

Oceanographic and demographic mechanisms affecting population structure of snow crabs in the northern Bering Sea

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ABSTRACT: Snow crabs *Chionoecetes opilio* are quite productive at suitable temperatures, but can also be abundant in water cold enough to depress settlement of larvae, growth, and reproduction. In much of the northern Bering Sea, bottom water temperatures are below -1°C for most or all of the year. Crab pelagic larvae prefer to settle at temperatures above 0°C , so we found high densities of juveniles only where intruding warm currents deposited larvae in localized areas. After settlement, maturing crabs appeared to exhibit ontogenetic migration toward deeper, warmer water. Cold temperatures excluded key predators, but decreased fecundity by restricting females to small body size (with associated small clutches) and to breeding every 2 yr. Migration to warmer water may allow females to breed annually and to encounter more adult males needed to fertilize subsequent clutches. Because older males also emigrate, remaining adolescent males probably inseminate newly maturing females. Without localized intrusion of warmer currents, snow crabs might not persist at high densities in such cold waters. However, they are currently very abundant, and export many pelagic larvae and adults.

KEY WORDS: Population structure · Larval advection · Larval settlement · Ontogenetic migration · Dispersion · Reproduction · *Chionoecetes opilio*

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INTRODUCTION

Snow crabs *Chionoecetes opilio* are abundant in both Atlantic and Pacific subpolar regions, where they support important commercial fisheries at temperatures generally $>0^{\circ}\text{C}$. Snow crabs can also be abundant where subzero temperatures for much or all of the year prevent them from growing to marketable size (Paul et al. 1997). Snow crab pelagic larvae prefer to settle at temperatures above 0°C (Dionne et al. 2003); in the laboratory at -1°C , snow crabs with carapace width (CW) up to 80 mm did not achieve

positive energy balance even when fed ad libitum (Thompson & Hawryluk 1990). Although field populations do grow at subzero temperatures, females are much smaller at maturity (Burmeister & Sainte-Marie 2010), with correspondingly smaller egg clutches (Haynes et al. 1976). Moreover, the longer incubation period at subzero temperatures limits females to producing clutches every 2 yr rather than annually (Rugolo et al. 2005). Despite these limiting factors, small snow crabs can be very abundant at such cold temperatures, with important trophic effects (Kolts et al. 2013a, Lovvorn et al. 2015). Given the potentially

low settlement rates of larvae at subzero temperatures (Dionne et al. 2003), and subsequent low growth and clutch size, it is unclear how these populations persist at such high densities, and what importance they may have to crab populations in adjacent warmer areas.

In the northern Bering Sea (Fig. 1), our surveys showed that snow crabs are the most abundant epibenthic predator (Lovvorn et al. 2015). Southward from St. Lawrence Island to St. Matthew Island, bottom water temperatures are $<0^{\circ}\text{C}$ (and often below -1°C) year-round. Northward from St. Lawrence Island to the Bering Strait (Chirikov Basin), bottom waters usually exceed 0°C only from July to November (Woodgate et al. 2005). Despite abundant food (Kolts et al. 2013a,b), most snow crabs in this region have a CW <55 mm and often much smaller, while the minimum legal size for fisheries is 78 mm and marketable size is >100 mm. Although snow crabs have been well studied in the southeast Bering Sea in areas of the commercial fishery, until recently few data were available for the very cold northern Bering Sea (Stevenson & Lauth 2012).

Direct measurement of the relative hydrographic transport of planktonic larvae to different locations in the northern Bering Sea would require comprehensive spatial sampling throughout the water column over a very large area for 3 to 4 mo (cf. Parada et al. 2010). Moreover, such measurements would not encompass effects of temperature or other conditions on settlement and early post-settlement survival. As a result of these difficulties, transport and successful settlement of decapod larvae into a given area are often inferred from sampling for settled recruits (Eggleston & Armstrong 1995, Garvine et al. 1997, Incze et al. 2000). There is typically a strong spatial correlation between densities of pelagic larvae and settled juveniles (Eggleston & Armstrong 1995, Incze et al. 2000). Simulation models that account for hydrographic flow and temperature do not always yield accurate predictions of local spatial patterns of larval advection and settled juveniles (Garvine et al. 1997, Incze & Naimie 2000). Thus, field measurements of juvenile recruitment to the benthos are often more reliable indicators of the combined processes of transport and settlement than are hydrodynamic models or water-column sampling.

Recent conceptual models of the southeast Bering Sea population (Parada et al. 2010) suggest that crabs recruited as juveniles into the cold north-central Bering Sea may emigrate southwestward into areas of active crab fishing, and might also provide pelagic larvae important to the fishery. Moreover, if these

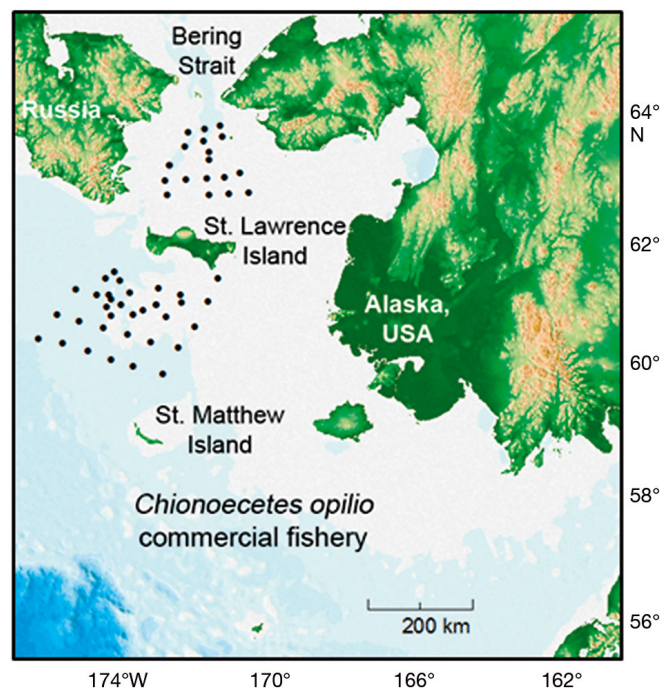


Fig. 1. Stations (black dots) sampled in the northern Bering Sea (St. Matthew Island to Bering Strait), relative to the general area of the snow crab *Chionoecetes opilio* commercial fishery in the southeast Bering Sea. The shelf break at about 200 m depth is seen at bottom left

larvae are carried northward they could contribute to populations in the Chukchi and possibly Beaufort Seas (Paul et al. 1997, Rand & Logerwell 2011), which are experiencing greater climate warming than the northern Bering Sea (Sigler et al. 2010). Thus, it is important to understand factors that allow the large snow crab population in the northern Bering Sea to persist in such cold conditions.

We investigated the spatial population structure and reproductive characteristics of snow crabs in cold waters of the northern Bering Sea. Our main questions were (1) by what demographic mechanisms do very cold temperatures limit the local productivity of snow crabs, (2) what oceanographic and demographic mechanisms can sustain populations in cold areas, and (3) could populations in cold areas contribute to production of harvestable crabs at larger spatial scales?

MATERIALS AND METHODS

Study system

Snow crabs mate in late winter and spring, and embryos develop under the abdomen of females for

either 1 or 2 yr, depending on bottom water temperatures. A switch to 2 yr embryo incubation occurs at temperatures below about 1°C in both the southeast Bering Sea (Rugolo et al. 2005) and the Gulf of St. Lawrence, Canada (Moriyasu & Lanteigne 1998). In spring to early summer (mid-June), eggs hatch to release pelagic larvae that are transported by currents for several months before settling to the sediments as megalopae (Parada et al. 2010). Specific cues that stimulate hatching of snow crab eggs have not been identified (Kuhn et al. 2011). Neither have cues for settlement of pelagic larvae, although a number of physical and biological variables have been described for other brachyuran crabs (see Sainte-Marie & Lafrance 2002), and snow crab larvae prefer to settle at bottom water temperatures of 0 to 2°C (Dionne et al. 2003).

