

Spatial distribution of juvenile and adult female Tanner crabs (*Chionoecetes bairdi*) in a glacial fjord ecosystem: implications for recruitment processes

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A systematic pot survey in Glacier Bay, Alaska, was conducted to characterize the spatial distribution of juvenile and adult female Tanner crabs, and their association with depth and temperature. The information was used to infer important recruitment processes for Tanner crabs in glaciated ecosystems. High-catch areas for juvenile and adult female Tanner crabs were identified using local autocorrelation statistics. Spatial segregation by size class corresponded to features in the glacial landscape: high-catch areas for juveniles were located at the distal ends of two narrow glacial fjords, and high-catch areas for adults were located in the open waters of the central Bay. Juvenile female Tanner crabs were found at nearly all sampled depths (15–439 m) and temperatures (4–8°C), but the biggest catches were at depths <150 m where adults were scarce. Because adults may prey on or compete with juveniles, the distribution of juveniles could be influenced by the distribution of adults. Areas where adults or predators are scarce, such as glacially influenced fjords, could serve as refuges for juvenile Tanner crabs.

Keywords: *Chionoecetes*, glacial habitat, juvenile, recruitment, refuge, spatial autocorrelation, spatial distribution, Tanner crab.

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Introduction

Tanner crabs (*Chionoecetes bairdi*) and snow crabs (*Chionoecetes opilio*) support valuable commercial fisheries in the North Pacific and North Atlantic oceans. There are commercial fisheries in the Gulf of Alaska from southeastern Alaska to the Aleutian Islands (Tanner crabs), in the Bering Sea (Tanner and snow crabs), and off the east coast of Canada (snow crabs). Tanner and snow crab stocks in the Bering Sea, where most of the Alaskan commercial harvest is taken, have independently experienced severe fluctuations and general declines in abundance in recent years. Resulting fishery closures (Rugolo *et al.*, 2006) have had a substantial economic impact and highlighted concerns about the health of fished stocks in Alaska (Orensanz *et al.*, 1998). It is not known whether these population fluctuations are caused by environmental variability (Anderson and Piatt, 1999; Zheng and Kruse, 2000; Orensanz *et al.*, 2004), intrinsic life history characteristics (Wahle, 2003), predation (Livingston, 1989), or commercial fishing (Orensanz *et al.*, 1998).

Different areas may have different recruitment patterns based on the relative magnitude and importance of environmental and biological variables. Efforts to understand the causes of fluctuations in abundance of *Chionoecetes* crabs in Alaska have largely focused on identifying the major variables that are likely

to affect recruitment (Zheng and Kruse, 2000, 2003, 2006; Rosenkranz *et al.*, 2001). Environmental and biological variables can affect recruitment of benthic crustaceans that have planktonic larvae by influencing the mortality or the distribution of larvae in the water column (Botsford *et al.*, 1998), the availability of suitable substratum for settlement (Wahle and Steneck, 1991), or post-settlement mortality (Heck *et al.*, 2001). For example, specific areas may receive a greater supply of larvae (Etherington and Eggleston, 2003), or provide the conditions for greater post-settlement survival of juveniles (Moksnes, 2002). Environmental conditions might also affect female fecundity and the reproductive cycle, growth rates, and almost all other aspects of crab biology.

Although the harvest of Tanner crabs in southeastern Alaska is an order of magnitude less than in the Bering Sea, the harvest has been more stable. Catches in the eastern Bering Sea have ranged between highs of 67 million pounds in 1977 and 40 million pounds in 1990 to lows near zero in 1985 and 1996 (Rugolo *et al.*, 2006). The fishery there was closed in 1986, 1987, and 1997–2004. In contrast, catches in southeastern Alaska have fluctuated between a high of 3.3 million pounds in 1982 and a low of 1 million pounds in 1985, and averaged 1.7 million pounds between 1969 and 2000 (Bishop *et al.*, 2002). There have

been no region-wide fisheries closures for Tanner crabs in southeastern Alaska. The difference in the extent of variation between harvests in the two areas suggests that the fundamental processes controlling fluctuations may differ.

Little is known about the spatial distribution of juvenile Tanner crabs in southeastern Alaska. In contrast to the Bering Sea, where National Marine Fisheries Service trawl surveys provide information on the distribution of both juveniles and adults (Zheng and Kruse, 2006), stock assessment surveys in southeastern Alaska are conducted using pots (Clark *et al.*, 1999b). The surveys neither provide information on the relative abundance of juveniles nor allow comparison of the spatial distribution of juveniles and adults.

We conducted a comprehensive systematic survey to determine the abundance and distribution of adult and juvenile Tanner crabs in Glacier Bay, a glacial fjord network within southeastern Alaska, as part of a study to understand the ecological effects of implementing marine protected areas. Here, we describe the spatial distributions of juvenile and adult Tanner crabs and relate them to depth and temperature. The findings are applied to improving understanding of the important recruitment variables for *Chionoecetes* crabs that may explain differences in recruitment patterns for *Chionoecetes* spp. from different parts of Alaska.

Methods

Study area

Glacier Bay is located in the northern portion of southeastern Alaska (Figure 1). Glaciers have dramatically altered and continue to strongly influence the landscape, and extended to the mouth of Glacier Bay at the neoglaciation maximum of the late 1700s (Lawrence, 1958). Since then, glaciers have retreated ~100 km, to form the present large (1255 km²) fjord-estuarine ecosystem. A central Bay splits into two more recently de-glaciated arms: the East Arm and the West Arm. Glacial discharge transfers large volumes of fresh water and sediment from the terrestrial to the marine environment and forces many of the oceanographic processes within the fjord (Matthews, 1981). Deep fjords, shallow sills, and large gradients in temperature, salinity, sedimentation, and ecological succession combine to create a highly heterogeneous marine environment that can affect the distribution of marine species including other species of crabs (Taggart *et al.*, 2003).

Tanner crabs are abundant in Glacier Bay. Compared with other commercial fishing districts in southeastern Alaska, Glacier Bay had the largest catch of Tanner crabs from 1983 to 1998 (Clark *et al.*, 1999b). The Tanner crab fishery is now being phased out following a 1998 United States congressional legislation to cease commercial fishing within the park to create a large, high latitude marine protected area (US Congress, 1998).

