TEMPERATURE-DEPENDENT GROWTH OF EARLY JUVENILE SOUTHERN TANNER CRAB \textit{CHIONOECETES BAIRDII}: IMPLICATIONS FOR COLD POOL EFFECTS AND CLIMATE CHANGE IN THE SOUTHEASTERN BERING SEA

CLIFFORD H. RYER,\textsuperscript{1,*} MICHÈLE OTTMAR,\textsuperscript{1} MARA SPENCER,\textsuperscript{1} JANET DUFFY ANDERSON\textsuperscript{2} AND DANIEL COOPER\textsuperscript{2}

\textsuperscript{1}Fisheries Behavioral Ecology Program, RACE Division, National Marine Fisheries Services, Alaska Fisheries Science Center–Hatfield Marine Science Center, 2030 Marine Science Drive, Newport, OR 97365; \textsuperscript{2}Recruitment Processes Program, RACE Division, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115

\textbf{ABSTRACT} Temperature strongly influences the growth of crustaceans and directly controls distribution. Despite being commercially important, there are no data on temperature effects upon growth in newly settled southern Tanner crab \textit{Chionoecetes bairdii}. Recently settled crabs were reared through three consecutive molts, both individually and in groups, at four different temperatures; 2°C, 6°C, 9°C, and 12°C. Survival was higher for crabs grown individually (92%) than those in groups (66%) owing to cannibalism, particularly during molting. There were no temperature effects on survival. Growth rate (mm/day) increased linearly with temperature, a product of exponential decline in intermolt period with increasing temperature and a molt increment that was relatively constant across temperatures. Growth rate, intermolt period, and growth increment did not differ between crabs grown singly or in groups. These data suggest that growth in 0 y aged southern Tanner crabs is strongly inhibited at temperatures less than 2°C. A small mesh beam trawl survey was conducted in the southeast Bering Sea during September 2012, a year when a cold pool (1°C bottom water) dominated the middle shelf. Southern Tanner crab less than 12 mm (carapace width) were concentrated just north of the Alaska Peninsula and along the outer shelf where bottom water was more than 2°C, but largely absent from the middle shelf. In contrast, adult southern Tanner crabs were widely distributed across the middle and outer shelves. It was hypothesized that early juvenile southern Tanner growth is inhibited by cold pool conditions, prolonging vulnerability to predation, and reducing survival. In the future, if sea temperature rises and sea ice is diminished, less frequent and less intense cold pool events may lead to increased persistence of thermally suitable juvenile southern Tanner crab habitat across the southeastern Bering Sea middle shelf region.

\textbf{KEY WORDS:} temperature-dependent growth, survival, recruitment, intermolt period, \textit{Chionoecetes bairdii}, crab

\textbf{INTRODUCTION}

Temperature is often the single most important environmental parameter influencing growth and survival in crustaceans (Hartnoll 1982). As a consequence, direct temperature effects upon growth and survival represent a logical starting point for developing models to forecast climate-driven changes in species distribution. Global mean sea surface temperature is predicted to increase, with warming most prominent at high latitudes (Overpeck et al. 1997). Bering Sea surface water temperature may increase 3°C by 2050 (Wang et al. 2012). This elevated sea surface temperature will likely result in later fall freezing, earlier spring melt, and decreased areal extent of sea ice (Holland et al. 2006, Wang et al. 2012). Lack of sea ice in turn will decrease surface albedo, accelerating the rise in sea surface temperature. In addition to the direct effects of temperature on physiology and growth, northward regress of seasonal sea ice will influence the timing of spring blooms, further altering trophic and ecosystem dynamics (Hunt et al. 2002, Stabeno et al. 2012).

