on ln-transformed data to assess if rate of change of median CW was proportional (isometry: expected slope = 1) to temperature and if it increased at the same rate in females and males. We tested for departures from isometry with a Student's $t$ test and for homogeneity of slopes by analysis of covariance (Sokal and Rolf 1995). We explored possible density-dependent effects on female adult size using simple regression with catch rates and multiple linear regression, combining temperature and catch rates simultaneously. Females were chosen over males because their numbers are presumably unaffected by fishing, whereas male numbers are reduced in fished localities. Fishing intensity is greatest in Holsteinsborg Dyb and Disko Bay (Burmeister and Siegstad 2008).

We constructed size frequency distributions (SFD) to resolve mean CW and proportion of individuals by instar for the two sampling sites (Kangerluarsuk and Disko Bay) that offered the combination of largest sample sizes and greatest difference in median CW at terminal moult. For a better representation of smaller versus larger crabs in SFDs, we used only data from the small-meshed traps. CWs were binned in size classes of 1.5 mm for males and

1.0 mm for females. Modes in histograms were resolved using mixture distribution analysis with MIX version 3.3 (MacDonald and Pitcher 1979). In males, we were able to resolve modes (instars) for adolescents >40 mm CW in the composite SFD from all sampling years but unable to do so for adults. In females, we resolved modes for preadults >20 mm CW and for primiparous adult females from selected years in which they were well represented (2004 and 2005 for Kangerluarsuk; 2000, 2001 and 2005 for Disko Bay). Resolution of modes for adult snow crabs is difficult, especially for males, because successive adult modes are poorly differentiated due to size differential probability of terminal moult across and within instars (i.e., larger females in an instar are more likely than smaller females to become mature at next moult, see Alunno-Bruscia and Sainte-Marie 1998) and/or to compounded variability from the accumulation of up to at least seven different year classes (Fonseca et al. 2008). Adjustment of modes to SFDs was guided by visual examination of raw and modeled SFDs, and $\chi^2$ test statistics. The analyses were constrained and instar numbers were attributed to modes based on prior knowledge of the range of values of mean CW and SD at instar for localities where the suite of instars from settlement to adulthood is partly or completely documented (Ito 1970; Kon 1980; Robichaud et al. 1989; Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998). Size at instar appears to be conservative for snow crab across a variety of habitats, i.e., differences in mean CW at instar $x$ are less between populations than differences in mean CW between instar $x$ and instar $x - 1$ or $x + 1$ within populations (Sainte-Marie et al. 1995, see Fig. 11 in Orensanz et al. 2007) and pre-adult instar structure is not blurred when crab sizes are integrated over large temporal and spatial scales (see Chabot et al. 2008). Modal analysis of SFDs for small crabs trawled in Kangerluarsuk served to reinforce our interpretation of instar structure. A Student's $t$ test compared mean CW at instar between sites or gears.

## Results

### Temperature, salinity and crab catch rates

The study sites differed much more in temperature than in salinity over the period 2000–2005. In the cold Kangerluarsuk and Itilleq fjords, mean bottom temperature varied annually from $-1.8$ to $+0.5°C$ and from $-0.5$ to $+1.3°C$, respectively, and salinity varied only from 33.6 to 33.7‰. In the warm Amerloq and Ikertooq fjords, mean bottom temperature varied annually from 1.0 to 2.5°C and salinity was constant at 34.2‰. In UF and Holsteinsborg Dyb, mean bottom temperature varied annually from 1.6 to

2.2°C and 2.3 to 2.8°C, respectively, and salinity was constant at 34.8‰. Finally, in Disko Bay, mean bottom temperature varied annually from 2.2 to 3.7°C and bottom salinity ranged only around 34.4–34.6‰. The coefficient of variation of mean temperature across the years was largest in Ikertooq (43.3%) and smallest in Holsteinsborg Dyb (14.8%) and Disko Bay (23.6%).

A total of 25,207 immature/adolescent males, 38,418 adult males, 3052 preadult females and 14,813 adult females were collected over all sites from 2000 to 2005. Mean catch rate (Table 1) varied across sites from 3.8 to 11.0 adult males per trap and from 5.7 to 43.1 adult females per trap; in both cases there was significant variability across sites (ANOVA, $F = 8.06$, $P < 0.001$ and Welch ANOVA $F = 6.20$, $P < 0.001$; respectively).