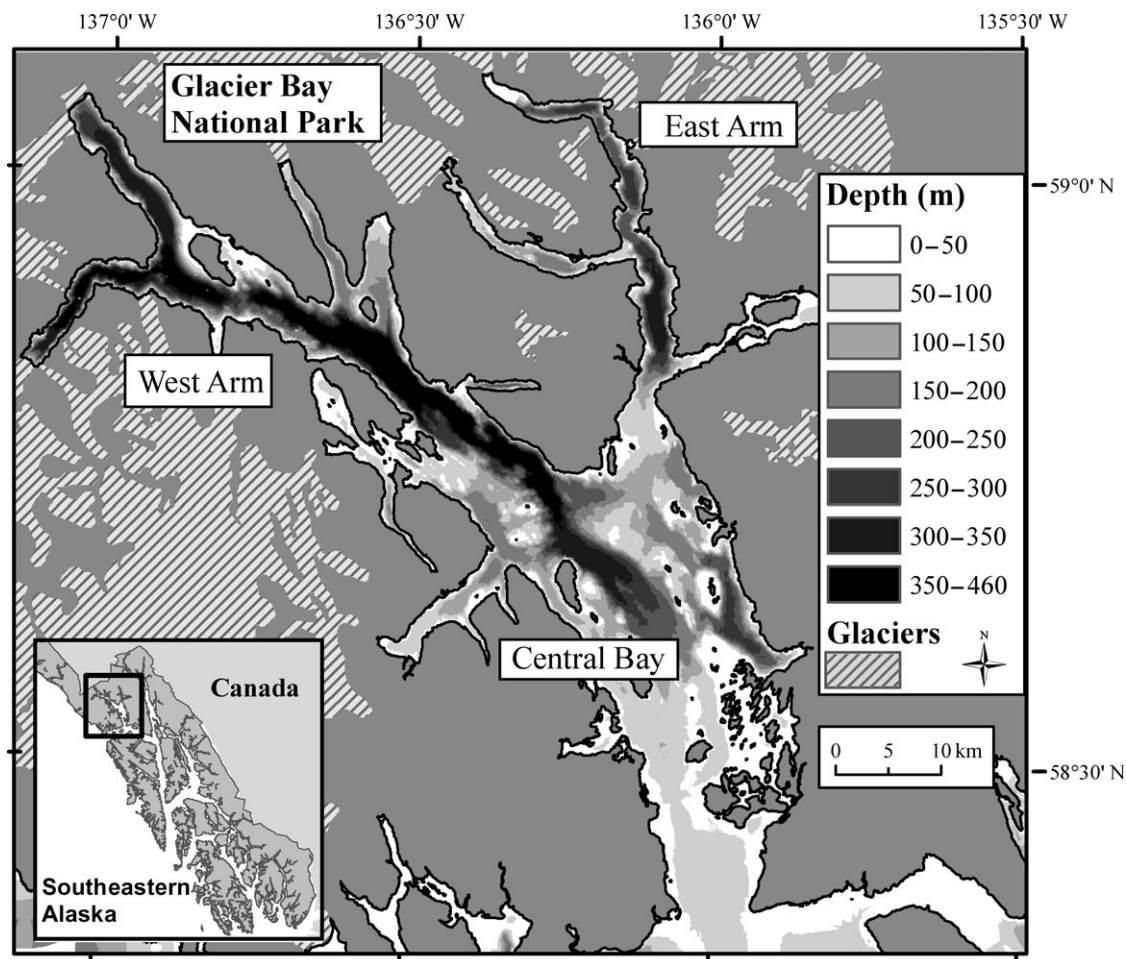


Figure 1. Map of the study area in Glacier Bay National Park, Alaska, including depth contours and locations of glaciers.

Sampling

During July and August of 2002, pots were set at 415 stations on a systematic grid covering the entire bay, except for two areas where access was prevented by shallow water or icebergs (Figure 2). Sampling stations were 1.5 km apart in areas closed to commercial fishing, and 1.8 km apart in areas that remain open to commercial fishing. At each station, a 2.5 × 1 m, 89-mm mesh, top loading, conical Tanner/king crab pot was used to sample adult crabs. A 1 × 0.5 m, 28.6-mm mesh shrimp pot, manufactured by Ladner Traps (Delta, British Columbia, Canada), was attached to the adult pot with a 20-m tether to sample juvenile crabs. Three tunnels with 76.2-mm stainless steel ring openings were located at equal intervals along the side of the shrimp pot. Crab pots were baited with chopped herring in two 1.9-l bait jars and 1/2 pink salmon hanging bait (Clark *et al.*, 1999a). Shrimp pots were baited with chopped herring in one 0.5-l bait jar and 1/4 pink salmon hanging bait. Pots were set in the afternoon and retrieved the following morning, usually in the same order they were set, to keep the soak times consistent. Average soak time was 18.1 h [± 2.4 h s.d. (standard deviation), minimum 10.0 h, maximum 25.2 h]. Temperature data-loggers (StowAway TidBiT, Onset Computer Corporation) were attached to each crab pot, and temperature was recorded in 0.15°C bins every 2.5 min. Depth (m) was recorded for each station at the times the pots were set. All Tanner crabs captured in the pots were counted and measured. For each, carapace width (CW), including spines, was measured with vernier calipers to the nearest millimetre, and shell condition was classified as premoult, soft, new, old, or very old-shell (Jadamec *et al.*, 1999). Catch per unit effort (cpue) was defined as the number of crabs caught at each station from both the crab pot and the shrimp pot. All bycatch (crabs, fish, shrimp, gastropods, echinoderms) collected from the pots were counted and identified to species.

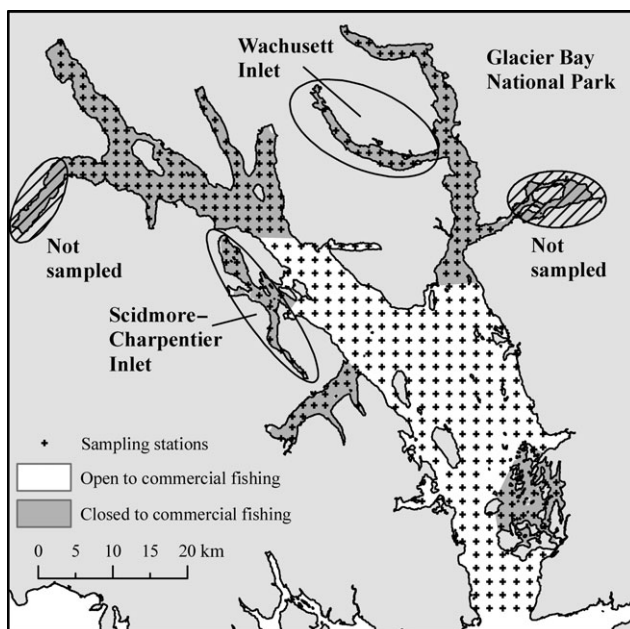


Figure 2. Systematic sampling grid for the Glacier Bay survey conducted in 2002 (areas not sampled are hatched, stations within Wachusett Inlet and Scidmore-Charpentier Inlet are circled, and areas closed to commercial fishing are in grey).

Analyses

Because the goal was to compare the distribution of adult and juvenile crabs, we limited most analyses to females because it is easier to classify them as either adult or juvenile; males are difficult to classify. During the female moult to adult morphology, the abdominal flap enlarges to cover the abdomen (Donaldson *et al.*, 1980). Females do not moult again after this post-pubertal moult, which is referred to as the terminal moult. Males also undergo a moult to adult morphology, during which the chela height (CH) enlarges relative to the CW (Conan and Comeau, 1986; Stone, 1999; Tamone *et al.*, 2005, 2007). Therefore, determination of male adult morphology requires measurement of CH (Somerton, 1980; Conan and Comeau, 1986; Stevens *et al.*, 1993). In this study, only female crabs could be categorized unambiguously as juvenile or adult, because male CH was not measured.