The southern reach of Bering Sea ice also controls the southward extent of the cold pool, a middle shelf bottom layer of cold less than 2°C water (Mueter & Litzow 2008). During cold years, with extensive sea ice formation, the cold pool extends to the southeastern middle shelf (~56° N). During periods of accelerated warming and restricted sea ice transport (1977 to 2008), the cold pool contracts to the northwest (~60° N). For many species, the geographic distribution of preferred habitat shifts poleward with increasing ambient temperature. During the 1977 to 2008 period of warming and resultant sea ice loss, there was a reorganization of communities by latitude, with subarctic species extending their range northward over bottom formerly dominated by the cold pool, whereas arctic species retreated northward (Mueter & Litzow 2008). Snow crab \textit{Chionoecetes opilio}, an arctic species, experienced a northward contraction of its distribution during this period (Orensanz et al. 2004). Potential economic consequences of changes in snow crab abundance and distribution are significant; in 2013 to 2014, the quota for Alaska landed snow crabs was 24,500 metric tons valued at $116 million.

Southern Tanner crabs (hereafter Tanner crabs, \textit{Chionoecetes bairdii}), along with king crabs \textit{Paralithodes} spp. and snow crab, have experienced severe population declines in recent decades, variously ascribed to climate-driven environmental changes (Zheng & Kruse 2000, Orensanz et al. 2004), predation (Livingston 1989), and overexploitation (Orensanz et al. 1998). Currently, Tanner crabs are taken as bycatch in the Bering Sea snow crab fishery, and in relatively small directed Bering Sea and Gulf of Alaska fisheries. In the northeastern Pacific, Tanner crabs occur in coastal waters of Washington and British Columbia, in the Gulf of Alaska, westward along the Aleutian Islands, and northward across a broad swath of the Bering Sea shelf from the Alaska Peninsula northward to approximately 58° N (Zheng & Kruse 2006, Nielsen et al. 2007, Zheng 2008). Adult and juvenile Tanner crabs are found at depths from 10 to more than 400 m (Nielsen et al. 2007) and are generally associated with...
In this depth range, across diverse oceanographic regions, Tanner crabs likely settle on seafloor characterized by a wide temperature range. Individuals typically molt between 6 and 10 times during the first 2–3 y, after which molting becomes annual or semiannual (Donaldson et al. 1981, Ryer et al. 2015). During these first 2 y, environmental parameters such as temperature may exert their greatest influence upon growth. If sexual maturation is size dependent (Zheng 2008), a crab that experiences two or three additional molts during its first year, would become sexually mature 2 or 3 y earlier than another crab with more limited first year growth. Alternatively, if maturation is age dependent, size at maturity would increase. Dawe et al. (2012) proposed that terminal molting in snow crabs is controlled by direct temperature effects on molt frequency during early ontogeny, as well as more indirect temperature and physiological influences upon the life-history decisions that control the incidence of skip-molting during later ontogeny. It is clear that temperature can greatly influence the age and size structure of populations, particularly those that draw recruits from large geographic areas encompassing variation in depth and bottom temperature (Stevens 1990).

Data on temperature dependence of growth in juvenile Tanner crab is restricted to specimens more than 10 mm in carapace width, mostly crabs in their second year of growth. Paul and Paul (2001) found that intermolt period, that is, days between successive molts, decreased from 3°C to 6°C, but did not decrease further between 6°C and 9°C. This would suggest that juvenile Tanner crabs accrue no growth benefit from occupancy of water more than 6°C; however, little is known about the ecology and growth of Tanner crab during their first year, as they are not typically captured during standard fisheries surveys conducted with trawls or pots. In a previous study around Kodiak Island, Gulf of Alaska, Tanner crab settlement onto the bottom in waters less than 20 m in depth, at densities up to 10 crabs/m², was observed. It was speculated that crabs settling in shallow water would experience more rapid growth owing to higher water temperatures when compared with crabs settling in deeper water and that decreased predator abundance in shallow water may further enhance survival (Ryer et al. 2010). For 0 y aged Tanner crabs to fully exploit these shallow waters, they would require the capacity for accelerated growth rates that are not apparent in crabs in their second postsettlement year (Paul & Paul 2001). The present laboratory study was designed to examine the temperature dependence of growth in recently settled C3–C5 stage crabs (instars); essentially those in their first post settlement year. These data would allow us to better understand the distribution of juvenile Tanner crab not only in the Gulf of Alaska but also in the Bering Sea where the presence/absence of the cold pool may influence juvenile habitat quality.