Size of adult crabs

The mean of annual values of adult median CW ranged from a low of 61.9 mm for females and 94.7 mm for males in Kangerluarsuk to a high of 72.8 mm for females and 117.8 mm for males in Holsteinsborg Dyb. Note that the largest adult female in our samples measured 103.5 mm CW, a verified value. The coefficient of variation for the mean of annual median CW was similar across sites and ranged from 8 to 12% for females and from 8 to 16% for males, with no clear pattern relative to mean temperature. Although median CW varied across sites, no latitudinal or longitudinal cline was apparent in either males or females. Adult median CW and mean temperature were significantly and positively correlated for both sexes (Fig. 2). The mean of median CW for adult females was unrelated to mean catch rate (CPUE) in simple linear regression ($F = 2.16$, $P = 0.201$) or in multiple linear regression with temperature ($T$) as an additional independent variable:

$$CW = -0.01\ CPUE + 3.48T + 62.92;\ F = 10.72,$$
$$P = 0.025;\ t_{CPUE} = -0.14,\ P = 0.897;$$
$$t_T = 3.71,\ P = 0.021.$$

The relationship between male and female adult size and temperature was further explored through simple linear regression analysis of annual values of Q1%, median and Q99% CW against temperature, after ln-transformation of data (Table 2). All regressions were positive and significant, but slope coefficients were much smaller than, and statistically different, from 1 (Student's $t$ test, $t > 4.30$ and $P < 0.001$ in all cases) indicating that CW did not increase proportionately to temperature. Slopes did not differ between females and males for CW Q1% (ANOVA, $F = 0.84$, $P = 0.363$) and median (ANOVA, $F = 0.19$, $P = 0.661$), however, CW Q99% increased more steeply in females than in males with increasing temperature
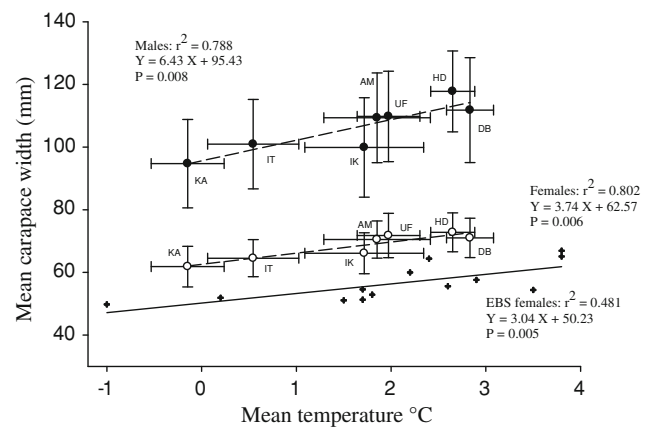


**Fig. 2** Relation between median carapace width (annual mean ± 1SD) and temperature (annual mean ± 1SD) at seven sites along the west coast of Greenland (see site abbreviations in Fig. 1) sampled from 2000 to 2005. Greenland adult males (*filled circle*) and females (*open circle*); Eastern Bering Sea (EBS) adult females (*plus symbol*)

**Table 2** Simple linear regression of natural logarithm of annual values of 1% (Q1%), 99% (Q99%) and 50% (median) quantiles of carapace width (CW, in mm) for male and female adult snow crab against the ln of mean temperature (+2, to make values positive) for seven sites sampled along the west coast of Greenland from 2000 to 2005

| Sex and simple linear regressions |
|---|
| **Adult males** |
| $\ln(CW_{Q1\%}) = 0.20 \ln(T + 2) + 4.00,\ r^2 = 0.606,\ P < 0.001$ |
| $\ln(CW_{Q99\%}) = 0.06 \ln(T + 2) + 4.85,\ r^2 = 0.562,\ P < 0.001$ |
| $\ln(CW_{median}) = 0.16 \ln(T + 2) + 4.46,\ r^2 = 0.531,\ P < 0.001$ |
| **Adult females** |
| $\ln(CW_{Q1\%}) = 0.16 \ln(T + 2) + 3.81,\ r^2 = 0.752,\ P < 0.001$ |
| $\ln(CW_{Q99\%}) = 0.12 \ln(T + 2) + 4.30,\ r^2 = 0.660,\ P < 0.001$ |
| $\ln(CW_{median}) = 0.15 \ln(T + 2) + 4.04,\ r^2 = 0.811,\ P < 0.001$ |

$N$ is 35 in all cases

(slopes 0.06 vs. 0.12, respectively; ANOVA, $F = 5.906$, $P = 0.017$). The index of SSD was always biased to males (mean SSD $= -0.55$) and was not correlated with temperature (Pearson correlation, $r = 0.47$, $P > 0.05$).