Female crabs were subdivided into three classes based on whether or not a crab exhibited adult morphology, and the shell condition (an estimate of the time since the previous moult) of adult crabs. Each female crab was categorized as a juvenile, a new-shell adult (estimated to be 2–12 months post-ecdysis), or an old-shell adult (estimated to be >13 months post-ecdysis) (Jadamec *et al.*, 1999). We refer to these classes as ontogenetic stages, because although the true crab age is unknown, these categories reflect a common progression in life history. Although some adult females were classified as very old-shell in the field, preliminary analyses indicated that the old- and very old-shell classes had similar spatial distributions and associations with habitat variables. Therefore, adult crabs in these two categories were combined to simplify analyses.

Because the size range of juveniles captured in the survey was large, we subdivided juvenile females into four size classes based on junctions in the size-frequency histogram (Figure 3). Juveniles in the two largest size classes (66–73 mm, and 74–95 mm) could moult either to adult morphology or to another juvenile instar based on the observed size frequency of adult females and moult increment data from a growth study in Kodiak, Alaska. In the growth study, the mean increment for a moult to adult morphology was 14 mm and to the next juvenile instar 18 mm (Donaldson *et al.*, 1980).

Although most of the analyses were conducted primarily with females, some did include males. For these analyses, males were partitioned into small (<80 mm CW) and large (≥ 80 mm CW) size classes. Most large males were capable of fertilizing females in a laboratory study conducted in Kodiak (Paul and Paul, 1990), whether or not they had undergone the moult to adult morphology.

Spatial distribution

We mapped cpue for each female ontogenetic stage and the proportion of juvenile female size classes present at each station with ArcGIS (ESRI, 2004) software. The software program GeoDistn, which computes a modified Cramer-von Mises test (Syrjala, 1996), was used to test for differences between the spatial distributions of each ontogenetic class (females) or size class (males). We also compared the spatial distribution of juveniles caught in shrimp pots with that of juveniles caught in crab pots. Values of *p* were calculated by comparing the observed test statistic to 1000 random permutations of the data.

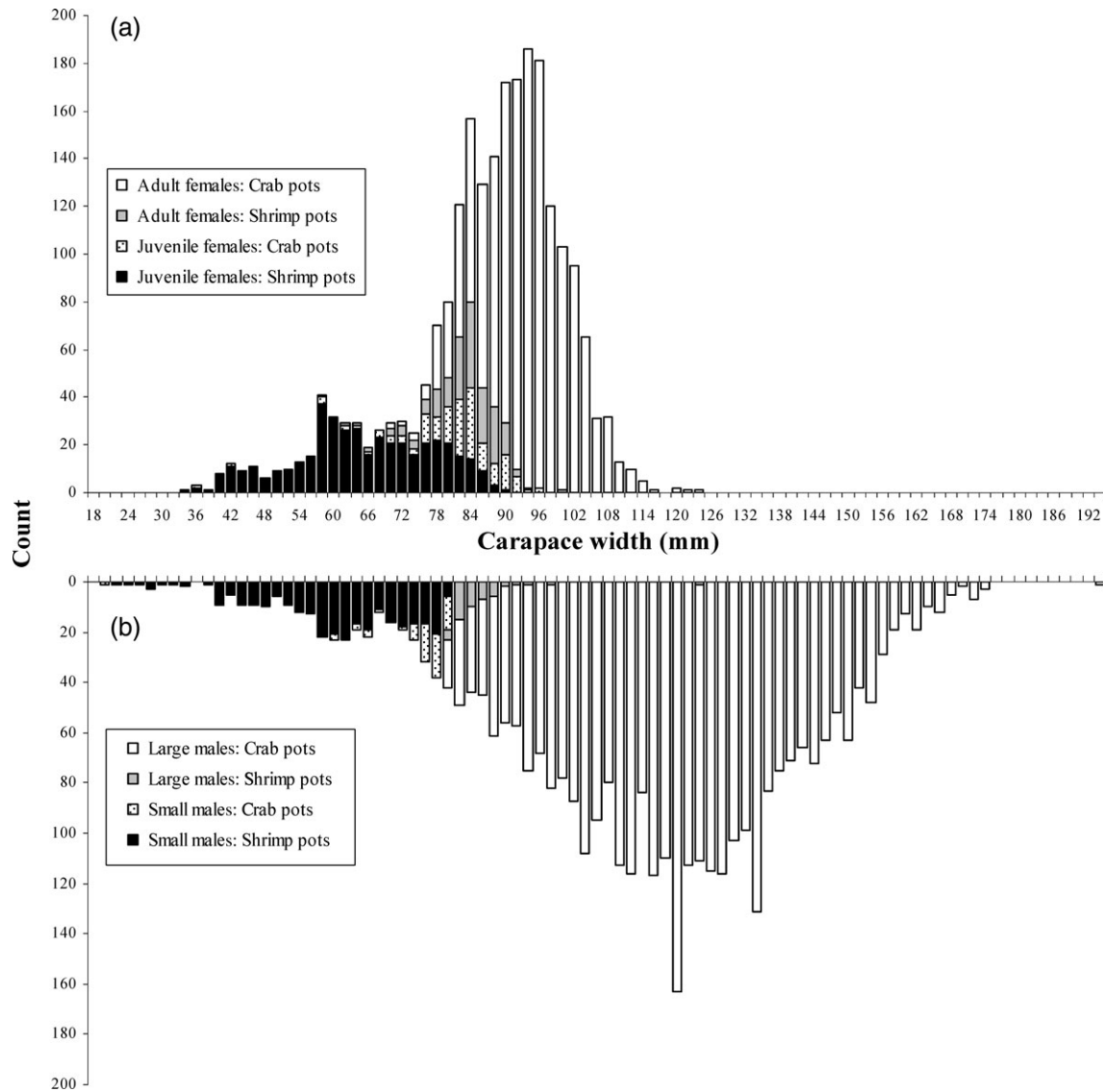


Figure 3. Size frequency distributions for (a) female and (b) male Tanner crabs. Juvenile females and small males (<80 mm CW) caught in shrimp pots are represented by black bars; those caught in crab pots are stippled. Adult females and large males caught in crab pots are represented by white bars; those caught in shrimp pots are grey.

Spatial autocorrelation

We characterized the magnitude and the range of spatial autocorrelation in cpue data for each female ontogenetic stage using a correlogram, for which Moran's index (I) was calculated as a function of distance (Oden, 1984; Perry *et al.*, 2002). Moran's I detects the degree of clustering for points within a given distance of each other by comparing the local variation (points j within distance d of point i) with the total variation:

$$I_d = \frac{n \sum_{i=1}^n \sum_{j=1}^n w_{ij} (y_i - \bar{y})(y_j - \bar{y})}{\sum_{i \neq j}^n \sum_{j=1}^n w_{ij} \sum_{i=1}^n (y_i - \bar{y})^2}, \quad (1)$$

where n is the number of observations, y_i and y_j attribute values at locations i and j , respectively, and w_{ij} the weight at distance d (1 if point j is within distance d from point i , otherwise 0). An I value close to +1 indicates clustering, whereas a value close

to -1 indicates dispersion (Moran, 1950). We used the minimum distance over water between stations as the distance d . In our application, Moran's I [I_d in Equation (1)] is the degree of clustering between stations separated by over-water distance d .