**MATERIALS AND METHODS**

**Crab Collection and Holding**

Second instar Tanner crabs (C2), recognizable by their size (2.9–4.1 mm carapace width) were collected during June 2011 from depths of 10–30 m in nearshore Kodiak Island Alaskan waters using an epibenthic sled (Ryer et al. 2015). A prior study (Ryer et al. 2015) mistakenly identified crabs in this size range as being first-stage (C1) crabs. Few actual C1 stage crabs were retained by the epibenthic sled they used in their study, which had a 3.0-mm mesh codend. This only came to light after Tanner crab larvae were cultured in the laboratory and 72 individuals that molted from megalopa to the first crab stage were measured and found to range from 2.0 to 2.8 mm in carapace width, with a median carapace width of 2.5 mm (C. H. Ryer, unpublished data).

Water temperature at collection sites was 5–7°C at the time of collection. After several days of holding at the Alaska Fisheries Science Center’s (AFSC) Kodiak Laboratory, crabs were shipped to the AFSC Newport Oregon Laboratory in insulated containers in 4–5°C seawater. Mortality during transit was negligible, and typically involved cannibalism upon crabs that molted during transit. In Newport, crabs were held for several days in flow-through seawater tanks (6°C, ~30 salinity) before being used in growth studies. During holding in Kodiak and Newport, crabs were fed daily diced krill, baitfish, squid, and/or bivalve.

**Individual Growth Experiment**

C2 crabs were grown individually in cells to track individual growth rates and to preclude cannibalism. The cells were cylinders (10 cm diameter, 17.5 cm high) made of stiff black plastic mesh (3 mm), with a mesh bottom and an open top. A 10-cm diameter, 5-cm tall piece of PVC pipe was inserted into the top of each mesh cylinder to prevent crabs from escaping. When placed into temperature-controlled seawater tanks, the mesh allowed water exchange between the cells and the larger tank. Each rectangular polyethylene tank (42 cm wide, 63 cm long, 30 cm deep) was supplied with a continuous flow (~35 ml/sec) of temperature-controlled sand-filtered seawater (28–33 ppt). There were two tanks for each experimental temperature (2°C, 6°C, 9°C, and 12°C), with 15 cells per tank. The bottom of each tank was covered with approximately 2 cm of fine sand, such that when cells were pushed down into the sand, the mesh bottom became buried, allowing crabs access to a sand bottom.

Crabs were placed into cells, one per cell, at a temperature of 7°C, after which the temperature was adjusted upward or downward 1°C each day until target temperatures were reached. Crabs that were missing appendages or appeared sluggish in their behavior were not used. Crabs were fed daily on an alternating ration of diced herring, krill, and bivalve, with all uneaten food removed the next day prior to feeding. Cells were systematically moved about each tank weekly to preclude bias and nutrient depletion. The cells were pushed down into the sand, the mesh bottom became buried, allowing crabs access to a sand bottom.

**Group Growth Experiments**

Growth experiments were conducted without cells in four tanks (42 cm wide, 63 cm long, 30 cm deep); one tank at each experimental temperature (2°C, 6°C, 9°C, and 12°C). Each tank contained 2 cm of sand and 2 bundles of black polypropylene mesh gill net material (~1.5 l each) that served as refuge to minimize cannibalism. As in the individual growth experiment,
each tank was supplied with a continuous flow (~35 ml/sec) of temperature-controlled sand-filtered seawater (28–33 salinity). Crabs were fed daily on herring, krill, and bivalve, with uneaten food from the prior day removed prior to each feeding. To initiate the experiment, 30 C2 crabs were placed into each tank, and the initial seawater temperature of 7°C was adjusted upward or downward 1°C each day until target temperatures were reached. For three of the temperature treatments, the experiment was terminated when mean crab carapace width reached 9 mm. This corresponded to roughly 80% of crabs having reached the C5 stage. The 12°C treatment was terminated at 98 days, 9°C at 154 days, and 6°C at 196 days. Because of logistical constraints, the 2°C treatment was terminated when crabs reached mean carapace width of 7.7 mm at 238 days.