For adult males (Fig. 3) and adult females (Fig. 4) both CW Q1% and Q99% increased with increasing median CW. In both sexes, the relationship was isometric for CW Q1% (Student's $t$ test, $t \leq 0.11$, $P > 0.05$) but not for CW Q99% where the slopes were 0.35 and 0.79 for males and females, respectively, and significantly different from 1 (Student's $t$ test, $|t| \geq 13.00$, $P < 0.001$) in both cases. The sexes had similar slopes for the relationship of Q1% on median CW (ANOVA, $F = 0.05$, $P = 0.826$) but not for the relationship of Q99% on median CW (ANOVA, $F = 21.36$, $P < 0.001$). A scatterplot illustrating the relationship between median CW of males and females (Fig. 5)
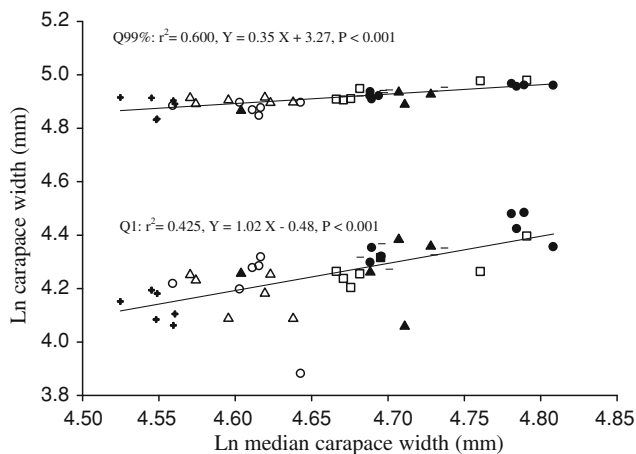
**Fig. 3** Natural logarithm (ln) of 1 and 99% quantiles of carapace width (CW) in relation to ln median CW of adult male snow crab by sampling site along the west coast of Greenland (*plus symbol* Kangerluarsuk, *open triangle* Ikertooq, *open circle* Itilleq, *filled triangle* Amerloq, *open square* Disko Bay, *minus symbol* inshore area outside the fjords, *filled circle* Holsteinsborg Dyb). Each site is represented by six data points representing annual medians for samples collected from 2000 to 2005
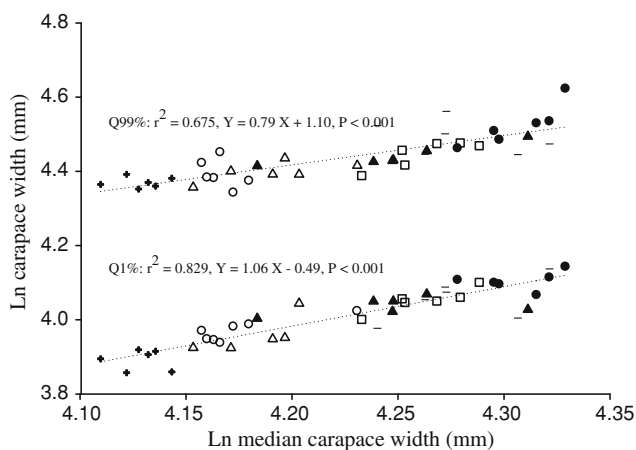


**Fig. 4** Natural logarithm (ln) of 1 and 99% quantiles of carapace width (CW) in relation to ln median CW of adult female snow crab by sampling site along the west coast of Greenland (*plus symbol* Kangerluarsuk, *open triangle* Ikertooq, *open circle* Itilleq, *filled triangle* Amerloq, *open square* Disko Bay, *minus symbol* inshore area outside the fjords, *filled circle* Holsteinsborg Dyb). Each site is represented by six data points representing the annual medians for samples collected from 2000 to 2005

demonstrates a strong positive relationship, suggesting again that both sexes are responding in a similar way to a common factor.

### Size frequency distributions

Few males and females captured in traps were smaller than 40 and 20 mm CW, respectively. Size frequency distributions (SFD) for adolescent males and preadult and adult
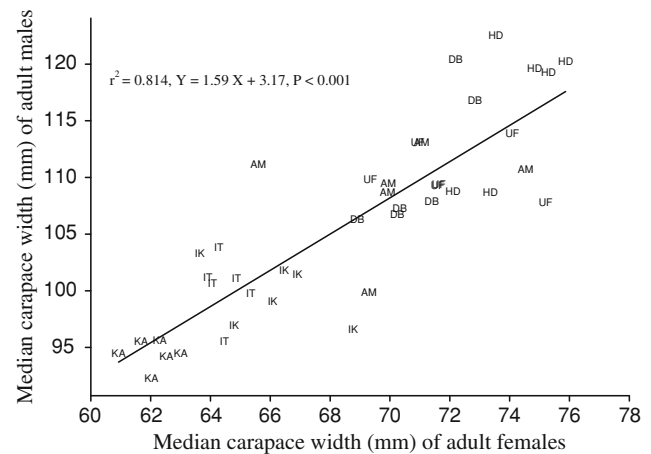
**Fig. 5** Relation between median carapace width (MCW) of adult males and MCW of adult females by sampling site along the west coast of Greenland. Each site is represented by six data points representing the annual medians for samples collected from 2000 to 2005. Refer to Fig. 1 for site abbreviations