Growth in snow crabs stops at their final molt into adults, typically during instars VIII to XI for females in the southeast Bering Sea (Orensanz et al. 2007). Males also undergo terminal molt over a range of instars, concurrent with an increase in the size of their chelae (claws) relative to their body size. Terminal molt in males occurs at a larger body size and 2 to 3 yr later post-settlement compared to females (Kon 1980, Alunno-Bruscia & Sainte-Marie 1998, Comeau et al. 1998). Males reach sexual maturity during one or more instars preceding the terminal molt (Sainte-Marie et al. 1995, Comeau et al. 1998), and males as small as 20–30 mm CW with spermatophores in their vas deferens have been captured in the cold waters of the Chukchi Sea (Paul et al. 1997). Following Sainte-Marie et al. (1995), we term such males that are sexually mature, but morphometrically immature, as ‘adolescents,’ and males with proportionately large claws as ‘adults.’ Because we did not evaluate ovarian development in all females collected, we term all females >20 mm CW that have not undergone terminal molt (based on shape of the belly flap) as ‘immature’ (Comeau et al. 1998). We refer to all crabs <20 mm CW (essentially instars I to V) as ‘juveniles.’ In the southeast Bering Sea, both males and females begin a southwestward migration toward deeper, warmer waters of the shelf break after undergoing terminal molt (Otto 1998, Zheng et al. 2001, Ernst et al. 2005). In that region 200 to 500 km south of our study area, migra-

tory movements of immature and adolescent crabs are not well understood.

Our sampling stations were between St. Matthew Island and the Bering Strait on the shallow continental shelf of the northern Bering Sea (Fig. 1). In the Chirikov Basin north of St. Lawrence Island (SLI) to the Bering Strait, stations varied in depth from 35 to 52 m. South of SLI, water depth increases from northeast to southwest, ranging from 30 to 96 m at our stations. During winter, near-bottom temperatures are uniformly cold (<−1°C) throughout our study area. However, at stations north of SLI and just south of its eastern end, bottom water temperatures increased to as high as 1°C during our cruise in late May to early June 2007 (Fig. 2) and through early August 2010 (Lauth 2011). A branch of the Anadyr Current diverges south of SLI to inject warm water and larvae (as indicated by settled juveniles, see ‘Results’) just south of the island (Fig. 3; Clement et al. 2005, Danielson et al. 2006). North of SLI, the Anadyr Current can be slowed and pushed eastward by northwesterly winds, also favoring settlement of larvae (Fig. 3). Most remaining stations south of SLI are covered year-round by a cold pool of bottom water (<0°C), which forms under sea ice during winter and lasts through summer due to very weak currents in this region of the shelf (Hu & Wang 2010). This mass

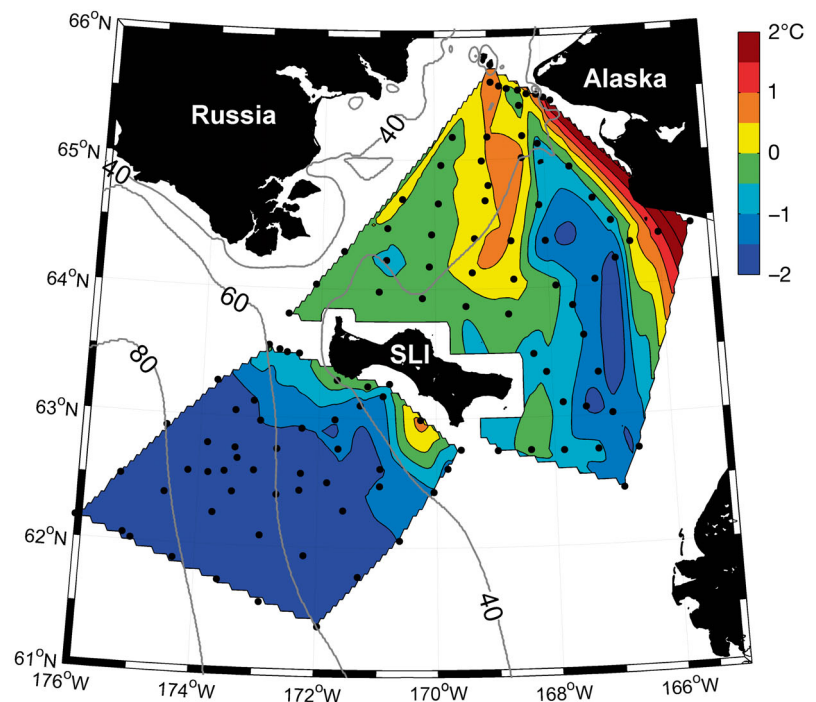


Fig. 2. Bottom water temperatures in the study area around St. Lawrence Island (SLI) from 18 May to 3 June 2007. Points show locations of temperature measurements ~2 m above the sea floor with a conductivity-temperature-depth instrument

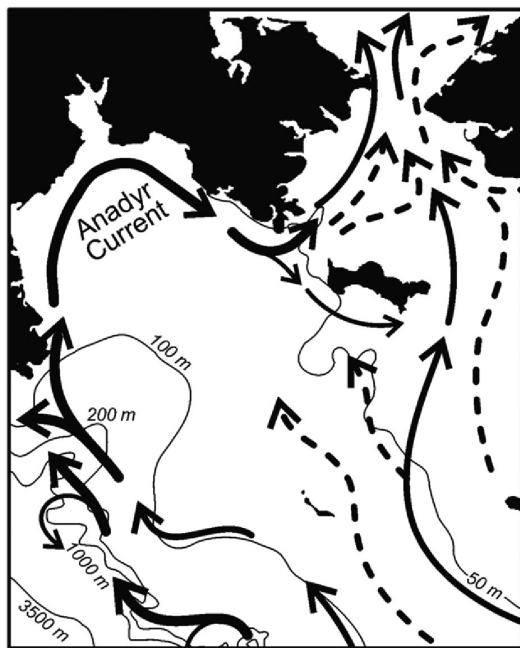


Fig. 3. Mean circulation in the northern Bering Sea (after Clement et al. 2005). Current volumes grade from high (bold solid lines) to moderate (finer solid lines) to low (dashed lines). Note the branch of the Anadyr Current that diverges south of St. Lawrence Island, and how the Anadyr Current can be slowed and displaced eastward by northwesterly winds in the Chirikov Basin north of St. Lawrence Island (dashed lines southeast of main line)

of cold water greatly affects the population dynamics of snow crabs, by mostly excluding species such as Pacific cod *Gadus macrocephalus* which are major predators of snow crabs in the southeast Bering Sea (Livingston 1989), and by decreasing growth rate and body size and increasing egg incubation periods for snow crabs compared to warmer areas farther south (Webb et al. 2007, Dawe et al. 2012).

Collection of specimens

We collected snow crabs from the US Coast Guard icebreaker 'Healy' from 18 May to 12 June 2007. We used a 4 m beam trawl with 3.7 mm (1.5 inch) stretched mesh to collect 31 179 snow crabs from 89 trawls at 53 stations. Because of widely varying densities of benthic animals across sampling stations, the duration of tows ranged from 3 to 20 min depending on anticipated magnitude of catch; however, most trawls lasted 10 min on the bottom as determined from continuous depth traces measured by a logger (Sensus Ultra Dive Data Recorder, ReefNet) inserted into the upper hollow frame of the beam trawl. Exact

distance traveled during time at the bottom was calculated from GPS locations. All trawls were conducted at ~2 knots (speed over ground) directly against any significant wind or current. After bringing the trawls on deck, crabs were separated by sex, counted, and immediately frozen at -80°C .