Measurements, Growth, and Statistical Analysis

For the individual growth experiment, cells were inspected daily for molts. Crabs that had molted during the preceding week were removed from cells and photographed using a digital camera attached to a dissecting scope. Crabs were then returned to their cells. For crabs grown in groups, individuals were similarly photographed every 14 days. Measurements of crab carapace widths were taken from digital photos.

In an initial comparison, difference in carapace width between temperature treatments at 70 days was tested. For individual growth experiments mean carapace width for each tank was calculated, using these values as the units of replication for testing temperature effects. For group growth, individual crabs were considered as the units of replication. Both individual and group carapace width data were normally distributed and homoscedastic. Temperature effects were tested using analysis of variance (ANOVA) and Tukey’s multiple comparisons (Sokal & Rohlf 1969). The frequency of various molt stages (C2, C3, C4, and C5) was compared between temperature treatments and experiments after 70 days of growth. In this analysis, for which log-linear models (Fienberg 1980) were used, individuals were the units of replication in both experiments.

Next, equations were derived to describe growth (mm/day) as a function of temperature. For crabs grown individually, the growth rate of the C3–C5 stage was calculated for each individual, and then the average for each tank was calculated. The resultant averages were homoscedastic and normally distributed, as indicated by Bartlett’s tests and examination of rankit plots (Sokal & Rohlf 1969). Tank averages where then regressed against temperature. For crabs grown in groups, mean carapace width was regressed against day for the duration of each temperature treatment. The resultant growth rates (regression coefficients) were then regressed against temperature. For individually grown crabs, where two replicate growth rates (i.e. 2 tanks) were available at each temperature, an ANOVA and Tukey’s multiple comparison test (Sokal and Rohlf 1969) was conducted to test for temperature effects upon growth.

Finally, for crabs grown individually, the components of growth were examined; intermolt period (molt interval) and size increment for each molt. Both intermolt period and increment were averaged by tank. Resultant intermolt period data were homoscedastic, normally distributed, and analyzed by ANOVA, testing for effects of temperature and molt stage (C3–C4 molt versus C4–C5 molt). In addition, a 2-parameter exponential decay curve was fit to the intermolt period data for each molt stage. Data for size increment were normally distributed, but were heteroscedastic; however, this nonequality in variances was not extreme, and ANOVA is generally robust to heteroscedasticity. Therefore, these data were analyzed using ANOVA, recognizing that an assumption of the analysis was violated.

Demersal Sampling over the Bering Sea Shelf

As part of another study (Hurst et al. 2015), small mesh beam trawling was conducted over the outer, middle, and inner Bering Sea continental shelf, from 60° N southward to the Alaskan Peninsula, during August and September 2012. Tows were made with a 3-m beam trawl, with 7-mm mesh and a 4-mm mesh codend liner, at a speed of 1.3 m/sec for 5–10 min. A depth sounder mounted on the net provided real-time data to allow determination of when the net was in contact with the bottom. Crabs were sorted from the catch, enumerated, and then frozen for later identification and measurement. Global positioning data were used to measure the length of each tow and correct catch to catch per unit effort (CPUE). In the laboratory, crab carapace widths were measured to the nearest 0.1 mm. Tanner crabs, snow crabs, and possible hybrids were discriminated following the methods of Urban et al. (2002). Eye color is, however, a less reliable character for distinguishing early juvenile Chionoecetes spp. (D. Urban, personal communication) and was further compromised by freezing. Therefore, epistome shape was considered as the primary diagnostic character for identifications. From this data set, data were taken on the spatial distribution of small Tanner crabs less than 11.4 mm carapace width (C2–C5 stages). Data on larger sexually mature Tanner crab from the Bering shelf in 2012 were available from the annual AFSC Bering Sea bottom trawl survey (Stauffer 2004, Lauth & Acuna 2007). Density data from these two sources were plotted on maps detailing depth and bottom temperature, allowing a visual comparison of the spatial distribution of recently settled versus older Tanner crabs. In addition, linear least squares regressions (Sokal & Rohlf 1969) were conducted for both juvenile and adult crab CPUE as a function of bottom temperature.

