**Abstract**—We examined depth distribution, habitat association, and growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) at 4 sites around the eastern end of Kodiak Island, Alaska, during 2010 and 2011. Settlement was from April through July, and crab density peaked during May–July, at 10 crabs/m$^2$ in 2010 and 2.3 crabs/m$^2$ in 2011. By the end of August most crabs had progressed through 3–5 molt stages (instars). An association between crabs and tubes of the ampharetid polychaete *Sabellides sibirica* was observed in 2010, but it was not seen in 2011 when both crabs and worms were less abundant. Crabs in protected embayments were larger in August than crabs at open coastal sites. Crabs at protected sites were also found in shallower water than at open coastal sites—a difference that may have exposed them to higher ambient water temperature and may have accelerated their growth. Accelerated growth may in turn result in earlier maturation. Southern Tanner crabs probably settle over a wide range of depths, but shallow embayments (depths <50 m) may play a disproportionately large role in providing recruits to the adult population, due to accelerated crab growth and survival.

# Depth distribution, habitat associations, and differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska

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Nursery habitats for many crab and fish species are often found in waters considerably shallower than those frequented by the adult population. Three features commonly characterize shallow-water juvenile nurseries. First, water temperatures are typically higher there than in adult habitat, a difference that can facilitate rapid growth (Yamashita et al., 2001; Ryer et al., 2012). Because mortality typically decreases with prey size (Sogard, 1997), rapid growth is a principal determinant of survival to adulthood. Second, shallow water usually is characterized by lower predation rates (Linehan et al., 2001; Manderson et al., 2004; Baker and Sheaves, 2007; Ryer et al., 2010). This feature follows from Heincke's Law (sensu Cushing, 1975), which holds that the abundance of larger predatory fishes increases with depth. Lastly, shallow-water nurseries often contain structurally complex habitat, such as

rooted aquatic vegetation, drift algae, bivalve shell, cobble, terrestrial litter, and polychaete tubes, which can mediate predator–prey interactions (Ryer et al., 2004; Long et al., 2011, 2013a) and, therefore, further reduce the risk of predation.

Red king crab (*Paralithodes camtschaticus*), snow crab (*Chionoecetes opilio*), and southern Tanner crab (*Chionoecetes bairdi*, hereafter "Tanner crab") stocks in the North Pacific have experienced significant declines over the last 3 decades. The reasons for stock declines are little understood but are generally attributed to overfishing or climatic changes (Orensanz et al., 1998; Woodby et al., 2005). Stocks currently are considered depressed or rebuilding, and closures have occurred throughout much of Alaska. Effective management of commercial species requires not only information on the current stock size but

also an understanding of ecological processes that contribute to the strength of upcoming year classes so that fisheries may be scaled to predicted future resource availability. For depressed stocks, recovery begins with the recruitment of one or more strong year classes. Establishment of a strong year class depends upon adequate spawning stock, transport of larvae from spawning to nursery grounds (Etherington and Eggleston, 2003), appropriate settlement substrate (Wahle and Steneck, 1991), and favorable postsettlement processes (Heck et al., 2001).

Little is known about nursery areas and preferred habitats for newly settled juveniles of these North Pacific crab species. Red king crab juveniles are strongly attracted to shallow-water, structured habitat, such as cobble, algae, and hydroids (Sundberg and Clausen[1]; McMurray et al.[2]; Loher and Armstrong, 2000), which mediates their interactions with predators and larger conspecifics (Loher and Armstrong, 2000; Stevens, 2003a; Stoner, 2009; Pirtle and Stoner, 2010, Sundberg and Clausen[1]; McMurray et al.[2]). Yet, most of this knowledge has been gained through laboratory studies or the outplanting of hatchery-reared crabs; too few juveniles are encountered in the wild to make firm conclusions. Similarly, newly settled Tanner crabs are not effectively sampled by conventional sampling gears, and there is a dearth of information on their habitat preferences and early ecology. Unlike king crabs (*Paralithodes* spp.), it is believed that Tanner crabs show an affinity for burial in unconsolidated sediment throughout their lives (Rosenkranz et al., 1998), indicating lower reliance on structured habitat during the juvenile period when crabs presumably experience high mortality.