We calculated Moran's I for nine lag distances from 2000 to 60 000 m using the Spatial Autocorrelation (Moran's I) tool in ArcGIS version 9.1. Initial lag distances (2000–4000 m) were selected to include similar numbers of stations in areas closed (1.5 km grid) and open (1.8 km grid) to commercial fishing. For both grid sizes, a lag distance of 2000 m includes adjacent stations at 90, 180, 270, and 360 degrees, and a lag distance of 2800 m includes adjacent stations in all directions. The distance lag of 4000 m includes similar numbers of stations from both grid sizes. Distance lags were gradually increased after 4000 m to reflect the scale of the study area, and were limited to half the maximum distance between stations (Rossi *et al.*, 1992).

Clustering for distances <2000 m could not be detected, because this distance represents the minimum resolution of the sampling grid.

A z score was calculated to test for significant departures from a random distribution for each I value in the correlogram:

$$z = \frac{I_d - E[I_d]}{\sqrt{\text{var}I_d}}, \quad (2)$$

where $E[I_d]$ (the expected value of I_d for a random distribution) = $-1/(n-1)$ (Getis and Ord, 1992). A Bonferroni criterion was used to ensure global significance of the correlogram. To meet this criterion, at least one of the I_d values in each distance lag had to be significant at the level of $0.05/k$, where k is the number of distance lags (Oden, 1984). This criterion corresponds to a z score of 2.78 for $k = 9$ (Zar, 1999).

High-catch areas

The local spatial autocorrelation statistic Getis-Ord G_i^* was used to locate areas of clusters of high cpue values for each female ontogenetic stage. The G_i^* statistic [Equation (3)] represents the proportion of the sum of the values of an attribute x within a distance d of point i to the sum of the values of x for the entire study area, and it also incorporates the statistical significance of each G_i^* value:

$$G_i^*(d) = \frac{\sum_j w_{ij}(d)x_j - W_i^* \bar{x}}{s\sqrt{[(ns_{ii}^*) - W_i^{*2}]/(n-1)}}, \quad (3)$$

where w_{ij} is the binary weighting variable (1 if point j is within distance d of point i , otherwise 0), x_j the attribute value at point j , W_i^* the number of points (including i) within distance d of point i , \bar{x} the mean of x for all points j , n the total number of observations, s the square root of the variance for all points j , and s_{ii}^* the sum of all weights within distance d of point i (if weights are binary, this value is equal to W_i^*) (Ord and Getis, 1995).

G_i^* values were calculated for each station using the Hot Spot Analysis tool in ArcGIS Version 9.1. The distance d chosen for this analysis corresponds to the distance lag with the highest z score in the Moran's I correlogram (Getis and Ord, 1992; Table 1); distance over water was used in the calculations. Stations with G_i^* values >1.96 ($p < 0.05$) were designated high-catch stations. High-catch stations for all female ontogenetic stages were mapped using ArcGIS software and plotted against depth and temperature.

Habitat associations

Habitat association analysis was used to determine relationships between the distribution of depth and temperature values sampled and the corresponding distribution of cpue for each female ontogenetic stage (Perry and Smith, 1994; Dionne *et al.*, 2003). A cumulative distribution function (CDF), $f(t)$, was developed for each habitat variable that characterized the range of values sampled:

$$f(t) = \sum \frac{1}{n}, \quad (4)$$

where t is the range of values for all stations (n), ordered from low to high (Perry and Smith, 1994). CDFs for juvenile, new-shell, and

Table 1. Moran's I correlogram with I values and corresponding z -values for each of nine distance lags for juvenile, new-shell adult, and old-shell adult females.

Distance lag (m)	Juvenile		New-shell adult		Old-shell adult	
	I	z	I	z	I	z
2 000	0.207	5.57*	0.164	4.15*	0.085	2.24
2 800	0.152	5.61*	0.124	4.32*	0.110	3.98*
4 000	0.140	6.71*	0.087	3.96*	0.061	2.89*
5 500	0.094	6.20*	0.079	4.95*	0.040	2.65
7 500	0.069	5.91*	0.072	5.85*	0.030	2.62
10 000	0.048	5.38*	0.046	4.88*	0.016	1.89
15 000	0.028	4.70*	0.023	3.74*	0.011	2.06
30 000	0.009	3.45*	0.008	3.03*	0.002	1.31
60 000	-0.003	-0.30	-0.002	0.13	-0.003	-0.63

Distance lags used to calculate Getis-Ord G_i^* for each female Tanner crab ontogenetic stage are emboldened.

*Satisfies Bonferroni criterion, $z > 2.78$.

old-shell adult females, $g(t)$, were developed that characterized the proportion of the catch with respect to each habitat variable:

$$g(t) = \sum \frac{y_t}{Y}, \quad (5)$$

where y_t is the cpue at each level of t , and Y the sum of cpue for all stations (n). CDFs for habitat variables and cpue were compared using a Kolmogorov-Smirnov two-sample test (Conover, 1999) with $\alpha = 0.05$, which is the maximum vertical distance between two CDFs (Perry and Smith, 1994). CDFs for the three ontogenetic stages relative to each habitat variable were also compared with each other. If there was no significant difference between the CDFs, we inferred that there was no difference in habitat association by ontogenetic stage. Habitat association analysis was performed using data from all stations in the survey ($n = 415$), stations in Wachusett Inlet and Scidmore-Charpentier Inlet combined (referred to subsequently as juvenile high-catch areas, $n = 26$), and all stations except those in juvenile high-catch areas ($n = 389$).

Results

Size-frequency distribution

Juvenile females collected during the survey were 33–95 mm CW, and adult females were 58–124 mm CW (Figure 3). The size frequency distribution for males was similar to that of juvenile females for sizes up to ~84 mm CW. Of the crabs caught in shrimp pots, 95% were between 39 and 88 mm CW; 97.5% of the crabs caught in the crab pots were >78 mm CW. Shrimp pots captured 73% juvenile females and 11% adult females.