RESULTS

Crabs grown individually experienced significantly higher survival (92%) during the first 70 days of the experiment, compared with crabs grown in groups (66%, $G = 25.33$, df = 1, $P < 0.001$). There was no independent effect of temperature upon survival, although there was a tendency, albeit insignificant ($G = 6.75$, df = 3, $P = 0.080$), for growth treatment (individual versus group) to interact with temperature in influencing survival. Although survival was fairly uniform between temperatures for individually grown crabs (87%–97%), there was a tendency for survival to decrease at higher temperatures in groups (77% for both 2°C and 6°C, 50% and 60% for 9°C and 12°C, respectively). Growth was strongly influenced by temperature, as demonstrated by the mean carapace width of crabs after 70 days (Fig. 1). Comparing crabs grown individually in cells ($F_{[3,1]} = 151.0$, $P < 0.001$), those at 12°C were significantly larger than those at the other temperatures (Tukey’s pairwise
comparisons, \( P < 0.05 \); crabs at 9°C and 6°C were similarly sized, but significantly larger than those grown at 2°C. Comparable results were observed among crabs grown in group tanks \( (F_{[3,7]} = 62.3, P < 0.001) \). Again, those at 12°C were significantly larger than those at the other temperatures, whereas crabs at 9°C and 6°C were similarly sized, but significantly larger than those grown at 2°C (Tukey’s pairwise comparisons, \( P < 0.05 \)).

These differences in growth between temperature treatments were also apparent in the molt stage frequency distributions in the two experiments (Fig. 2). After 70 days, crabs from the 2°C treatments were largely dominated by C3 stage crabs, whereas those from the 12°C treatments were largely C5 stage crabs \( (G = 11.94, df = 11, P < 0.001) \). The treatments of 6°C and 9°C were a mixture C3, C4, and C5 stage crabs. Whether crabs were grown individually or in group tanks had no influence upon the temperature dependence of these molt stage distributions \( (G = 9.78, df = 6, P = 0.134) \).

Crab growth rate (mm/day) increased linearly with increasing temperature (Fig. 3). The carapace width of crabs grown individually increased 0.02 mm/day at 2°C, 0.03 mm/day at 6°C, 0.06 mm/day at 9°C, and 0.07 mm/day at 12°C. Slightly lower, but similar rates of growth were seen in crabs grown in groups.

This temperature effect was largely attributable to changes in intermolt period (days between successive molts). Intermolt period decreased with increasing temperature \( (F_{[3,4]} = 225.7, P < 0.001) \). Although the intermolt period was longer for the C4–C5 transition than for the C3–C4 transition \( (F_{[1,4]} = 228.09, P < 0.001) \), the effect of temperature was consistent (molt–temperature interaction: \( F_{[3,4]} = 4.12, P = 0.102 \)). Consequently, the intermolt period at each successive temperature differed significantly from the next temperature (Tukey’s pairwise comparisons, \( P < 0.05 \)). The intermolt from C3 to C4, which was 81 days at 2°C, was reduced by 36 days (44.5%) at 6°C, 51 days (63%) at 9°C, and 58 days (72%) at 12°C. Similarly, the period from C4 to C5, which was 100 days at 2°C, was reduced by 39 days at 6°C, 57 days at 9°C, and 66 days at 12°C.