We have conducted studies on the ecology and habitat preferences of juvenile flatfish species that use shallow-water nurseries around Kodiak Island in the Gulf of Alaska since 2002. During 2002 and 2003, we conducted beam trawl hauls in Pillar Creek Cove (hereafter Pillar) and estimated densities of age-0 Tanner crabs to be <0.05 crabs/m$^2$ (senior author, unpubl. data). Although not quantified in subsequent years, densities of age-0 Tanner crabs appeared to remain low. However, in 2009, we began to encounter larger numbers of age-0 Tanner crabs in beam trawl hauls and, again, began enumerating them. Beam trawl hauls conducted over a range of depths indicated that crabs were at their highest density, ~2 crabs/m$^2$, at depths of 15–30 m (senior author, unpubl. data). This depth range also corresponded to the depths where we docu-

mented extensive areas of habitat created by the tubes of the ampharetid polychaete *Sabellides sibirica*. This polychaete has been shown to influence the depth distribution of juvenile northern rock sole (*Lepidopsetta polyxystra*) (Ryer et al., 2013).

The densities of juvenile Tanner crabs during summer in Kodiak embayments remained high from 2009 through 2011, in the range of 2–10 crabs/m$^2$. Although it is too soon to conclude that populations of Tanner crabs are rebuilding in the Gulf of Alaska, the occurrence of high densities of juvenile crabs has provided an opportunity to study early life-stage ecology of a commercially important species in Alaska waters. In this study, we specifically examined 1) the depth distribution of newly settled crabs and how it changes through the summer, 2) the possible association between crabs and habitat created by polychaete worm tubes, and 3) differences in crab size and distribution between embayments with varying characteristics of sediment and physical exposure. Together, these efforts represent the first significant study aimed at understanding important facets of the habitat ecology of newly settled Tanner crabs.

## Material and methods

### Study sites

Field work was conducted at 4 sites in the coastal waters around the eastern end of Kodiak Island, Alaska (Fig. 1). Two of these sites, Holiday Beach (hereafter Holiday; 57°41.344′N, 152°27.958′W) and Pillar (57°49.136′N, 152°25.314′W), have been the focus of juvenile flatfish habitat studies (Hurst and Abookire, 2006: Ryer et al., 2007; Stoner et al., 2007; Ryer et al., 2013). Both sites have gently sloping, sandy bottoms just offshore from beaches that are exposed to wave action from the Gulf of Alaska. The third site, in Kalsin Bay (hereafter Kalsin; 57°36.207′N, 152°26.890′W), also is characterized by a gently sloping bottom, but it has finer sediments because of its more protected location near the head of the bay. The last site, Womens Bay (hereafter Womens; 57°42.800′N, 152°31.134′W), has a narrow entrance with a relatively shallow sill (depth ~11 m) and offshore islands, which protect the inner bay from wave action. This fourth site is also characterized by a gently sloping bottom, but sediments are finer there than at the other 3 sites being composed of silty sands and muds.

Salinity and water temperature in spring and summer were generally comparable between sites, ranging from 28–32 and 5–11°C, respectively, for all 4 sites. During 2011, temperature loggers were deployed on the bottom at each site at a depth of 15 m mean lower low water (MLLW) on 20 May and recovered on 22 August. After recovery of loggers, temperature data were downloaded, averaged by day for each site, and then analyzed with analysis of variance (ANOVA) to determine if there were differences between sites.

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[1] Sundberg, K., and D. Clausen. 1977. Post-larval king crab (*Paralithodes camtschatica*) distribution and abundance in Kachemak Bay, Lower Cook Inlet, Alaska, 1976, vol. 5, 36 p. Environmental studies of Kachemk Bay and Lower Cook Inlet (L. Trasky, L. Flagg, and D. Burbank, eds.). Alaska Dep. Fish Game, Anchorage, AK.