Measurements of crabs

For each crab collected, we measured CW, height of right chela in males, and abdomen width in a subset of females (Jadamec et al. 1999) to the nearest 0.1 mm with a digital caliper. Immature and adult females were distinguished based on abdominal flap morphometry (Jadamec et al. 1999). Maturity in males was determined by the ratio of chela height (CH) to CW. On plots of $\ln \text{CH}$ versus $\ln \text{CW}$, we divided clouds of points for 92 adult males versus 1453 immature and adolescent (sexually mature but morphologically immature) males by the canonical discriminant function $\ln \text{CH} = 1.028 \ln \text{CW} - 1.816$ (Fig. 4), determined with PROC DISCRIM of the SAS software (SAS Institute; cf. Comeau et al. 1991). Shell condition was scored according to US National Oceanic and Atmospheric Administration (NOAA) Fisheries protocols (Rugolo et al. 2006).

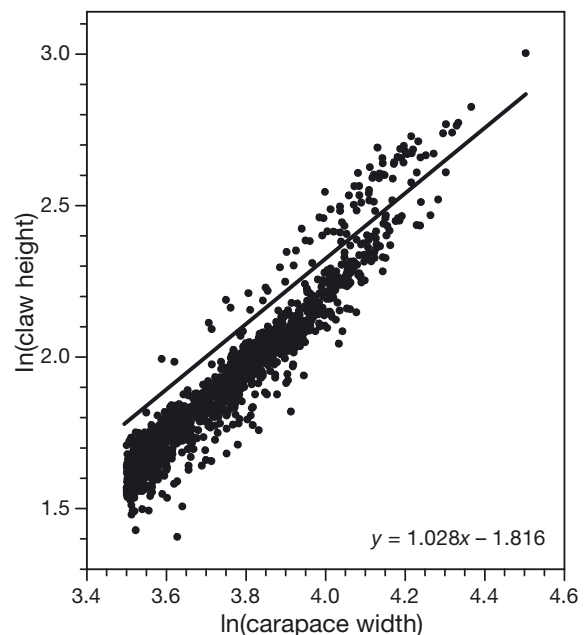


Fig. 4. Natural logarithmic plot of right chela (claw) height (CH) versus carapace width (CW) of male snow crabs *Chionoecetes opilio* in the northern Bering Sea with $\text{CW} > 3.5 \text{ mm}$, and the discriminant function used to separate large-clawed adult males from small-clawed adolescent males

Reproductive status

We processed egg clutches from adult female crabs at sites representative of their geographic range in our study area. Adult females were classified as primiparous or multiparous (whether producing first or subsequent broods) based on shell condition and clutch development (Sainte-Marie 1993). Regarding shell condition, we used Alaska Fisheries Science Center criteria for distinguishing primiparous from multiparous females in the eastern Bering Sea; however, it is possible that shells do not wear as quickly in the northern Bering Sea, so that a fraction of females we graded as second-year primiparous were possibly multiparous females. We removed clutches from all of the 32 multiparous (old-shell) crabs collected, which ranged from 40 to 68 mm CW, as well as from 41 primiparous (new-shell) crabs ranging from 40 to 64 mm CW.

For each clutch, we estimated the percentage of clutch remaining (Jadamec et al. 1999), percentage yolk, and embryonic development stage (when possible) according to the NOAA Fisheries scoring system (Rugolo et al. 2004). Total eggs per clutch were calculated from the dry mass of an entire clutch, and desiccated mass per egg was calculated from a subsample of 250 to 300 eggs removed from the clutch and counted with a dissecting microscope. An additional subsample of ~40 eggs was removed and stained with Bouin's solution for evaluating developmental stage (Moriyasu & Lanteigne 1998). We dried the larger subsample and remaining clutch at 60°C for a minimum of 64 h in a drying oven. Eggs close to hatching had a much thinner protective coat than those in early development; as a result, these older eggs were sometimes destroyed by freezing and could not be counted. Also, some females that had recently molted to maturity had not completely extruded their broods, so their eggs could not be counted.

To distinguish an annual versus biennial cycle of reproduction, we examined both eggs and ovaries. The time of year of our sampling (18 May to 12 June) corresponds to a period in which many of the females would have just extruded a fresh clutch of eggs and exhibited barren ovaries, whereas others at the end of the reproductive cycle would have clutches approaching hatching as well as ripened ovaries. The presence of females with eggs at intermediate stages of development (see Kon 1980, Moriyasu & Lanteigne 1998) and maturing ovaries indicates that those individuals were following a biennial reproductive cycle. However, it was not possible to make this judgment for all individuals.

RESULTS

For analyses, we divided our study area into 3 sectors (Fig. 5) based on distinct assemblages of epibenthic macrofauna. Cluster analysis separated stations north of SLI in the Chirikov Basin sector from those in the south, which were further divided into East and West sectors (see Supplement for Kolts et al. 2013a at www.int-res.com/articles/suppl/m483p209_supp.pdf).

Demographic structure

Overall abundance of snow crabs was greatest in the Chirikov Basin (Fig. 5), where we also found highest densities of all sizes of crabs except those over 45 mm CW (Fig. 6). Overall densities of crabs were lowest in the West sector, where epibenthic biomass was dominated by brittle stars *Ophiura sarsi* and the densities of benthic predators such as sea stars, whelks, and larger snow crabs were relatively low (Lovvorn et al. 2015).

Juvenile snow crabs were most abundant at the northernmost stations in the Chirikov Basin (Table 1;

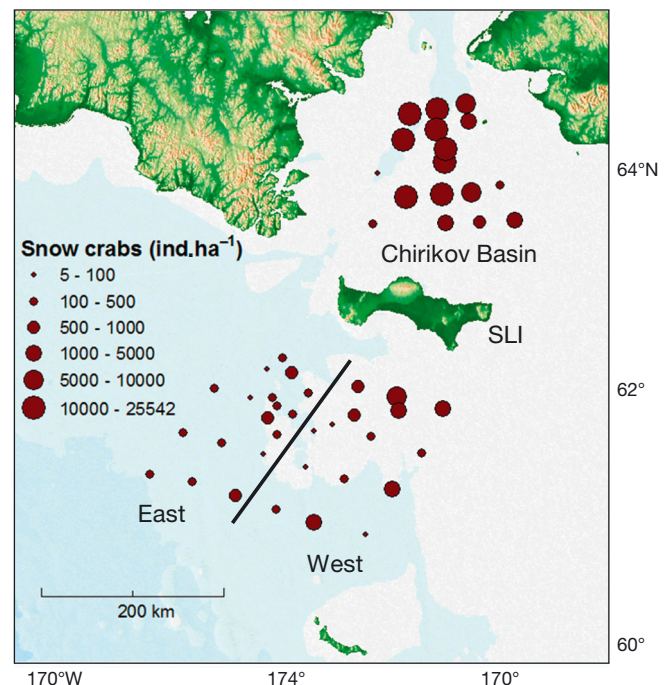


Fig. 5. Density (ind. ha⁻¹) and distribution of snow crabs *Chionoecetes opilio* (all ages and sexes combined) at sampling stations in the northern Bering Sea, May to June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors

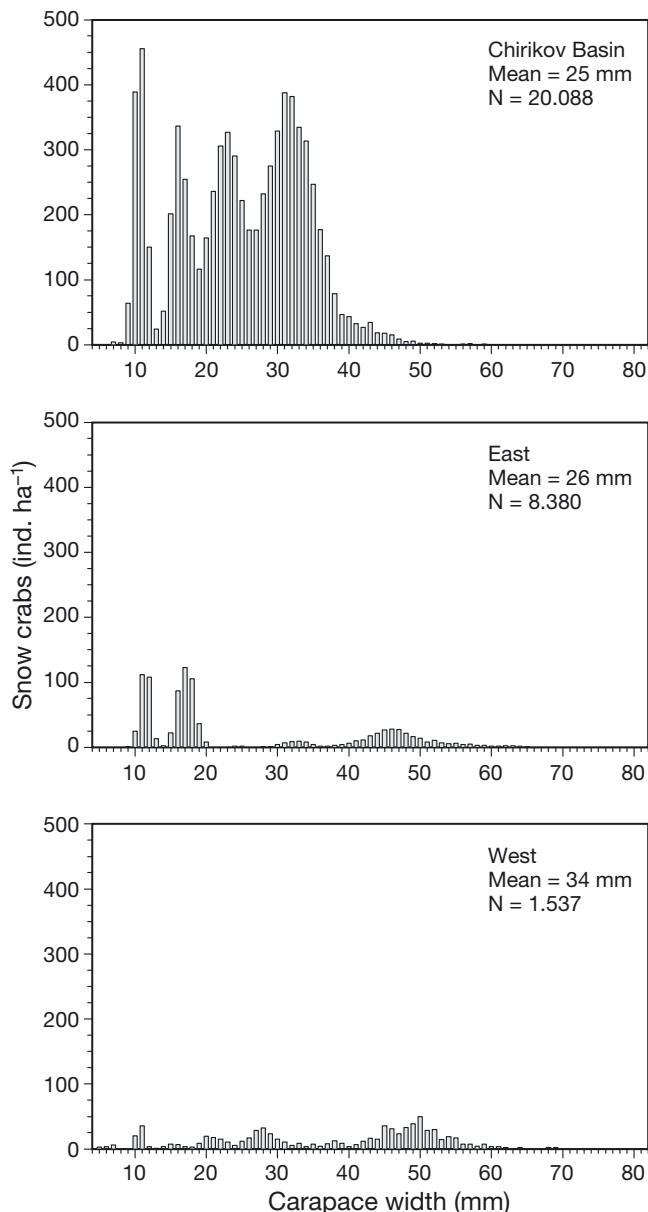


Fig. 6. Size structure of snow crabs *Chionoecetes opilio* (both sexes combined) in each sector of our study area (see Fig. 5) in the northern Bering Sea, May to June 2007

Figs. 6 & 7a). This pattern appears to result from slowing and eastward deflection of the Anadyr Current by northwesterly winds (Fig. 3), probably enhancing deposition of crab larvae. Highest densities of juveniles were found at our stations closest to the Bering Strait, while juveniles were absent at most stations in the southern Chirikov Basin (Fig. 7a). In contrast, immature and adolescent crabs >20 mm CW were very abundant at these southern stations of the Chirikov sector (Fig. 7b,c). Juveniles were also abundant in a small area in the northern East sector where there were almost no adults (Figs. 7a,d). In the latter area, a southward branch of the Anadyr Current transports warm water and crab larvae into a region that is otherwise too cold to support high crab recruitment (cf. Figs. 2 & 3).

Adult females were more abundant south of SLI, with the most consistent highest densities at stations along the southern edge of our sampling grid (Table 1, Fig. 8). Adult females composed only 0.03% of all females collected in the Chirikov Basin, compared to 4.5% at stations south of SLI. Adult females ranged from 49 to 59 mm CW in the Chirikov Basin, and from 40 to 68 mm south of SLI. Mean CW of adult females did not differ (*t*-test, $p = 0.13$) between the Chirikov Basin (53.8 ± 7.1 mm SD; $N = 13$) and south of SLI (50.5 ± 4.8 mm; $N = 462$). We captured immature females as large as 62 mm CW.

Adult males occurred at low densities at a number of stations in our study area (Table 1, Fig. 9). Adult males ranged from 36 to 90 mm CW, and we captured adolescent males as large as 78 mm CW. We found no clear latitudinal gradient in size of adult males within our southern or northern areas, and adult males varied by up to 40 mm CW at a single station. However, mean CW at maturity south of SLI (59.4 ± 9.2 mm SD; $N = 156$) was significantly higher (*t*-test, $p < 0.001$) than in the Chirikov Basin (50.6 ± 9.1 ; $N = 20$).

Modal components ('humps') in size-frequency histograms (cf. Fig. 6), which are typically interpreted as instars, were apparent at many but not all

Table 1. Mean (SE in parentheses) number of juvenile (≤ 20 mm carapace width, CW), immature and adolescent (20–40 mm CW), and adult female and male snow crabs *Chionoecetes opilio* per hectare at stations in the 3 sectors (see Fig. 5) of our study area in the northern Bering Sea, May to June 2007. Immature and adolescent crabs >40 mm CW are not included. Estimates for juveniles include few individuals <9 mm CW due to the mesh size of our sampling gear

Sector	No. of stations	Females			Males		
		Adult	Immature	Juvenile	Adult	Immature/Adolescent	Juvenile
Chirikov Basin	18	1.11 (0.68)	2703.79 (551.25)	1712.97 (660.83)	8.99 (4.57)	3582.55 (801.53)	1924.36 (752.54)
East	16	15.35 (6.10)	53.66 (24.69)	484.40 (289.76)	5.93 (2.07)	42.68 (16.70)	266.08 (160.05)
West	17	19.85 (6.39)	52.25 (21.01)	49.24 (13.55)	3.09 (0.89)	45.47 (19.75)	51.77 (13.12)

stations (data not shown). These instars may have included several ages due to irregular reduction of molt frequency at these low temperatures (Dawe et al. 2012). Size of mature females was highly variable within different sectors of our study area. Thus,

although size at instar could be determined for a few intermediate instars (either large instars IV to VII or small instars V to IX), the actual age at those instars and at maturity (and associated growth rates) could not be inferred.