Spatial distribution and autocorrelation

Tanner crabs were spatially segregated by ontogenetic stage, with specific areas dominated by either juveniles or adults. Almost half (44%) of the juvenile crabs were caught in two narrow glacial fjords, Wachusett Inlet and Scidmore-Charpentier Inlet, where adult cpue was low (Figures 4a and 5b). In contrast, catches of old-shell adult females were large mainly in the middle and northeastern areas of the central Bay, near the entrance of the East Arm

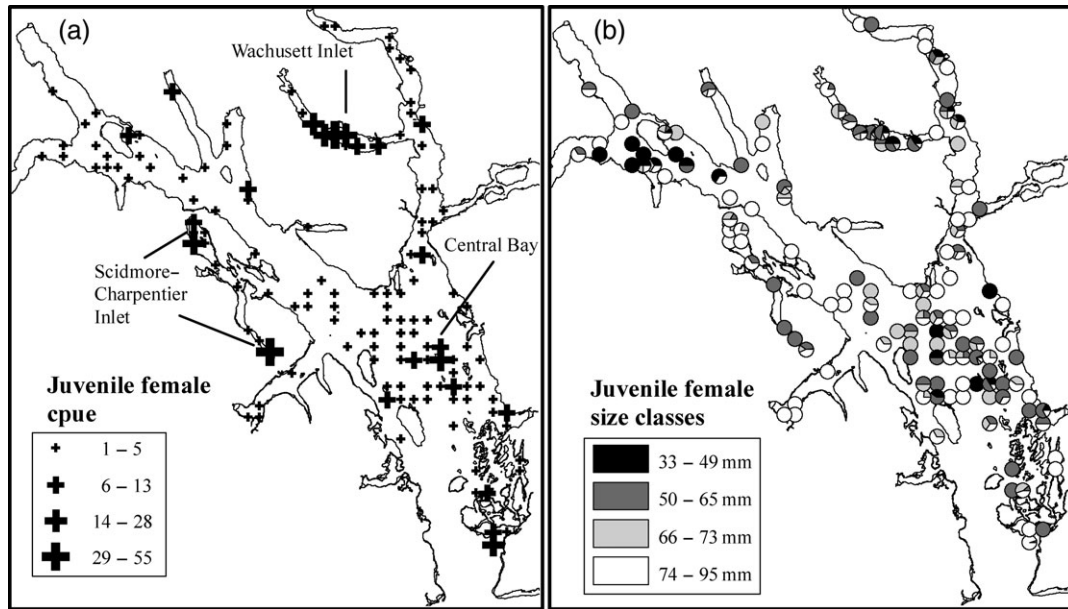


Figure 4. (a) Spatial distribution of cpue for all juvenile females, and (b) size class proportions for juvenile females caught at each station.

(Figure 5b). Juvenile females were also caught in lower numbers on a shallow shelf in the central Bay adjacent to areas of large catches of adults (Figure 4a). New-shell adult females were found in conjunction with large numbers of old-shell adult females and in areas where large numbers of juveniles were caught (Figure 5a).

No clear pattern in the spatial distribution of juvenile females by size class was observed (Figure 4b). More than one juvenile size class was present at 76% of the stations where juvenile female cpue was >2 .

The spatial distribution of juvenile females was significantly different from old-shell adult females ($p = 0.048$) and large males ($p = 0.008$), based on the modified Cramer-von Mises test. The distribution of new-shell adult females was also significantly different from that of old-shell adult females ($p = 0.024$). However, there was no significant difference between the spatial distributions of juvenile females and small males ($p = 0.191$), old-shell females and large males ($p = 0.188$), or juvenile females caught in shrimp vs. crab pots ($p = 0.53$).

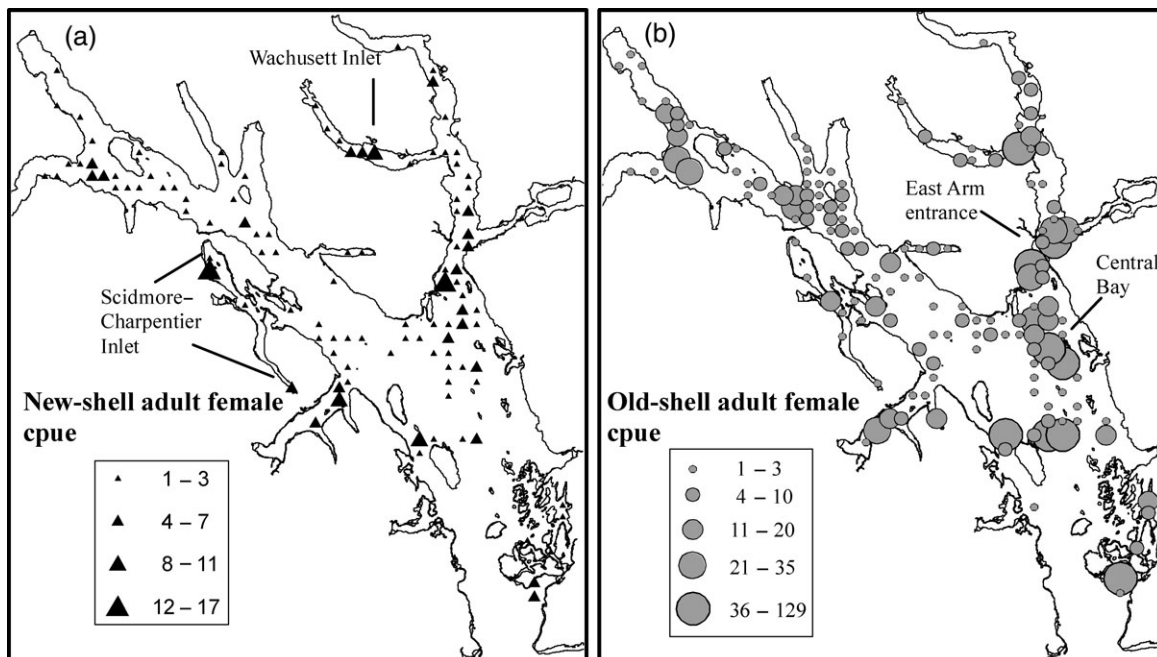


Figure 5. Spatial distribution of cpue for (a) new-shell adult female, and (b) old-shell adult female Tanner crabs.

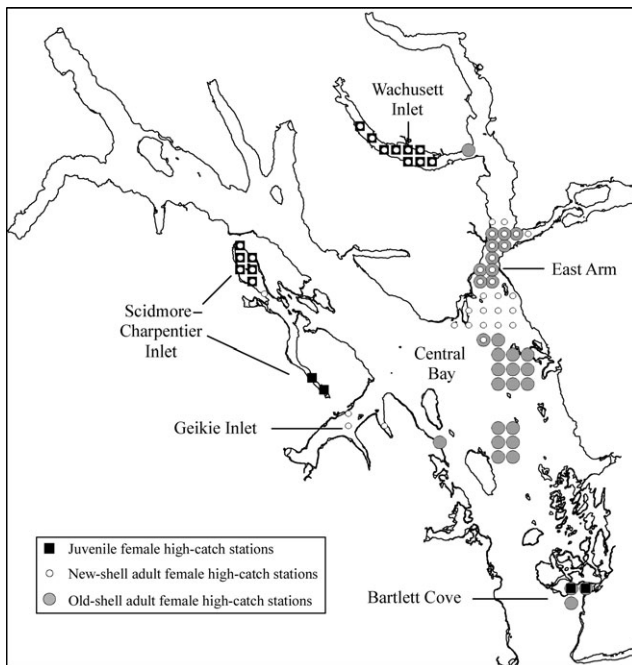


Figure 6. High-catch areas for juvenile, new-shell adult, and old-shell adult female Tanner crabs based on the Getis-Ord G_i^* statistic.

The distribution of juvenile females was more clustered than that of both new- and old-shell adult females. Juvenile females had the highest value of I_d , followed by new-shell and old-shell adults, for lag distances up to 5500 m (Table 1). Spatial autocorrelation was observed for all female ontogenetic classes. With the exception of the 2000 m lag for old-shell adult females, I_d values for all classes decreased monotonically with distance. The range of autocorrelation (the distance at which I_d approaches 0), and therefore patch size (Perry *et al.*, 2002), for old-shell females was less than that of both juvenile and new-shell adult females. However, it is possible that juvenile and new-shell adult females

were also autocorrelated at distances less than the minimum grid resolution.