Increase in carapace width, expressed as percent increase, differed between molts \( (F_{[1,4]} = 33.60, P = 0.004) \), with mean percent increases of 37% for the C3–C4 molt, and 30% for the
C4–C5 molt. There was no overall influence of temperature upon percent increase in carapace width ($F_{[3,4]} = 0.08, P = 0.997$). There was however a trend, albeit insignificant, for temperature effects that differed between molts ($F_{[3,4]} = 4.68, P = 0.085$). Percent carapace increase was similar, 33.5%, at 6°C but tended to increase at both higher and lower temperatures for the C3–C4 molt, whereas trending lower for the C4–C5 molt.

Survey data from the southeastern Bering Sea demonstrate that early juvenile Tanner crab (C2–C5 stage) had a very different spatial distribution during the summer 2012 than older sexually mature Tanner crabs (Fig. 4A, B). Juveniles were concentrated along the outer shelf and in the vicinity of the Alaska Peninsula, but were largely absent from the middle shelf, which was characterized by cold pool bottom temperatures (<2°C). In contrast, adult Tanner crab distribution extended from the outer shelf onshore through much of the middle shelf and the cold pool. To consider only the core area of juvenile Tanner crab distribution in the southeastern Bering Sea, stations in Bristol Bay and the inner shelf along the Alaska mainland were eliminated. In the remaining area of juvenile Tanner crab concentration, there was a clear positive linear relationship between bottom temperature and natural log-transformed juvenile CPUE ($r^2 = 0.327, F_{[1,41]} = 19.92, P < 0.001; $Fig. 4C). For adult crabs, stations in Bristol Bay and the inner shelf along the Alaska mainland were similarly eliminated, but also eliminated those north of 58°N. In this core area of adult distribution, there was no significant relationship between temperature and natural log-transformed CPUE ($r^2 < 0.001, F_{[1,162]} = 0.06, P = 0.814; $Fig. 4D).

**DISCUSSION**

Tanner crabs go through multiple molts during their first 2 y, or perhaps 3 y, afterward molting more or less annually (Donaldson et al. 1981). Consequently, this is an ontogenetic period when environmental factors may strongly influence ultimate population structure. Our results indicate that growth of Tanner crabs, and hence the number of molts, during their first year is highly temperature dependent. Intermolt periods and their pattern of temperature dependence were very similar to those reported for red king crab *Paralithodes camtschaticus* (Stoner et al. 2010) and blue king crab *Paralithodes platypus* (Stoner et al. 2013). Tanner C3–C4 intermolt period ranged from 81 days at 2°C to 23 days at 12°C. Similarly, the C4–C5 intermolt period ranged from 100 days at 2°C to 34 days at 12°C. From these data, the potential cumulative effect of temperature upon juvenile growth as well as the age and/or size structure of Tanner crab populations is apparent. Temperature-dependent growth will be an important consideration in predicting the consequences of climate change. As sea temperature rises, the age-at-size and recruitment age of Tanner crab can be expected to decrease in their current range. In an analysis of temperature records and red king crab growth, Stevens (1990) concluded that crab age at recruitment in the eastern Bering Sea had decreased from 9.5 to 7.5 y during warming that occurred during the 1980s.

The Bering Sea has a broad continental shelf, over which depth and bottom temperature changes gradually over great distances during any given year. A prominent, yet ephemeral thermal feature of the southern Bering Sea is the cold pool. It is a layer of cold (<2°C) bottom water on the middle shelf, formed through sea ice melting, which can extend almost to the Alaska Peninsula during cold years but contracts farther northwest during warm years (Stabeno et al. 2012). During the summer, it is bounded by warmer more than 2°C inner and outer shelf bottom waters. The middle shelf has experienced moderate to
strong cold pools years since 2006, with a particularly strong cold pool in 2012. During the summer of 2012, juvenile Tanner crab presumed to be less than 3 y old were concentrated on the outer shelf, absent from the inner shelf, and largely absent from the middle shelf, except immediately north of the Alaska Peninsula and around the Pribilof Islands. The only bottom water that did not dip well below 2°C during 2012 was the outer shelf, where early juvenile Tanners were concentrated. In contrast, adult and subadult Tanners were widely distributed across the middle shelf in 2012. Tanner crab larvae are widely distributed across the outer and middle shelf during spring and early summer (Incze et al. 1987). Therefore, it is likely that Tanner crab larvae settle widely across the outer and middle shelf during the summer, given circulation patterns that promote larval retention (Parada et al. 2010). The absence of juveniles on the middle shelf during 2012, after a 6-y string of moderate to strong cold pools, may have been a consequence of low postsettlement survival. We suspect that temperatures less than 2°C severely limited the survival of juvenile Tanner crab either directly, or indirectly, by slowing their growth and extending the time during which they are vulnerable to predation. Juvenile Tanner crab are a dominant prey for Pacific cod *Gadus macrocephalus*, which consume an estimated 84%–94% of 1 y aged crabs annually (Livingston 1989).