[2] McMurray, G., A. H. Vogel, and P. A. Fishman. 1984. Distribution of larval and juvenile red king crabs (*Paralithodes camtschatica*) in Bristol Bay. OCSEAP Final Rep. 53:267–477.
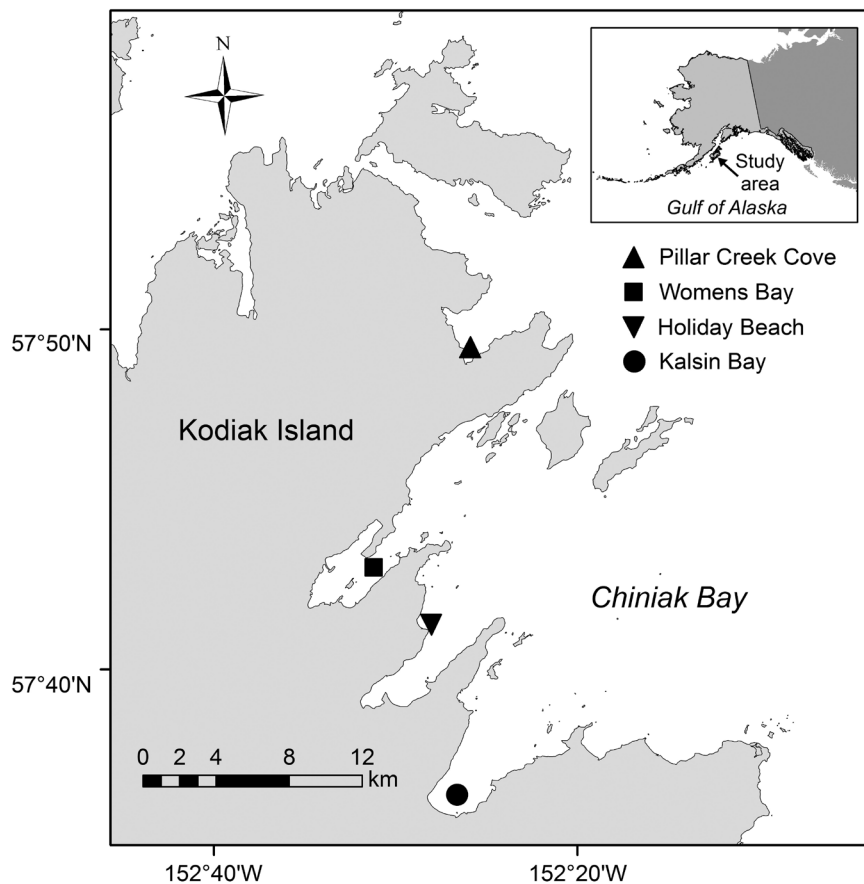
**Figure 1**

Map of locations of the 4 study sites around the eastern end of Kodiak Island, Alaska, where scrape tows and beam trawl hauls were conducted from May through August in 2010 and 2011 to examine the depth distribution, habitat association, and growth of newly settled southern Tanner crab (*Chionoecetes bairdi*). Inset shows location of Kodiak Island in relation to the Gulf of Alaska and Bering Sea.

**Scrape estimation of crab density**

Crab densities were estimated from sampling conducted with a video camera sled (Spencer et al., 2005; Stoner et al., 2007; Ryer et al., 2013). Hereafter referred to as a "scrape," the sled was augmented with a cutter bar and a codend that was 3 m long and had a 3-mm seine mesh. The tubular aluminum frame measured 114 cm long by 67 cm wide by 42 cm high. An aluminum cutter bar (width: 5 cm, thickness: 0.5 cm), mounted across the rear of the scrape between the runners and at an angle of 45°, scraped off the upper 2–3 cm of the sediment surface as the scrape was towed along the bottom of the seafloor. Fastened to the rear of the scrape and immediately behind the cutter bar, the codend had a lead line attached along its leading edge, to maintain contact with the bottom. Sediment displaced by the cutter bar passed over the lead line and into the codend. A video camera positioned just forward of the codend, at the top of the scrape, provided an oblique

view of the bottom traversed. The video images were transmitted by a cable to the vessel and were recorded.

Scrape tows were made parallel to shore at depths ranging from 3 to 25 m, at a speed of 0.5 m/s for ~30 m. The actual distance towed was determined with the GPS coordinates of the start and end of each tow. On deck, the codend was briefly rinsed with seawater to remove any remaining sediment, and the contents were deposited into a plastic tray, sorted, and all Tanner crabs were enumerated. During 2010, 121 tows were made at Holiday (May: 30, June: 32, July: 29, August: 30) and 168 were completed at Pillar (May: 48, June: 47, July: 36, August: 37). In a more limited effort, we made 23 tows at Womens (July: 4, August: 19) and 4 tows at Kalsin (August: 4). During 2011, 111 tows were made at Holiday (May: 26, June: 35, July: 30, August: 20), 89 were conducted at Pillar (May: 23, June: 26, July: 20, August: 20), 132 at Womens (May: 13, June: 34, July: 42, August: 43), and 105 were completed at Kalsin (May: 25, June: 30, July: 30, August: 20). Dur-

ing each month, all tows at the 4 sites were conducted within 6 days of one another. From each scrape tow, the number of crabs per square meter was calculated on the basis of the area swept. For the purpose of analyses, scrape tows were grouped into 5-m depth bins centered on 2.5, 7.5, 12.5, 17.5, and 22.5 m.