High-catch areas

High-catch areas for juvenile females were located in Scidmore-Charpentier Inlet, Wachusett Inlet, and two stations in Bartlett Cove (Figure 6). Most (79%) juvenile female high-catch stations overlapped with new-shell adult female high-catch stations. High-catch stations for new-shell adult females overlapped juvenile female high-catch stations in Wachusett and Scidmore-Charpentier Inlets and old-shell adult female high-catch stations in the mouth of the East Arm. New-shell adult female high-catch stations were also located in Geikie Inlet. Bartlett Cove was the only location where high-catch areas of juvenile females and old-shell adult females overlapped.

Bottom temperatures were colder (with the exception of Bartlett Cove) at juvenile female high-catch stations than at old-shell adult female high-catch stations at similar depth. New-shell adult female high-catch stations overlapped both juvenile female and old-shell adult female high-catch stations in terms of depth and temperature (Figure 7).

Habitat associations

Juvenile females occurred at almost all depths sampled (15–439 m), but 50% were caught at depths <97 m and 85% at depths <166 m (Figure 8a). In contrast, 50% of the old-shell adult females were caught at depths <161 m, and 85% at depths <344 m. Half of the new-shell adult females were caught at depths <148 m, and 85% at depths <307 m.

Juvenile female associations with depth differed from those of old-shell adult females, and these associations were reversed in the juvenile high-catch areas compared with all other stations. In juvenile high-catch areas, juvenile females were associated with deeper water relative to the range of depths sampled, and their distribution was deeper than that of old-shell adult females (Figure 8c, Table 2). However, for all stations except those in juvenile high-catch areas, juveniles were associated with shallower water relative to the range of depths sampled, and their

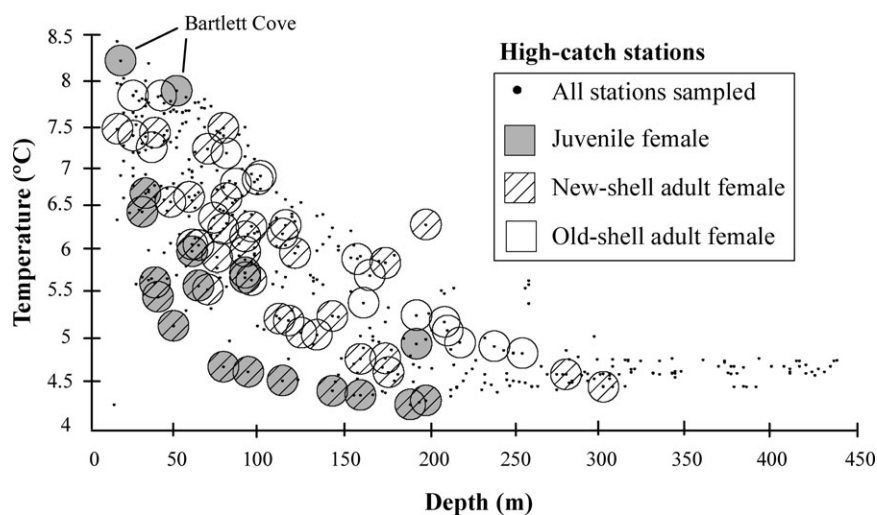


Figure 7. Relationship between depth and temperature for all stations sampled (black dots), juvenile female high-catch stations (shaded circles), new-shell adult female high-catch stations (striped circles), and old-shell adult female high-catch stations (white circles).

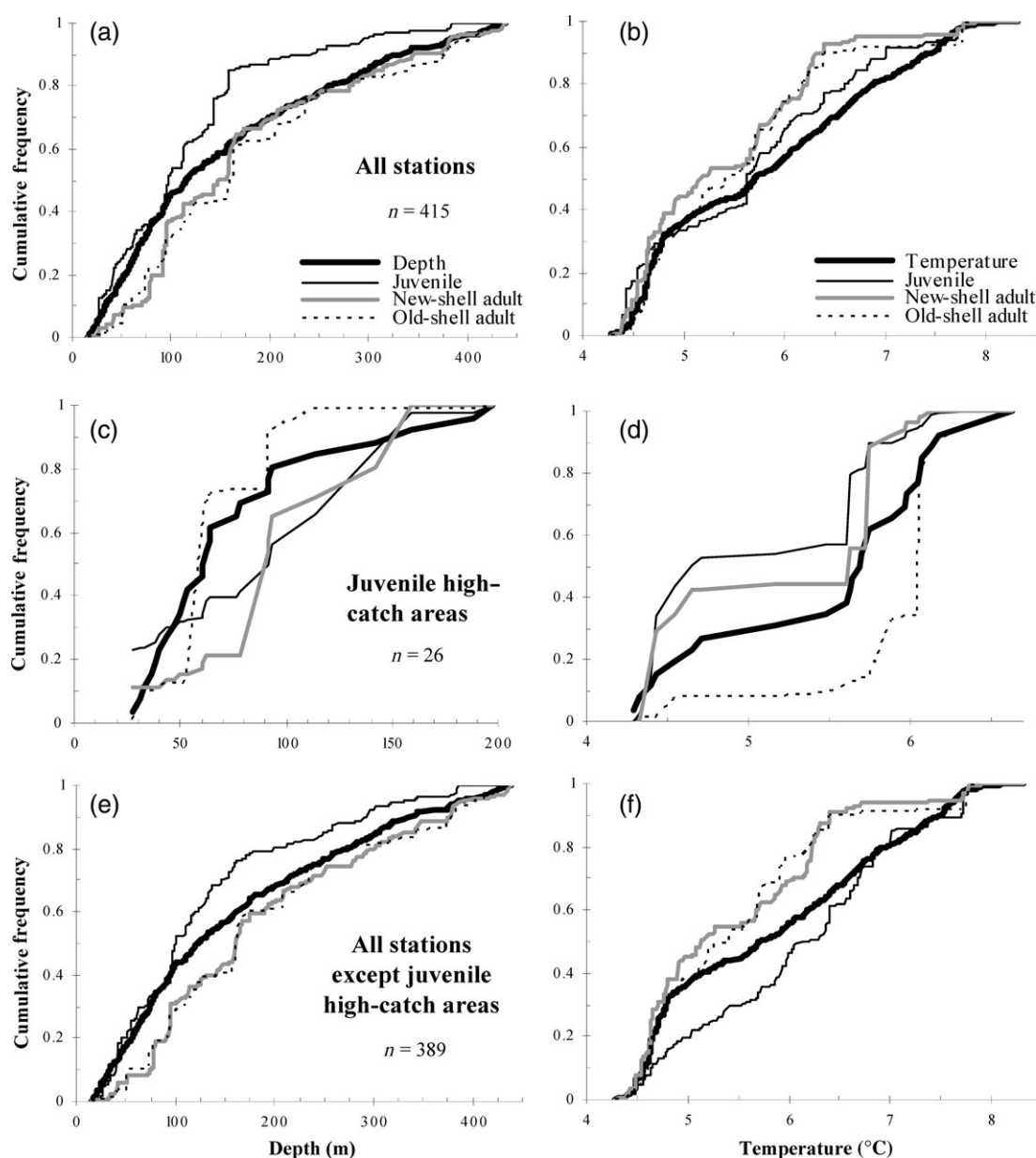


Figure 8. CDFs for juvenile, new-shell adult, and old-shell adult females relative to depth and temperature for (a, b) all stations, (c, d) juvenile high-catch areas, and (e, f) all stations except those in juvenile high-catch areas.

distribution was shallower than that of old-shell adult females (Figure 8e, Table 2).