The crabs used in our growth experiments were collected from the Gulf of Alaska, around Kodiak Island. Although there is genetic differentiation in Tanner crab populations throughout their range in the North Pacific, levels of genetic diversity are low (Merkouris et al. 1998). This is a consequence of larval dispersal via the Alaska Coastal Current, which moves north-westward along mainland Alaska in the Gulf of Alaska, then through Unimak Pass into the Bering Sea (Bunch et al. 1998). Nonetheless, there is some genetic differentiation between Tanner crabs around the Pribilof Islands and those farther eastward in the southeastern Bering Sea (Bunch et al. 1998), which is also reflected in female size at maturity (Somerton 1981). We consider it reasonable to assume that temperature-dependent growth rates, derived from experiments with Kodiak crab, are...
representative of crabs in the Bering Sea; however, comparison of growth characteristics from throughout the Tanner crab range is clearly needed.

If early juvenile Tanner crabs are indeed limited by temperatures less than 2°C, this is in stark contrast with what little is known for snow crab, an arctic species widely distributed in the North Pacific, Arctic, and north Atlantic Oceans (Adams 1979, Ernst et al. 2012). In the southeastern Bering Sea, snow crab are most abundant in areas routinely subjected to cold pool temperatures (<2°C). While Tanner crab have accelerated growth at temperatures up to 12°C, it has been speculated that juvenile snow crab may have very narrow temperature tolerances and are associated with bottom waters less than 3°C (Dionne et al. 2003). As such, recently settled snow crab may be particularly vulnerable to negative effects of ocean warming, representing the “weak link” for this species (Dionne et al. 2003).

Our predictions regarding current and future distributions of Tanner crab assume that temperature plays a decisive role. Clearly, other factors such as larval supply and advection (Roughgarden et al. 1988), primary production and its timing (Hunt & Stabeno 2002), predation, and the availability of suitable habitat (Stoner 2009) are also important. A combination of these factors has been suggested to explain the recent poleward contraction of snow crab distribution in the Bering Sea (Orensanz et al. 2004, Mueter & Litow 2008). Sea ice retreat during a period of accelerated warming (1975 to 1979), and resultant increased bottom temperature, is believed to have shifted favorable juvenile habitat to the northwest. Once extirpated from the southeastern Bering Sea, it may be difficult for juveniles to become reestablished (“environmental ratchet hypothesis”; Orensanz et al. 2004). Even though adults may migrate southward, currents over the middle shelf generally move larvae northward. In addition, a northward expansion of Pacific cod occurred, increasing mortality rates for juvenile crabs (Livingston 1989). We consider it logical that, as with snow crab, temperature will be a major driver of Tanner crab distribution in the future, with other physical and biological factors acting to modify this relationship. Importantly, because the center of Tanner crab distribution is to the south, along the Alaska Peninsula and in the Gulf of Alaska, the generally northward currents should allow Tanner crab to rapidly occupy areas of the Bering Sea vacated by snow crab as the southerly extent of the cold pool moves northward.