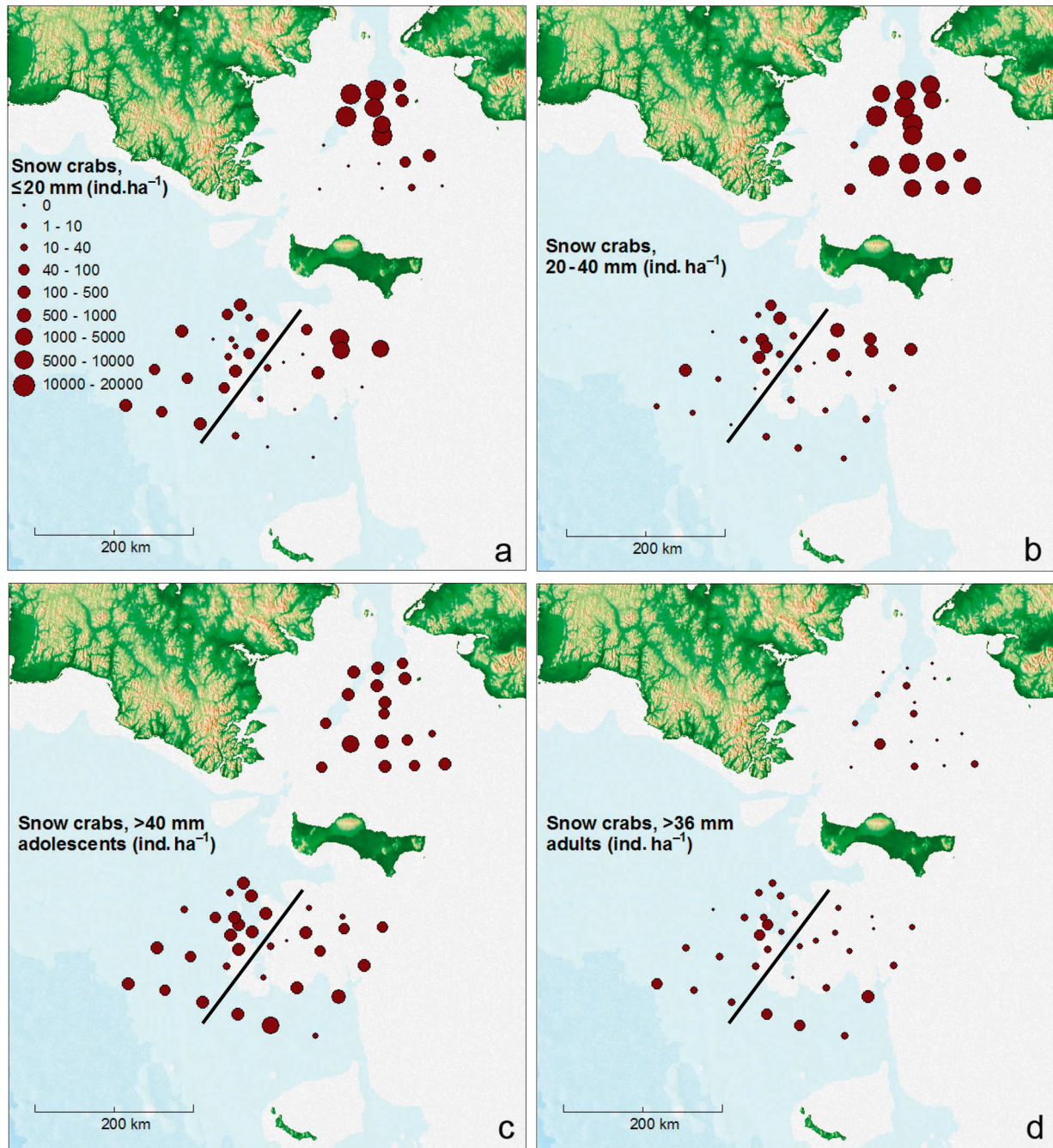


Fig. 7. Density (ind. ha⁻¹) and distribution of snow crabs *Chionoecetes opilio*: (a) juveniles <20 mm carapace width (CW), (b) immatures and adolescents 20–40 mm CW, (c) adolescents (males only) >40 mm CW, and (d) adults >36 mm CW at stations in the northern Bering Sea, May to June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors

Reproductive status

All adult females in the Chirikov sector ($N = 3$) carried eggs, as did 99% in the East and West sectors

($N = 268$). Most adult females collected were primiparous (according to their new shell condition), bearing spent ovaries and a clutch of bright-orange, uneyed eggs in early development stages (stages

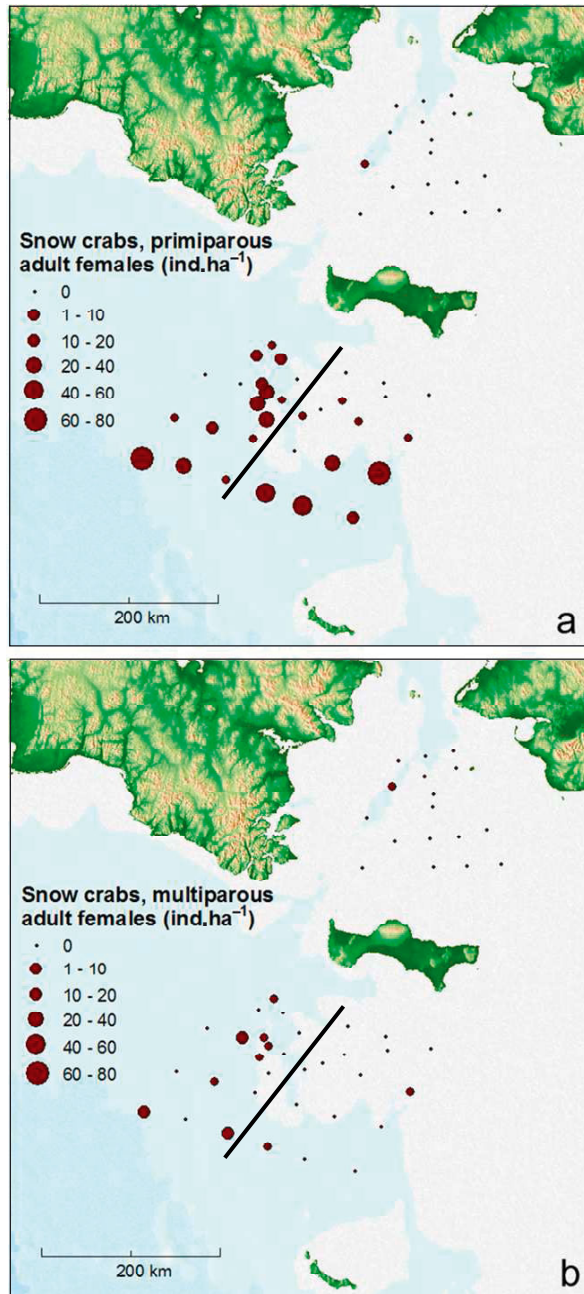


Fig. 8. Density (ind. ha^{-1}) and distribution of adult female snow crabs *Chionoecetes opilio* that were (a) primiparous (first time breeding) and (b) multiparous (subsequent breedings) at sampling stations in the northern Bering Sea, May to June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors

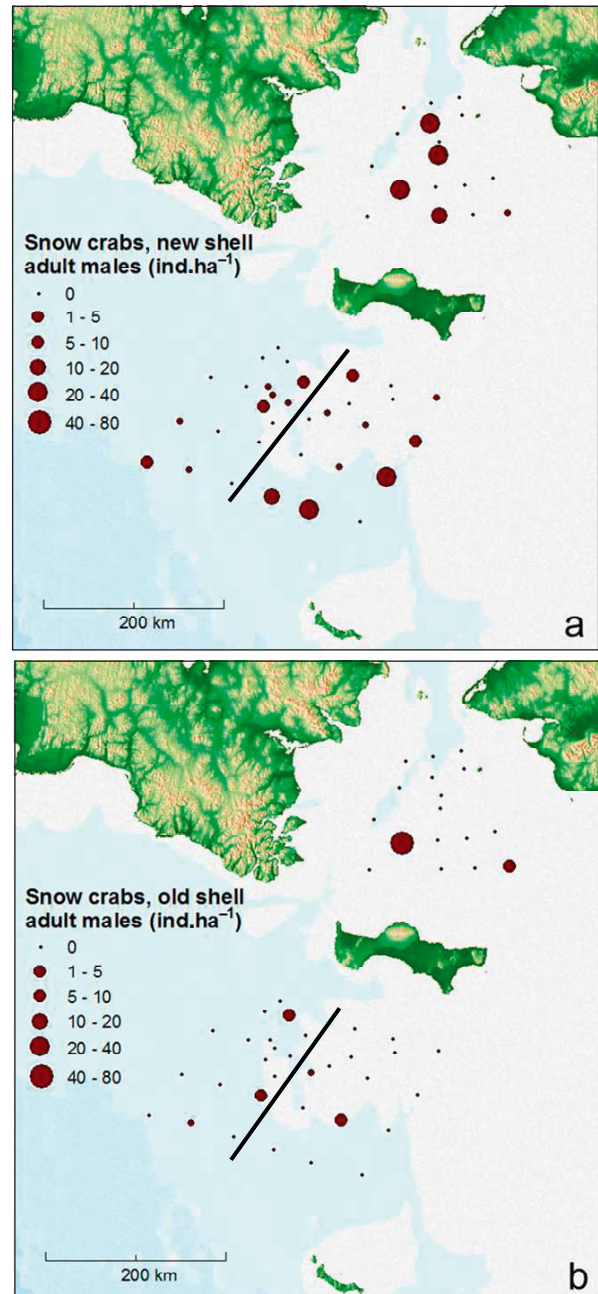


Fig. 9. Density (ind. ha^{-1}) and distribution of (a) shell condition 1 and 2 (soft-shell and new hard-shell) and (b) shell condition 3 (old-shell) morphometrically mature male snow crabs *Chionoecetes opilio* at stations in the northern Bering Sea, May to June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors

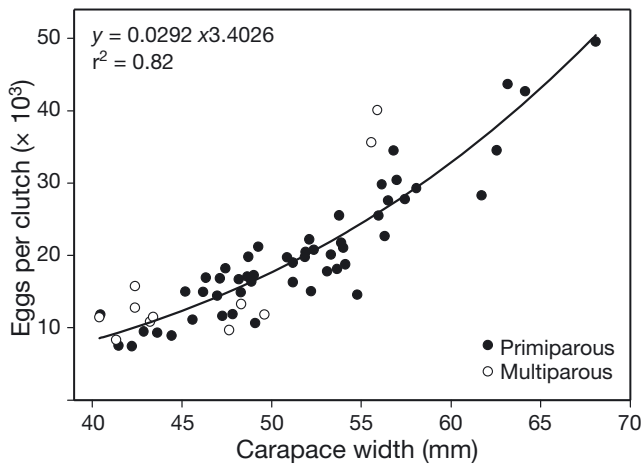


Fig. 10. Number of eggs per clutch for primiparous (first time breeding) and multiparous (subsequent breedings) snow crabs *Chionoecetes opilio* in the northern Bering Sea, May to June 2007. Clutch sizes for multiparous crabs with 45–50 mm carapace width are low, as most crabs in this category bore hatching eggs with 2 yr of incubation time in which to lose eggs from the clutch

1–4, Moriyasu & Lanteigne 1998). We encountered many crabs with soft or pliable shells that had very recently extruded their first clutch.

Multiparous female crabs were rare throughout our study area (Fig. 8b), and nearly all were found in the West sector at the greatest depths of our study area. Of the 32 adult females graded as old- or very old-shell, only 14 appeared to be definitively multiparous with a second or third clutch at stages varying between early development and prehatching. Six primiparous females had clutches in the prehatching stages, while 12 bore clutches entering a second year of development as indicated by orange eggs in yolkereduction stages and maturing ovaries. Clutch size increased with CW and was higher in multiparous than in primiparous females of the same CW interval (Fig. 10, analysis of covariance, $p < 0.001$).

We compared eggs per clutch for snow crabs of a given CW in our East and West sectors versus outside of our study area (southeast Bering Sea; northeast and southeast Chukchi Sea; Gulf of St. Lawrence, Canada). We found no consistent difference across the range of CWs between the southeast and northern Bering Sea (south of SLI) and the Gulf of St. Lawrence, but saw consistently higher values in the Chukchi Sea (Fig. 11). Water temperature is below -1°C over most of our study area south of SLI throughout the year (see Fig. 2), but can be 5 to 6°C warmer during summer at the other locations. Despite this substantial temperature difference among regions, there appears to be no consistent difference

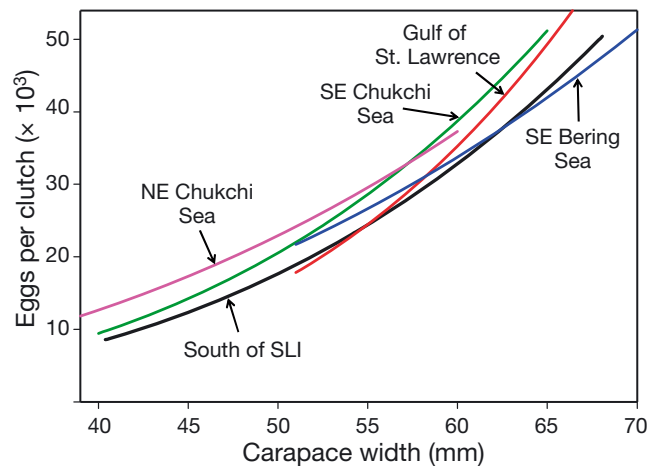


Fig. 11. Number of eggs per clutch (y) for female snow crabs *Chionoecetes opilio* with different carapace widths (x) in the northern Bering Sea south of St. Lawrence Island (SLI, $y = 0.0292 x^{3.4026}$), in the southeast Bering Sea ($y = 0.4905 x^{2.7206}$, Jewett 1981), northeast Chukchi Sea ($y = 0.0292 x^{3.4026}$, Paul et al. 1997), southeast Chukchi Sea ($y = 0.0249 x^{3.4822}$, Jewett 1981), and Gulf of St. Lawrence ($y = 0.0012 x^{4.2000}$, Jewett 1981). Females that were primiparous, multiparous, and of unknown status are included

in number of eggs per clutch at a given CW owing to the lower temperature south of SLI (Fig. 11). Clutch size was, however, consistently smaller for smaller females, and mature females are smaller at colder temperatures.

We found little relationship between individual egg mass and clutch size (eggs per clutch; $r^2 = 0.053$, $p = 0.064$, $N = 66$). Smaller clutches (< 25000 eggs) exhibited much greater variation in individual egg mass ($\text{CV} = 0.119$, $N = 50$) than larger clutches (> 25000 eggs; $\text{CV} = 0.057$; $N = 15$), but the sample size of large clutches was quite small. Mean mass per individual egg was similar (t -test, $p = 0.74$) for primiparous ($6.38 \times 10^{-5} \pm 7.45 \times 10^{-6}$ g SD; $N = 39$) versus multiparous (6.29×10^{-5} g $\pm 1.16 \times 10^{-5}$ g; $N = 9$) females with recently extruded clutches.

We were unable to calculate fertilization rates for clutches. Dead eggs were rarely present, and we saw only a few when they were, suggesting high fertilization rates. For clutches of eyed and prehatching eggs, no uneyed or otherwise undeveloped eggs were noted in any subsamples examined under a dissecting microscope. However, most females collected had eggs at stages 1 to 3, and it is not possible to distinguish fertilized from unfertilized eggs at these early stages (Moriyasu & Lanteigne 1998; but see Sainte-Marie & Carrière 1995 for a DNA-staining approach). Unfertilized eggs remain in the clutch for only 4 to 6 mo (Moriyasu & Lanteigne 1998), and any

unfertilized eggs would likely have been lost by the time we captured crabs with eggs in their second or final year of development. We did not encounter egg parasites in any clutches we examined.

Less than 1 % of 23846 male crabs captured were adults. Adult males occurred at a number of stations throughout our study area, but always at low densities with no apparent spatial pattern (Table 1, Fig. 9). New-shell (soft-shell and new hard-shell) crabs composed 56 % of adult males north of SLI and 71 % in the south. Adolescent male crabs were much more common and occurred in all sectors of our study area (Table 1, Fig. 7c). We observed spermatophores in the vas deferens of males 30 to 35 mm CW, but did not check the vas deferens of all captured males for signs of sexual maturity. Therefore, it is not clear at what size most males begin producing spermatophores in our study area.