Juvenile females were also found throughout the range of temperatures sampled (4.3–8.3°C), but 50% were caught where temperatures were <4.6°C and 85% where temperatures were <6.8°C (Figure 8b). In contrast, 50% of old-shell adult females were caught at temperatures <5.4°C and 85% at temperatures <6.3°C. Half of the new-shell adults were caught where temperatures were <5.6°C, and 85% where temperatures were <6.8°C.

Juvenile female associations with temperature also differed from that of adults, and these were also reversed in juvenile high-catch areas compared with all other stations. All female ontogenetic stages were associated with cooler temperatures relative to the distribution of all temperatures sampled, but adults (both new- and old-shell) were associated with cooler temperatures than

juveniles (Figure 8b, Table 2). In juvenile high-catch areas, juveniles were associated with colder water and adults were associated with warmer temperatures relative to the range of temperatures sampled (Figure 8d, Table 2). However, for all stations except those in the juvenile high-catch areas, juveniles were associated with warmer temperatures than both temperatures sampled and old-shell adult females (Figure 8f, Table 2).

Discussion

Tanner crab distribution in Glacier Bay

The distribution of Tanner crabs in Glacier Bay was characterized by spatial segregation of juveniles and adults that corresponded to features in the glacial landscape. Glacier-proximal areas in Wachusett Inlet and Scidmore–Charpentier Inlet were high-catch

Table 2. Kolmogorov–Smirnov test statistic (and *p*-values) for comparisons of (top) depth-CDFs, and (bottom) temperature-CDFs for all stations, juvenile high-catch areas (stations in Wachusett Inlet and Scidmore–Charpentier Inlet), and all stations excluding juvenile high-catch areas.

Comparison	Depth	Juvenile	New-shell adult
Depth			
All stations (<i>n</i> = 415)			
Juvenile	0.231 (<0.001)		
New-shell adult	0.227 (<0.001)	0.284 (<0.001)	
Old-shell adult	0.169 (<0.001)	0.375 (<0.001)	0.126 (<0.001)
Juvenile high-catch areas (<i>n</i> = 26)			
Juvenile	0.314 (<0.01)		
New-shell adult	0.481 (<0.001)	0.201 (>0.05)	
Old-shell adult	0.271 (<0.05)	0.507 (<0.001)	0.674 (<0.001)
All stations except juvenile high-catch areas (<i>n</i> = 389)			
Juvenile	0.162 (<0.001)		
New-shell adult	0.216 (<0.001)	0.298 (<0.001)	
Old-shell adult	0.186 (<0.001)	0.331 (<0.001)	0.072 (<0.05)
Temperature			
All stations (<i>n</i> = 415)			
Juvenile	0.121 (<0.001)		
New-shell adult	0.258 (<0.001)	0.181 (<0.001)	
Old-shell adult	0.230 (<0.001)	0.152 (<0.001)	0.124 (<0.001)
Juvenile high-catch areas (<i>n</i> = 26)			
Juvenile	0.373 (<0.001)		
New-shell adult	0.269 (<0.05)	0.259 (=0.05)	
Old-shell adult	0.476 (<0.001)	0.757 (<0.001)	0.745 (<0.001)
All stations except juvenile high-catch areas (<i>n</i> = 389)			
Juvenile	0.177 (<0.001)		
New-shell adult	0.260 (<0.001)	0.355 (<0.001)	
Old-shell adult	0.247 (<0.001)	0.340 (<0.001)	0.105 (<0.001)

areas for juvenile females, whereas old-shell adult females were scarce and found mostly at the mouths of these inlets. High-catch areas for old-shell adult females were mostly in the central portion of Glacier Bay on low gradient, highly bioturbated soft-sediment seabed (Harney *et al.*, 2006) at depths of ~150 m. Few juvenile females were caught in these areas, but there were moderate numbers on a shallow shelf with sloping, mixed sediment seabed adjacent to high-catch adult areas.

The distribution of juvenile female Tanner crab abundance does not appear strongly related to depth or temperature, although we cannot be sure that depth or temperature does not affect settlement or early life history because we were unable to sample very small crabs. Juvenile females were found throughout the range of depths sampled in Glacier Bay, so their distribution was not limited by depth. Juvenile females were also found in relatively high densities at both the warmest and the coldest temperatures sampled, so we infer that temperature did not limit their distribution. Juvenile female associations with both depth and temperature were reversed in juvenile high-catch areas compared with all other stations. Instead, a consistent pattern of opposing associations with depth and temperature between juvenile females and old-shell adult females in all areas reflects a general tendency for segregation of juveniles and adults.

The segregated distribution of juvenile and adult females could be a result of several different underlying processes including: (i) intercohort cannibalism, (ii) competition between adult and juvenile Tanner crabs, (iii) interspecific predation on juveniles,

(iv) differential juvenile and adult associations with substratum or infaunal food resources, or (v) ontogenetic movement.

Cannibalism can have strong effects on population dynamics and age structure in many animal species (Fox, 1975). In addition to *Chionoecetes* species (Paul *et al.*, 1979; Jewett and Feder, 1983; Dutil *et al.*, 1997; Lovrich and Sainte-Marie, 1997; Sainte-Marie and Lafrance, 2002; Squires and Dawe, 2003), cannibalism has been observed in the Dungeness crab *Cancer magister* (Stevens *et al.*, 1982; Fernandez *et al.*, 1993a, b; Fernandez, 1999), the blue crab *Callinectes sapidus* (Hines and Ruiz, 1995; Moksnes *et al.*, 1997; Ryer *et al.*, 1997; Moody, 2003), the shore crab *Carcinus maenas* (Moksnes *et al.*, 1998; Moksnes, 2004), the stone crab *Homalaspis plana* (Fernandez and Castilla, 2000), and other crab species (Luppi *et al.*, 2002; Kuroda *et al.*, 2005). Intercohort cannibalism, combined with movement of juvenile crabs with ontogeny, is thought to result in the spatial segregation of juvenile and adult blue crabs (Dittel *et al.*, 1995; Hines and Ruiz, 1995) and has also been proposed to result in spatial segregation of juvenile and adult snow crabs (Dutil *et al.*, 1997). Seasonal movement of male snow crabs to shallow-water refuges has been proposed as a mechanism for avoiding cannibalism during moulting (Lovrich *et al.*, 1995).

Competition between juveniles and adults could also result in segregated distribution. Although competition between juvenile and adult Tanner crabs has not been documented, prey types for adults and juveniles were similar in Kodiak (Jewett and Feder, 1983).