females from Disko Bay and Kangerluarsuk are shown in Fig. 6. In Disko Bay, the SFD of adolescent males revealed four outstanding modes and a fifth small mode could be discerned; these modes were designated instars IX–XIII. The SFD of preadult females showed four clear modes designated instars VIII–XI. In Kangerluarsuk, three modes were obvious in the SFD of adolescent males and these were designated instars IX–XI. Preadult females showed six clear modes designated instars VI and VIII–X and two other modes designated XI and XII could be discerned. SFD for adult females were comparatively featureless and appeared to be almost unimodal, especially in Disko Bay, although one or two additional smaller modes could be inferred to the right of the SFDs.

The mixture distribution models that maximized the log-likelihood $\chi^2$ value while providing biologically plausible results based on trap data are shown in Table 3. These models resolved one small additional mode in each of the SFDs of Disko Bay preadult females (instar XII), Kangerluarsuk adolescent males (instar XII) and Kangerluarsuk preadult females (instar VII). For adult females, using only the constraint that SD be consistent with well-grounded observations elsewhere (Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998), we resolved several instars whose composite distribution approximated normality. In general crabs were somewhat larger at instar in Kangerluarsuk compared to Disko Bay (Table 3). Notable exceptions to the trend of larger size at instar occurred for female preadult instars X–XII. A Student's *t* test detected a significant difference in mean CW at instar between the two sites for adolescent males at instars IX, X and XI, and for preadult females at instar X (Table 3).

**Fig. 6** Size frequency distribution (SFD) of immature/adolescent males (**a, d**) and preadult (**b, e**) and adult primiparous (**c, f**) females from Disko Bay and Kangerluarsuk. *Gray dashed line* represents raw data, *thin black line* represents individual modes (instars indicated by roman numerals) adjusted by mixture distribution analysis, and *heavy black line* represents composite distribution of adjusted modes. SFDs for immature/adolescent males and preadult females are based on pooled data from 2000 to 2005; SFDS for primiparous females are based on pooled data from 2000, 2001 and 2005 in Disko Bay, and 2004 and 2005 in Kangerluarsuk
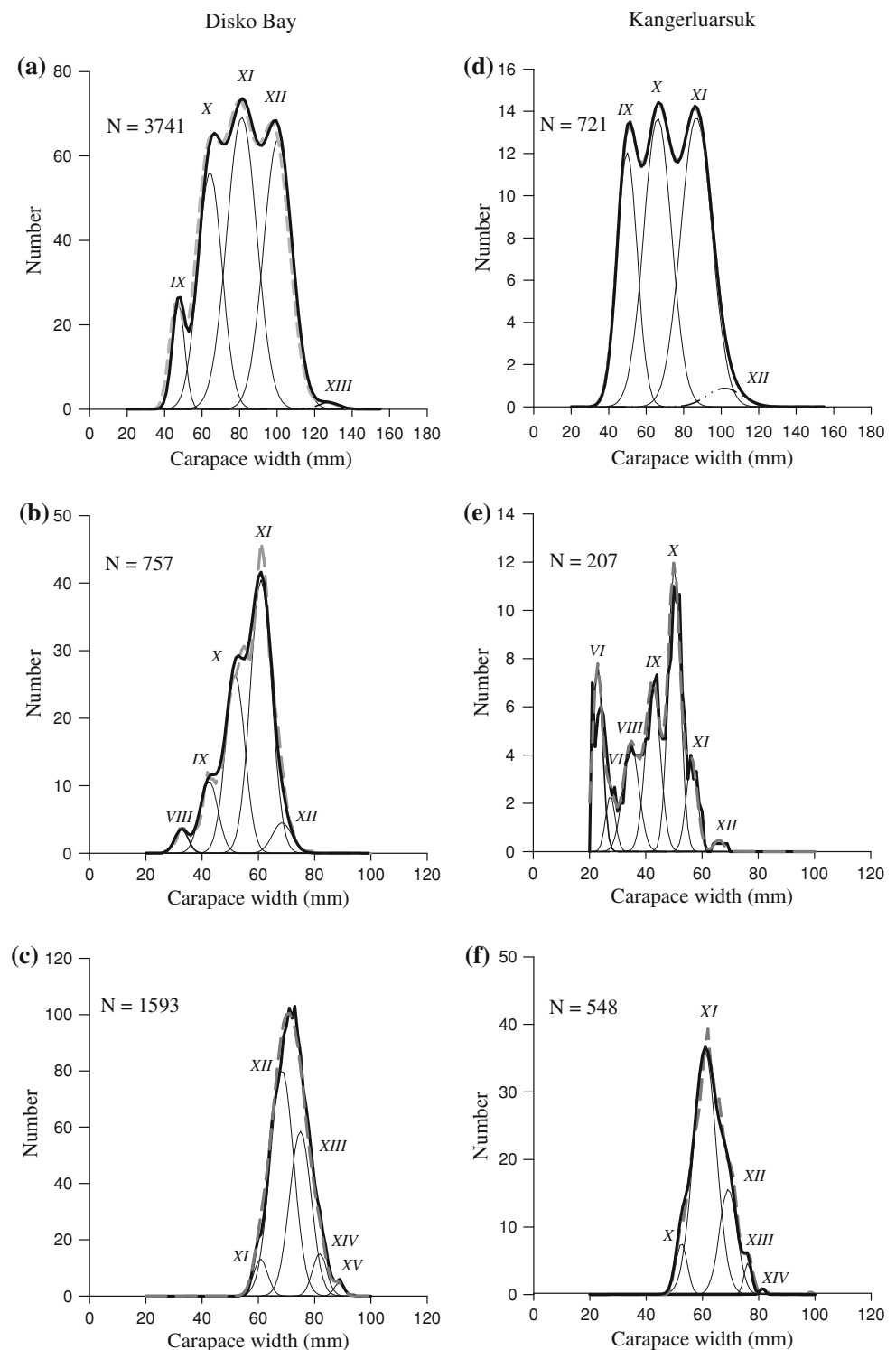