DISCUSSION

Our data suggest that south of SLI during the years of our sampling, localized intrusion of a warm current provided many juvenile recruits in an area that otherwise had temperatures well below those preferred by settling larvae of snow crabs. However, the prevailing low temperatures appear to strongly limit growth, which restricts females to small body size (and associated small clutches) and to breeding only every 2 yr. Growth of males is also inhibited, probably putting them at a disadvantage in mating with older females that are breeding for a second or subsequent time. Thus, there are compelling fitness benefits for both males and females to emigrate to warmer areas before reaching final size at maturity, and for females that have already matured at smaller size to reach areas where higher temperatures allow annual breeding. Although adolescent males may breed with newly maturing females more often than they would if most adult males had not emigrated, they generally do not mate with multiparous females (Sainte-Marie et al. 2008). Our results suggest that the abundance of small crabs south of SLI depends on larvae deposited by a localized warm current into a region that is otherwise unsuitably cold, and that these recruits transit the area during development on their way to more favorable, warmer conditions. With key predators excluded by the cold, these small crabs reach high densities, and the area exports many adult crabs and pelagic larvae to adjacent warmer areas. North of SLI in the Chirikov Basin, very high densities of juvenile snow crabs depend entirely on

larvae advected from other regions (cf. Parada et al. 2010), as females appear to migrate out of this area before reaching maturity.

Temperature effects on reproduction

In our study area, it appears that cold temperatures are the greatest limitation on snow crab production. Low temperatures inhibit growth, size at maturity, clutch size, and development rate of eggs. We will discuss each of these aspects.

In snow crabs, molt increment (size increase at molting) and size-at-instar are thought to be quite conservative (Comeau et al. 1998). However, at colder temperatures the age-at-instar and number of molts during development may vary greatly due to longer intervals between molts (see review by Dawe et al. 2012). In the southeast Bering Sea and coastal waters of West Greenland, low temperatures are thought to decrease molt frequency, mostly among juveniles (Orensanz et al. 2007, Burmeister & Sainte-Marie 2010). Older stages appear to follow a more rigid molt schedule regardless of temperature (Sainte-Marie et al. 1995), except that adolescent males may skip molt, molt to another adolescent instar, or molt to maturity depending on the density of adult males in the area (Comeau et al. 1998). Thus, for females, final size may be set by temperature during the first few years after settlement (Sainte-Marie & Gilbert 1998, Orensanz et al. 2007). For males, final size might be affected by temperature during early instars, but may ultimately depend on demographic conditions during late adolescence. It has also been suggested that temperature effects on final adult size are mediated by achievement of a threshold physiological condition that increases the probability of surviving the terminal molt (Dawe et al. 2012).

Compared to larger females farther south, the clutch size of females in our study area was greatly reduced by their small size at maturity and resulting smaller clutches. Their lifetime reproductive potential would be further limited by a biennial reproductive cycle exhibited by females for which this characterization was possible. Female crabs reproducing annually are expected to produce 2.6 to 2.8 times more eggs over their lifetime than females of similar size that breed biennially, which probably produce only 2 to 3 clutches over their life span (Mallet et al. 1993, Sainte-Marie 1993, Moriyasu & Lanteigne 1998, see also Drouineau et al. 2013). Embryo size, survivorship, and overall viability might also be reduced for clutches incubated for 2 yr, due to para-

sites and limited nutritional reserves (Moriyasu & Lanteigne 1998, Rugolo et al. 2004). However, no egg parasites were noted in any clutches we examined.

Most egg production in our study area was by primiparous (first time breeding) females. Primiparous females have up to 32% smaller clutches than young multiparous females (second and later breeding; Somerton & Meyers 1983, Sainte-Marie 1993). This difference likely results from the smaller body size of primiparous females which mate just before growing their final exoskeleton (Hines 1982), as well as the greater concurrent energy costs of growth and molting (Elner & Beninger 1992, Kruse et al. 2007). We found only a weak correlation between the mean mass of individual eggs and clutch size, and no difference in individual egg mass between primiparous and multiparous females. For a given CW, there was no consistent difference in clutch size of females south of SLI versus the southeast Bering Sea or Gulf of St. Lawrence (Fig. 11), despite much lower temperature during the summer growing season south of SLI. We conclude that temperature did not affect clutch size or egg size directly, but that temperature controlled clutch size indirectly via effects on body size at terminal molt.

Effects of hydrography

Snow crab populations in our very cold study area are supported by currents which bring in both larvae and warmer waters ($>0^{\circ}\text{C}$) that favor recruitment to the benthos. The largest concentration of juvenile crabs was in the Chirikov Basin (Fig. 6a). However, there were almost no adult females in that area (Fig. 7), indicating that these juveniles were advected there either as planktonic larvae or after initial settlement elsewhere (Blackmon & Eggleston 2001). The same was true of the many juveniles just south of SLI, in an area lacking adult females but where a small bifurcation of the Anadyr Current flows eastward and creates a localized area of warmer water (Figs. 2 & 3; Spaulding et al. 1987, Muench et al. 1988, Danielson et al. 2006). The first instar we consistently caught in our trawls (IV) was likely 1 to 2 yr old, depending on the frequency of molts, so we do not know whether initial recruitment to these areas is by settling larvae or possibly by post-settlement dispersal of instars I to III (cf. Lovrich et al. 1995, Etherington & Eggleston 2000, Blackmon & Eggleston 2001). Regardless, it is clear that these very high juvenile densities are maintained by reproduction elsewhere, and that habitat for breeding females is often disjunct from nursery areas for

recruiting juveniles (cf. Parada et al. 2010). Segregation between juvenile and older snow crabs has also been noted in eastern Canada: very small, sedentary instars inhabited shallower waters with coarser, gravelly sediments that provided refuge from predators, whereas larger, older instars moved into deeper waters with finer, muddy sediments (Coulombe et al. 1985, Lovrich et al. 1995, Comeau et al. 1998).

In snow crabs, settling larvae and early juveniles are thought to have narrow temperature tolerance (Dionne et al. 2003). In our study area, most snow crab megalopae probably settle from mid- to late summer (Kon et al. 2003, Parada et al. 2010). During our sampling from late May to early June 2007, the area of high juvenile density just south of SLI was the part of our southern study area that was closest to the suggested $0\text{--}2^{\circ}\text{C}$ preference of early instars (cf. Figs. 2 & 6a; Dionne et al. 2003). This spatial pattern of temperature was also evident in midsummer during the 2010 NOAA survey (Chilton et al. 2011). In the laboratory, small snow crabs could not maintain positive energy balance at temperatures $<0^{\circ}\text{C}$ regardless of food availability (Thompson & Hawryluk 1990), so this region may be the only part of our southern study area where snow crabs can thrive upon settlement. Warmer water in the current moving eastward just south of SLI (Fig. 3) appears to accumulate near the east end of the island, as affected by local winds and the slowing of tidal currents along the concave southern shoreline (Muench et al. 1988, Danielson & Kowalik 2005, Danielson et al. 2006). Thus, in addition to warmer temperatures being a strong settlement cue for advecting larvae, slowing waters probably also favor larval deposition.

The other major concentration of juveniles was in the northern Chirikov Basin (Fig. 6a). Bottom temperatures near the Bering Strait are typically above 0°C from July to November (Woodgate et al. 2005); thus, we expect temperatures in the area of high juvenile density just south of the strait to be $0\text{--}2^{\circ}\text{C}$ during the early fall period of megalopal settlement. In that area, water velocity is often slowed by northerly winds, convergence of major water masses, and slowing of tidal currents, with slowest water movements typically in the area where juvenile snow crabs were most abundant (cf. Figs. 3 & 6a; Coachman 1993, Kowalik 1999, Clement et al. 2005).