Co-occurrence of high numbers of predators that differentially prey on juveniles in adult high-catch areas could also cause an

apparent negative relationship between juvenile and adult Tanner crabs. Pacific cod (*Gadus macrocephalus*) is a frequent predator of juvenile Tanner crabs, and heavy cod predation has been proposed to regulate Tanner crab recruitment in the Bering Sea and Gulf of Alaska (Jewett, 1982; Livingston, 1989). Sculpins, flatfish, and skates are also major predators of juvenile Tanner crabs (Jewett, 1982). Many of these fish species have been documented within Glacier Bay (J. F. Piatt, USGS Alaska Science Center, and SJT, unpublished data), although their spatial distribution within Glacier Bay has not been quantified. Invertebrate species such as red king crabs (*Paralithodes camtschaticus*) may also prey on Tanner crabs (Jewett, 1982; Jewett and Feder, 1982). Red king crabs were sampled concurrently with Tanner crabs in this study. Their distribution was extremely aggregated and centred in the East Arm of Glacier Bay (SJT, unpublished data). In this study, very few juveniles, but large numbers of adult Tanner crabs, were found where densities of red king crab were high.

The spatial distribution of adults and juveniles could also vary based on the spatial distribution of substratum type or food resources. Substratum is thought to be a primary variable in explaining the distribution of juvenile snow crabs in the Gulf of St Lawrence (Brethes *et al.*, 1987; Robichaud *et al.*, 1989; Dionne *et al.*, 2003), and distributions of other crab species have been positively correlated to prey densities (Seitz *et al.*, 2003). Information on substratum and infaunal community was not available for comparison with Tanner crab distribution data from this survey, but much of the study area has been mapped using multibeam sonar (Harney *et al.*, 2006). Future studies should compare substratum type, infaunal community structure, and Tanner crab diet and distribution among juvenile and old-shell adult high-catch areas to determine whether associations with these variables might help to explain the spatial segregation observed.

Maintenance of juvenile and adult spatial structure over time depends on whether juveniles move to adult areas with ontogeny. In this study, such movement is suggested by the spatial, depth, and temperature distributions of new-shell adult female Tanner crabs. The spatial distribution of new-shell adult females overlapped those of both juvenile and old-shell adult females, whereas juvenile and old-shell adult female spatial distributions generally did not overlap. Habitat associations for new-shell adult females were similar to old-shell adult females for all stations excluding juvenile high-catch areas, but were more similar to juvenile females in the juvenile female high-catch areas of Wachusett and Scidmore–Charpentier Inlets. These data suggest that movement from juvenile to adult areas takes place at the new-shell adult female stage of ontogeny; such movement is consistent with the hypothesized ontogenetic movement of new-shell adult female snow crabs from juvenile to adult areas in the Bering Sea (Ernst *et al.*, 2005).

Glacier-proximal habitat

Because the largest numbers of juveniles were caught near glaciers, glacier-proximal habitat could be particularly important for juveniles. Areas near glaciers could: (i) possess low numbers of predators, and therefore serve as large-scale refuges, (ii) provide optimal prey for juveniles, or (iii) possess higher levels of larval supply through increased larval retention at the distal ends of glacial fjords.

Adult Tanner crabs or other predators could be in lesser densities near glaciers as a result of a general decline in prey availability with increasing glacial influence. Glacial processes such as

sedimentation (Gorlich *et al.*, 1987; Fetzer *et al.*, 2002) or infaunal community succession following glacial retreat (Włodarska–Kowalczyk *et al.*, 1998) can affect the infaunal community that serves as the prey for Tanner crabs. Infaunal abundance and biomass typically increase along a gradient from head to mouth in glacial fjords (Hoskin *et al.*, 1976; Gorlich *et al.*, 1987; Włodarska–Kowalczyk *et al.*, 1998; Fetzer *et al.*, 2002). Infaunal species that dominate near glaciers are often smaller than those at the mouths (Włodarska–Kowalczyk *et al.*, 1998; Nielsen, 2005), so the infaunal community near glaciers might provide adequate food resources or optimal prey size for juvenile crabs, but not for adults. As adult male Tanner crabs are mobile and capable of moving >40 km (Donaldson, 1983), they can presumably move to preferred habitats that offer high quality food resources. Demersal fish abundance and diversity appears to decline as glacial influence increases in Glacier Bay (J. F. Piatt, unpublished data), so glacier-proximal areas could contain fewer fish predators.

Cold bottom temperatures (Pickard and Stanton, 1980) and fine, muddy substrata (Powell, 1983) associated with glaciers may also provide an advantage for survival and growth of early benthic stages of Tanner crab. Although little information is available on temperature preferences or limitations for Tanner crab, cold temperatures and muddy substrata are the main factors explaining the spatial distribution of early benthic stages of snow crab in the Gulf of St Lawrence (Brethes *et al.*, 1987). Smaller snow crab instars selected colder temperatures than larger instars, and all juveniles preferred muddy substrata in laboratory experiments (Dionne *et al.*, 2003). Colder temperatures appear to provide a metabolic advantage for adult snow crabs; energetic costs may exceed energetic intake at temperatures >7°C (Foyle *et al.*, 1989). Juvenile Tanner crabs preferred muddy substrata in a laboratory study (Moles and Stone, 2002), and Tanner crabs burrow in mud, sometimes until only parts of the dorsal carapace and chelipeds are visible (Stevens *et al.*, 1994; Zhou and Shirley, 1998). Most (78.6%) of the snow crabs observed buried in mud in a video survey in the Gulf of St Lawrence were <100 mm CW (Conan and Maynard, 1987).

Abundance of juveniles can also be correlated with the magnitude of larval supply to an area (Botsford *et al.*, 1998). Fjord estuarine circulation can transport and concentrate zooplankton at the heads of fjords (Weslawski *et al.*, 2000; Zhou *et al.*, 2005), and Tanner crab larvae might be concentrated near glaciers in Glacier Bay by similar processes.

Because Wachusett and Scidmore–Charpentier Inlets had many more juveniles than other areas where juveniles were found, glacier-proximal habitat could serve as nursery areas if crabs leave these areas with ontogeny (Beck *et al.*, 2001). Additional research is needed to determine whether the large numbers of juveniles in these areas are a consequence of increased survival rates, increased larval supply, or a combination of both processes.

Implications for recruitment

A combination of spatial refuges or nursery areas for juveniles and ontogenetic movement of crabs from juvenile to adult areas could explain the segregated distribution of juveniles and adults in Glacier Bay. If so, specific locations are likely to be important for determining the magnitude of recruitment in a given area.

Refuges caused by spatial heterogeneity can increase the abundance and decrease the interannual variability in recruitment for

species exposed to size-selective predation (Wright, 1990; Benoit *et al.*, 1998). The small-scale heterogeneity observed in glaciated systems could mean that southeastern Alaska has more refuges than other areas where Tanner crabs are found, especially the broad, flat eastern Bering Sea shelf. Therefore, recruitment per unit area might be higher, and fluctuations in abundance reduced, in areas with more spatial refuges.

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