The range of five instars for female adulthood was shifted one instar down in Kangerluarsuk (instars X–XIV) compared to Disko Bay (instars XI–XV). The vast majority of females at each site reached adulthood in one of two successive instars: 87.6% of adult females belonged to instar XI or XII in Kangerluarsuk compared to 89.8% to instar XII or XIII in Disko Bay (Table 3). At each site, the distribution of females was biased toward the first of the two predominant instars and more heavily so in Kangerluarsuk (67.5% in instar XI) than in Disko Bay (52.3% in instar XII). The onset of terminal moult at a lower instar and the stronger proportional bias toward

**Table 3** Mean and standard deviation (SD) of carapace width (CW, in mm) at instar and proportion of individuals by instar for immature/adolescent males, and preadult and adult (primiparous) females of snow crab from Disko Bay (DB) and Kangerluarsuk (KA)

| Instar | Disko Bay | | | Kangerluarsuk | | | Student's $t$ test |
|---|---|---|---|---|---|---|---|
| | % | Mean CW | SD | % | Mean CW | SD | |
| Preadult males | | | | | | | |
| IX | 5.6 | 45.9 | 0.1 | 22.3 | 44.9 | 6.9 | −8.2* |
| X | 24.1 | 62.7 | 3.3 | 35.5 | 66.1 | 13.4 | −6.9* |
| XI | 37.0 | 79.7 | 6.2 | 39.5 | 86.8 | 11.8 | −14.1* |
| XII | 32.7 | 96.0 | 29.5 | 2.8 | 101.7 | 13.9 | −0.9 ns |
| XIII | 0.6 | 126.0 | 0.01 | – | – | – | – |
| | $\chi^2 = 14.81$, $P = 1.00$, $df = 64$ | | | $\chi^2 = 16.58$, $P = 1.00$, $df = 57$ | | | |
| Preadult females | | | | | | | |
| VI | – | – | – | 16.7 | 22.9 | 2.2 | – |
| VII | – | – | – | 4.7 | 27.5 | 3.8 | – |
| VIII | 2.8 | 32.7 | 3.0 | 15.3 | 34.8 | 5.0 | −1.7 ns |
| IX | 11.3 | 42.5 | 5.1 | 22.1 | 42.6 | 4.5 | −0.1 ns |
| X | 30.2 | 51.8 | 6.0 | 31.0 | 50.2 | 3.2 | 2.4* |
| XI | 50.6 | 61.0 | 5.4 | 9.2 | 56.4 | 2.7 | −0.1 ns |
| XII | 5.1 | 68.5 | 5.0 | 1.0 | 66.0 | 1.9 | −1.3 ns |
| | $\chi^2 = 5.52$, $P = 1.00$, $df = 54$ | | | $\chi^2 = 10.89$, $P = 1.00$, $df = 43$ | | | |
| Adult females | | | | | | | |
| X | – | – | – | 7.0 | 52.6 | 3.1 | – |
| XI | 5.2 | 60.8 | 4.6 | 67.5 | 60.9 | 5.6 | −0.1 ns |
| XII | 52.3 | 68.4 | 6.5 | 22.3 | 69.2 | 5.1 | ns |
| XIII | 35.3 | 75.0 | 6.4 | 2.4 | 76.1 | 1.9 | ns |
| XIV | 6.1 | 81.8 | 4.7 | 0.4 | 81.5 | 1.2 | ns |
| XV | 1.2 | 88.6 | 2.3 | – | – | – | – |
| | $\chi^2 = 6.71$, $P = 1.00$, $df = 38$ | | | $\chi^2 = 3.31$, $P = 1.00$, $df = 32$ | | | |