Low predation on juveniles

The high densities of snow crabs in our study area appear to be favored by low predation on juvenile

crabs of the sizes we sampled (instar III and older). The 2 areas with extremely high concentrations of juvenile snow crabs (Fig. 6a), and our entire study area in general, had low biomass of ectotherm predators of snow crabs (Cui et al. 2009, Lovvorn et al. 2015). In the southeast Bering Sea, Pacific cod are the main predator of juvenile snow crabs (Livingston 1989, Livingston et al. 1993) and may be important in limiting the population (Orensanz et al. 2004, Zheng & Kruse 2006). However, Pacific cod are mostly excluded by temperatures $<2^{\circ}\text{C}$ (Alderdice & Forrester 1971) and were rare or absent in our study area (Cui et al. 2009). An isolated group of 25 to 37 cm short-horn sculpins *Myoxocephalus scorpius* which had eaten mainly immature and adolescent snow crabs (20–40 mm CW) were found at a single station north of SLI (Cui et al. 2009). These large sculpins were the only major predators of snow crabs among fish that we captured. Cannibalism was mainly by large adolescent and adult snow crabs at our southernmost stations south of SLI and was very rare in the areas of high juvenile density (Kolts et al. 2013a). Brachyuran crabs (including both snow crabs and *Hyas coarctatus*) composed 34 to 40% volume of the diet of bearded seals *Erignathus barbatus* at the northern and southern ends of the Chirikov Basin (Lowry et al. 1980). Densities of bearded seals in our area are unknown, but they occur mainly from December through April when sea ice is present (see Simpkins et al. 2003).

Ontogenetic migration

South of SLI, we found few old-shell multiparous females and few primiparous females with clutches in their second year of development (Fig. 8). This scarcity likely resulted from southwestward migration of recently mated primiparous females out of our study area toward deeper, warmer waters near the shelf break. Southwestward ontogenetic migration toward deeper water has also been noted for adult snow crabs in the southeast Bering Sea (Otto 1998, Zheng et al. 2001, Ernst et al. 2005).

North of SLI, juvenile snow crabs were very abundant in the central Chirikov Basin, although adult females were essentially absent there. We suggest that this lack of adult females may have resulted from ontogenetic migration in which crabs pass through the Bering Strait into the Chukchi Sea, perhaps aided by converging, northward-flowing currents and movements of crabs toward warmer waters associated with those currents (Wyllie-Echeverria et al.

1997). Being affected by Anadyr, Bering Shelf, and Alaska Coastal waters, seasonal bottom temperatures in the central Chirikov Basin resemble those in the eastern Chukchi Sea (cf. Ahlnas & Garrison 1984, Johnson 1989, Miyake et al. 1994, Weingartner et al. 2005). Summer temperatures in those areas can be over 5°C higher than in the cold pool south of SLI. Moreover, prey for snow crabs are abundant in the Chirikov Basin (Kolts et al. 2013a). These aspects indicate that growth to maturity in the Chirikov Basin is not limited directly by temperature or food, but rather by ontogenetic emigration.

Directional movements of immature snow crabs (as opposed to adult females, Ernst et al. 2005) are not well documented in the Bering Sea. However, in Bonne Bay, Newfoundland, instar V to VII crabs moved from shallower waters with coarser sediments to deeper, muddier habitats (Comeau et al. 1998). Distributions of snow crab size classes south of SLI (Figs. 6, 7 & 9) suggest that both males and females begin migrating toward the shelf break before reaching maturity. Essentially no adults and few adolescents occurred in the area of very high juvenile density in the northern East sector (Fig. 6). Moreover, highest densities of immature and adolescent crabs were at stations southwest of that juvenile concentration, areas we would expect crabs to migrate through on their way to deeper, warmer waters. As in eastern Canada (Comeau et al. 1998), snow crabs appeared to move from the shallow region of juvenile settlement near SLI to deeper water, where maturation occurs and stimulates migration out of our study area.

In the southeast Bering Sea, gradients in near-bottom temperature are thought to be the cue for ontogenetic migrations of snow crabs (Ernst et al. 2005). However, in most of our study area south of SLI where adult females were found, there was no positive directional temperature gradient (Fig. 2; Chilton et al. 2011). Although the ultimate reason may be to seek higher temperatures of the outer shelf, ontogenetic migration in our study area south of SLI appears to follow bathymetry toward deeper water and not temperature per se.

The near absence of adult females and scarcity of adult males throughout the Chirikov Basin (Figs. 7 & 9) indicate that ontogenetic migration in this sector may also begin for both sexes before reaching maturity. High densities of adolescent crabs at stations in the southern Chirikov Basin (Fig. 6c), where juveniles are mostly absent (Fig. 6a), are further evidence of pre-maturity migrations. While megalopae might not regularly settle at our stations in the southern Chirikov Basin, we suggest that immature and ado-

lescent crabs from peripheral areas may migrate into this region toward warmer waters in the northern and eastern parts of the basin.

Adolescent males are thought not to mate with multiparous females when adult males are present (Sainte-Marie et al. 2008, Turnock & Rugolo 2008), as in much of the southeast Bering Sea. However, adolescent males may be important to reproduction by primiparous females that dominate our southern study area, where adult males are rare but adolescent males are more common. Southwestward migration out of our study area by females after their first mating would place them in areas where larger, adult males are more abundant. Because multiparous females are believed to be inseminated only by adult males (Conan & Comeau 1986, Comeau & Conan 1992, Sainte-Marie et al. 2008), southward emigration of females would be important to ensuring fertilization of their subsequent broods. Flow of current capable of transporting pelagic larvae is greater closer to the shelf break, and much of this westward flow ultimately carries larvae northward into the Chukchi Sea (Fig. 3; Clement et al. 2005, Hu & Wang 2010). Thus, southwestward migration of females probably increases their reproductive input to populations north of the Bering Sea.

Climatic controls on snow crab abundance

South of SLI, snow crabs are very abundant and are the dominant ectotherm predator (J. R. Lovvorn unpubl. data), despite bottom temperatures that may be too low for high rates of settlement and reproduction. Our results indicate that these high crab densities are supported by a localized current that carries larvae from distant sources (cf. Parada et al. 2010) and that infuses warmer temperatures for larval settlement into an area that is otherwise unsuitably cold. Although cold temperatures reduce predation and cannibalism on these juvenile recruits, they also severely limit growth. As a result, females have small size at maturity which reduces their clutch size, and they can breed only every 2 yr. To escape constraints of cold temperatures, both males and females appear to emigrate toward warmer waters. In Alaska, the legal size for this fishery is >78 mm CW and marketable size is >100 mm, whereas all adult females we captured were <68 mm and all adult males were <90 mm. Despite their abundance, crabs in this region will not achieve marketable size without a substantial increase in temperature, but they do contribute pelagic larvae and likely adult crabs to other areas.

The branch of the Anadyr Current that flows eastward just south of SLI is a relatively minor physical flow on a regional scale (Fig. 3), but appears to be quite important to snow crabs and biotic assemblages they affect (Kolts et al. 2013a, J. R. Lovvorn unpubl. data). The magnitude of this small current probably varies with the strength of the large Anadyr Current, which flows eastward toward the island before turning mainly northward but with a portion diverging south of the island (Spaulding et al. 1987, Muench et al. 1988, Clement et al. 2005). The fraction of the Anadyr flow that bifurcates south of the island probably also depends on the strength of northerly versus southerly winds, with southerly winds decreasing the southern diversion of flow (Clement et al. 2005). Positions of the Aleutian Low and related atmospheric systems control the dominance of northerly versus southerly winds, which also control the extent of winter sea ice and the associated cold pool of bottom water (Overland & Pease 1982, Hu & Wang 2010). Thus, long-term climatic shifts in these atmospheric systems (Overland et al. 1999, 2002) might affect this snow crab population by altering not only water temperature, but also the magnitude of juvenile recruitment that is driven by localized currents.

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