In contrast to the Bering Sea, thermal habitats in the Gulf of Alaska are more spatially varied. A narrow continental shelf with numerous coastal embayments, and in the southeast, inland fjord systems (Nielsen et al. 2007), produces a complex mosaic of nearshore bottom temperatures. In nearshore waters, crabs may experience more than 13°C bottom water during the summer, in contrast to 5°C bottom water several miles offshore (Ryer et al. 2015). Around Kodiak Island, juvenile Tanner crabs grow more rapidly in protected embayments with fine sediments, compared with other more exposed nearshore locations (Ryer et al. 2015). It is suspected that elevated temperatures associated with shallows in these bays accelerate crab growth, particularly immediately postsettlement (May and June) when bottom temperatures at depths of 15–30 m have yet to reach summer highs of 12°C and 13°C. As bottom temperatures rise in coming decades, more coastal embayments will experience summer bottom temperatures in the range of 12–13°C earlier in the spring and later in the fall, expanding thermal opportunities for growth. Experiments in this study, however, only examined temperature up to 12°C. How summer bottom temperatures of 15°C or higher influence growth and survival in 0 y aged Tanner crabs is unknown.

Sources of mortality for recently settled Tanner crabs are largely unknown. Although Pacific cod prey extensively upon larger 1 y aged Tanner crab, annually consuming 84%–95% of the eastern Bering Sea population (Livingston 1989), there is a dearth of information on 0 y aged crabs. Cannibalism is common among crustaceans, both in nature and in hatcheries. Survival of juvenile Tanners grown individually was relatively high, at 92%, and was uninfluenced by temperature. In contrast, survival was significantly lower in groups, and there was a trend toward greater mortality at higher temperatures. We attribute this lower group survival to cannibalism, as intermolt crabs consuming newly molted crabs were periodically observed. The incidence of cannibalism may increase as size disparity increases between slow and fast growing individuals. Sainte-Marie and Lafrance (2002) reported greater cannibalism in laboratory populations with mixed cohorts. Individuals of many species seek out refugia when molting (Tamm & Cobb 1978, Hines et al. 1987), or synchronize their molting with other individuals, so as to swamp potential predators/cannibals (Reaka 1976, Ryer et al. 1997). This suggests that cannibalism may play a role in mortality in natural habitats, particularly where crabs have aggregated into favorable habitats at densities of up to 10 individuals/m² (Ryer et al. 2015). Cannibalism also has implications for potential aquaculture with Tanner crab. The decline in northeastern Pacific crab stocks has generated interest in the efficacy of crab enhancement, wherein juvenile crabs are cultured and then released into the wild to reestablish stocks and/or support fisheries. Cannibalism in the hatchery can be a major problem, wherein natural agonistic behavior is exacerbated in high-density culture environments (Zmora et al. 2005).

In summary, during the first year, temperature has a strong effect upon growth in juvenile Tanner crab; however, this temperature dependence appears to become less pronounced during the second year (Donaldson et al. 1981), perhaps indicating an ontogenetic shift in habitat temperature/depth preference. The temperature of early juvenile habitat has the potential to greatly influence age and size structure of Tanner populations, as those crabs spending their first year in warmer water may grow larger or mature earlier than crabs settling onto colder bottom. Decrease in the duration of size-related vulnerability to predation will also likely increase the survival of Tanner crab settling in warmer bottom waters, shallow in the Gulf of Alaska, deeper in the southeastern Bering Sea. This temperature dependence in growth may be a principle factor governing the distribution of Tanner crab in the southeastern Bering Sea, where recently settled Tanner crabs appear to be absent from bottom recently subjected to cold pool temperatures. It is proposed that less frequent and decreased sea ice coverage, with resultant cold pool contraction, will set up the prerequisite thermal conditions for further poleward contraction of snow crabs, with concurrent expansion of early juvenile Tanner crab habitat throughout the southeastern Bering Sea middle shelf region. Additional data on the growth and survival of early juveniles at temperatures less than 2°C, along with continued sampling of early juvenile abundances relative to cool
pool expansion and contraction in future years will allow for a more rigorous evaluation of this hypothesis.

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LITERATURE CITED