Values were obtained by mixture distribution analysis of size frequency distributions (SFD) shown in Fig. 6: $\chi^2$ value and accompanying statistics describe the model that was adjusted to the SFD. A Student's $t$ test was used to check for significant differences in mean CW at instar between sites (*$P < 0.05$, $ns$ not significant)

the lowest adult instars in Kangerluarsuk can explain the inversion at instars IX–X of the relative size differential at instar (from positive to negative) between preadult females from the two sites, as larger females were removed from the pool of preadults by terminal moulting earlier in the instar sequence in Kangerluarsuk relative to Disko Bay.

SFD for immature snow crab collected by trawl in Kangerluarsuk allowed to resolve mean and SD of CW for five instars: $8.4 \pm 1.2$ mm for instar III, $12.6 \pm 2.6$ mm for instar IV, $16.9 \pm 2.5$ mm for instar V, $22.7 \pm 4.4$ mm for instar VI and $29.4 \pm 1.4$ mm for instar VII ($\chi^2 = 1.23$, $P = 1.00$, $df = 11$). Trawl data from another cold fjord, Eqaluit Paarliit, produced very similar and statistically indistinguishable mean CW values for instars III to VI. There was no difference between trawl and trap data in the mean CW of instars VI and VII resolved for Kangerluarsuk (Student's $t$ test, $P > 0.05$).

## Discussion

### Intersex coherence and causes of spatial patterns in adult size

This study confirms that minimum, median and maximum adult sizes are geographically variable in female snow crab and demonstrates the same pattern in males. Adult size in both sexes responds to a common factor which is temperature or an environmental covariate (see below). The rate (i.e., slope) of increase in Q1% and median adult CW with increasing temperature, when expressed with ln-transformed data, did not differ significantly between males and females suggesting proportionally similar effects in both sexes. The lesser rate of increase in Q99% for males than for females may be caused by selective fishery removal of large males in conjunction with lesser fishing effort in the cold fjords than at other sites (Burmeister and Siegstad

2008). Below we discuss why temperature is the most likely factor in spatial variability of adult size in snow crab and elaborate on the mechanisms determining change in size. We focus on females because they have been better studied. However, we are of the opinion that the causes and mechanisms of size change are the same in both sexes.

A negative cline in adult size of female snow crab with increasing latitude has repeatedly been demonstrated in the eastern Bering Sea (e.g., Otto 1998; Zheng et al. 2001). This converse Jame's cline was initially attributed to genotypic variation by Somerton (1981), an interpretation convincingly refuted by Orensanz et al. (2007) who suggested instead that the pattern reflects phenotypic variation. These authors argued that temperature per se is the most likely environmental cause of clinal variation in female adult size. Orensanz et al. (2007) discounted season length, which is correlated to latitudinal gradients of temperature, as a more direct cause of the size cline. Indeed, contrary to most terrestrial ectotherm examples provided to support the idea that converse Bergmann/Jame's clines can be explained by season length, female snow crab are long lived (>5 year lifespan from metamorphosis and settlement to terminal moult) and feed and grow somatically and gonadically year-round (Alunno-Bruscia and Sainte-Marie 1998). In eastern Canada, females complete the critical life history events of terminal moult and first mating during winter months at subzero temperature (Lovrich et al. 1995) and this is likely the case elsewhere (Ernst et al. 2005).

This and other studies provide further support against season length or local adaptation as explanations of geographic size variability for adult female snow crabs. Indeed, there is no latitudinal cline in female adult size along the west coast of Greenland, while there is a positive relationship with temperature. Similarly, along the north shore of the Gulf of St. Lawrence the positive cline in female adult size is longitudinal and relates to increasing temperature (Sainte-Marie and Gilbert 1998), not changing season length. Moreover, variability in female adult size along West Greenland or north Gulf of St. Lawrence coasts are unlikely to reflect local adaptation because populations within each area are not genetically differentiated, being well mixed through an extended larval phase lasting 3–5 months (Puebla et al. 2008). Importantly, variation in adult size across the fragmented snow crab habitats of west Greenland or along the continuous but narrow and extended (>1,000 km) snow crab habitat of the north Gulf of St. Lawrence is indicative of a direct temperature effect on growth (see below) rather than a size-dependent temperature preferendum expressed by females during post-terminal moult migration, which is oriented from shallow to deep bottoms (see Lovrich et al. 1995; Ernst et al. 2005).

The size-temperature relationship observed for snow crab in our study could conceivably reflect food limitation by quality or quantity if colder habitats are less productive than warmer habitats. Ectotherms and crustaceans specifically may mature later and/or at a smaller size when growth rate is reduced as a consequence of lesser food quality or quantity (e.g., Wenner et al. 1985; Berrigan and Charnov 1994; Atkinson and Sibly 1997). Few studies of the benthos have been conducted along West Greenland and information about species composition, diversity, abundance and productivity in relation to temperature or ice cover is limited (Sejr et al. 2009a). The growth of some filter feeders and herbivores declines from sub- to high arctic along the Greenland coast, probably in relation to food availability which may be inversely related to temporal extent of ice cover (Blicher et al. 2007; Sejr et al. 2009b). However, the Disko Bay "warm" site where snow crabs reached large sizes is normally covered by ice during winter, whereas the fjords near Sisimiut whether "cold" or "warm" are rarely covered by ice except during very cold winters. Moreover, snow crab is mainly carnivorous and its preys include many large and often long-lived invertebrates (Lovrich and Sainte-Marie 1997) that may be available year-round. Under food limitation, one would expect crabs to experience a reduction in relative moult increment resulting in a smaller size at instar (reviewed in Hartnoll 2001). However, the mean CW at instar for preadult females and males and all adult females either did not differ significantly between Disko Bay and Kangerluarsuk or was greater in Kangerluarsuk, with the exception of male adolescent instar IX. Thus, for the time being, the cline in snow crab adult size along west Greenland (and elsewhere) does not appear to be related to differences in food supply—but more research is needed before this can be concluded definitively. Overall, our results support the view that a universal cause is unlikely to explain all ectotherm examples of converse Bergmann/Jame's clines.

Our observations provide evidence for other possible sources of within or between population variability in adult size of snow crab. First, interannual variability in median adult size, evident in Fig. 2, has been related to the interplay of episodic or periodic multiyear recruitment pulses and limited post-terminal-moult life expectancy (Orensanz et al. 2007; Sainte-Marie et al. 2008). For example, median size increases through a recruitment pulse because crabs first recruit to and die out from the smallest of potential successive adult instars, subsequently median size decreases when the last and largest of recruited adults begin to die out and a new recruitment pulse begins. Second, the relationship between female mean CW and temperature in the Eastern Bering Sea is indiscernible from ours in terms of slope value (Fig. 2; ANOVA, $F = 0.149$, $P = 0.701$), but has a conspicuously smaller $y$-intercept. This in part may reflect the sampling of crabs by trawl in Orensanz et al. (2007) compared to traps in our study, but the difference

holds true and is of the same magnitude when minimum or maximum size are considered and these values may be less sensitive to sampling method. In fact, we compared Q1%, median and Q99% adult CW between trap and trawl samples in Kangerluarsuk and found a significant difference between gears only in Q99%, which was greater in trap than in trawl samples. Thus, the difference between Bering Sea and Greenland snow crab suggests that other factors may account for the shift in the intercept of the size-temperature relationship: these could include basin-scale effects (e.g., adaptation) or observation bias (e.g., crabs are no longer in the same temperature conditions that determined their size, due for instance to migration).

## Mechanisms of variability in adult size

The observation of a similar or larger mean CW at instar in "cold" Kangerluarsuk compared to "warm" Disko Bay is consistent with the finding among majoid crabs that the relative moult increment usually is invariable with temperature [as seen in both sexes of *Inachus dorsettensis* and in male and terminally moulting female *Hyas coarctatus* (Hartnoll et al. 1993), in male *C. bairdi* (Paul and Paul 2001) and in *Mithraculus forceps* (Penha-Lopes et al. 2006)] or declines weakly with increasing temperature [as seen in female and male *Pyromaia tuberculata* (Furota 1996) and in immature female *H. coarctatus* (Hartnoll et al. 1993)], all other things being equal. Moult increments were identical in another majoid (*Scyra acutifrons*) between two populations that exhibited large differences in female adult size (Hines 1989).

The principal mechanism leading to differences or clines in adult size among majoid populations is generally inferred to be a difference in the number of instars prior to terminal moult (Hines 1989; Hartnoll et al. 1993). A shift to a higher instar number with increasing temperature is the only possible mechanism for explaining our results, given that pre-adult crabs were of equal or larger size at instar in Kangerluarsuk than in Disko Bay. This conclusion is also supported by the analysis of instar composition for adult females, although one might argue that interpretation of adult SFDs is tenuous and that alternative solutions involving fewer instars would not be statistically rejected. However, the proposed solutions of modal composition in SFDs are consistent with observations elsewhere in that adult females are predominately represented by two consecutive instars (Ito 1970; Kon 1980; Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998; Orensanz et al. 2007), the moult increments for pre-adult and terminal moulters are very similar to expectation (see laboratory and fields data in Alunno-Bruscia and Sainte-Marie 1998), and there is a reduction of SD for individual preadult instars after minimum instar for adulthood (Alunno-Bruscia and Sainte-Marie 1998). Forcing a uni- or bimodal model to adult female SFDs

would result in moult increments and standard deviation of modal components (instars) that are not plausible.

In this study, the progressive upward shift in Q1%, median and Q99% CW of adult females with increasing temperature can likely be explained by a gradual change in the proportional distribution of crabs from the lower to the higher instars, which respectively reduces or increases a gradual range of CW values associated with each instar because range is related to sample size in a normally distributed variable. This process culminates in the loss of the smallest instar and addition of a larger instar. Over a wider span of habitat temperatures than represented in this study, as seen for example in the Bering Sea (Orensanz et al. 2007, see Fig. 2 herein), it is likely that the instar distribution of adult females may shift upward by two instars.

The shift toward higher instars in warmer waters is not a short-term (months) or immediate (weeks to days) effect of temperature operating on pre-terminal-moult females. Indeed, among pubescent females, the proportion moulting to maturity and the average moult increment are invariable with temperature over the range of about 0.5–3.7°C after holding for up to 8–10 months in the laboratory (Sainte-Marie et al. in review and unpublished data). Instead, it is likely that females are conditioned for maturity at lower or higher instars in the early phase of their life as hypothesized by Sainte-Marie and Gilbert (1998) and Orensanz et al. (2007). Briefly, it is postulated that immature females are able to achieve more moults in a "warm" than in a "cold" environment before the onset of pre-puberty, when ovaries begin to develop and the moult cycle becomes annual (Alunno-Bruscia and Sainte-Marie 1998), and that the resulting size advantage at the pre-puberty moult carries over to the terminal moult because development time is fixed. This hypothesis rests on the assumptions that (1) moult increment is largely temperature independent (see above), (2) intermoult period decreases with increasing temperature during the immature phase, and (3) there exists an age-related trigger for the pre-puberty and terminal moults. The three assumptions require testing but are reasonable given a variety of clues expounded in detail by Orensanz et al. (2007). Note that if this hypothesis is correct, the development of reliable predictive regressions for adult size will require information on temperature in juvenile habitat which may differ somewhat from temperature in adult habitat, even though both are likely to be positively correlated.

Slowing of growth due to longer intermolt period in "cold" versus "warm" habitats has been demonstrated in many other decapod crustaceans and results from temperature-induced reduction of metabolism (e.g., *Pandalus borealis* in Daoud et al. 2007). Moreover, in some marine invertebrates cold tolerance is limited by a critical temperature which forces the transition from aerobic to

anaerobic metabolism (Burggren and Roberts 1991). In reptant crustacean decapods, which include crabs, this temperature threshold may be mediated by hemolymph concentration of $Mg^{2+}$. In the majoid *H. araneus*, for example, below a temperature threshold of about 2°C cardiac performance, hemolymph circulation and general activity are severely depressed (Frederich et al. 2000a). Reptant decapods including some investigated majoid crabs are apparently unable to downregulate hemolymph $Mg^{2+}$, which acts as an anesthetic, and this may explain why this group of decapods has not colonized the coldest polar areas (Frederich et al. 2000b, 2001). Whether this applies to snow crab, arguably the best cold adapted of all crabs, remains to be tested.

Implications for conservation

Our findings have important applied implications. They suggest that climate may affect per capita reproductive output in both females and males, because individual fecundity scales exponentially to body size, and the proportion of adult males that become vulnerable to the fishery under a fixed minimum legal size limit. With rising temperature, potential reproductive output will increase more substantially in females than in males because the allometric relationship of fecundity to body size is steeper in females than in males (Sainte-Marie et al. 2008) and also because females shift from a biennial to an annual reproductive mode (Moriyasu and Lanteigne 1998; Burmeister 2002; Webb et al. 2007). At the same time, an increasingly large proportion of males may outgrow the minimum legal size and become vulnerable to fishing, thereby accentuating sex ratio bias due to male-only fishing and reducing sperm supply. Other more subtle effects of changing size structure on the mating system are possible (Sainte-Marie et al. 2008).

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