During both 2010 and 2011, we also conducted a smaller number of tows with a 2-m plumb-staff beam trawl (hereafter referred to as a "trawl") with a 3-mm-mesh codend. This gear allowed us to sample crabs at greater depths than with the scrape, which has an operational depth limit of ~30 m. Tows were conducted at Pillar at depths of 3–80 m, parallel to shore, during July and August. We towed the trawl 200 m, and confirmed that length with GPS readings at the beginning and end of each tow. In 2010, 35 tows were completed (July: 18, August: 17), and 46 tows were made in 2011 (July: 23, August: 23). Crabs were sorted from the catch of these tows and enumerated in the laboratory. The number of crabs per square meter also was calculated on the basis of the area swept, and the resulting density values were grouped into 10-m depth bins and analyzed.

Using video from scrape tows, we characterized the relative abundance of worm tubes along each tow. During video analysis, each tow was divided into 5-s segments. For each segment, an observer assigned an index score for the relative abundance of worm tubes on the seafloor passing between the scrape's runners. The index was scored on a 5-point scale (0–4), with 0 representing worm absence and 4 representing a contiguous "worm turf" (Stoner et al., 2007; Ryer et al., 2013). The vast majority of worm tubes were easily identifiable as belonging to *S. sibirica*, following prior positive identification from benthic samples taken during 2008 (Jewett[3]).The tubes of *S. sibirica* are distinctive: 1.00–1.25 mm in diameter and up to 12 cm long, with approximately 70% of the tube emergent and upright above the sediment surface. For each tow, the average worm index score was calculated.

Crab density data followed a Poisson distribution. To analyze this data, we used generalized linear models (GLMs), incorporating a Poisson log-linear link function, and we used the Wald chi-square statistic for tests of significance (Wald, 1943). Crab densities were first converted to an expanded integer scale through multiplication by 10, augmentation by 1, and rounded to the nearest whole integer. We tested the resultant data for independent and interactive effects of site, month, and depth, with the worm index as a covariate. We conducted separate analyses for each year. For 2010, we excluded data for Womens and Kalsin from the analysis because of the lack of consistent temporal and depth coverage at these sites. For 2011, all 4 sites were included in analysis. Trawl data also followed a Poission distribution and were analyzed with GLM with a

Poisson log-linear link, which allowed us to test for the effects of depth on crab distribution.

## Diver estimation of crab density

During June, July, and August of 2010, divers used quadrats to estimate densities of crabs and worm tubes. During each dive, multiple squares made of PVC pipe were haphazardly placed on the bottom to mark the 0.25-m² quadrats that would be surveyed. A second square was positioned haphazardly within each of the 0.25-m² quadrats, marking an area of 0.10 m² for enumeration of worm tubes. After worm tubes were counted, the 0.10-m² square was removed. Then, using a metal tooth comb, a diver methodically worked over the sediment within the 0.25-m² quadrat, dislodging crabs and enumerating them. During the course of 10 dives, 222 paired (crab and worm tube) quadrats were sampled, with 69, 74, 59, and 20 pairs from depths of 8, 13, 17, and 23 m, respectively. Data followed a Poisson distribution and were analyzed with GLM with a Poisson log-linear link. We tested for independent and interactive effects of month and depth on crab density, with worm density included as a covariate.

## Measurements of crab carapace width

We measured the carapace width of crabs from scrape tows conducted during only July and August of 2010 and during all 4 months in 2011. For tows from which more than 100 crabs were sampled, we measured a subsample of 50–100 crabs. Carapace width was measured to the nearest 0.1 mm with digital calipers. On the basis of visual examination of a cumulative size-frequency distribution, break points between peaks (instars) were identified and used to classify individuals into molt stages (C1–C5 instars). Using this classification scheme and G-tests (Sokal and Rohlf, 1969), we tested for differences in the frequency distribution of molt stages between sites for each month. In addition, we compared mean carapace width using ANOVA (Sokal and Rohlf, 1969). Where the ANOVA indicated a significant effect, group means were compared with Tukey's honestly significant difference (HSD) test (Sokal and Rohlf, 1969). Where data did not meet parametric assumptions, a Kruskal-Wallis ANOVA was used, and when significant effects were found, the associated multiple range test for differences between means was used (Conover, 1971). In these comparisons, we eliminated from consideration those crabs that were not, in our estimation, representative of the age-0 cohort (i.e., crabs of age 1 or older).

## Results

### Distribution of age-0 crabs

Crab densities estimated from catches of scrape tows conducted during 2010 increased from May through

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[3] Jewett, S. 2008. Personal commun. Institute of Marine Science, Univ. Alaska Fairbanks, Fairbanks, AK 99775-7220.
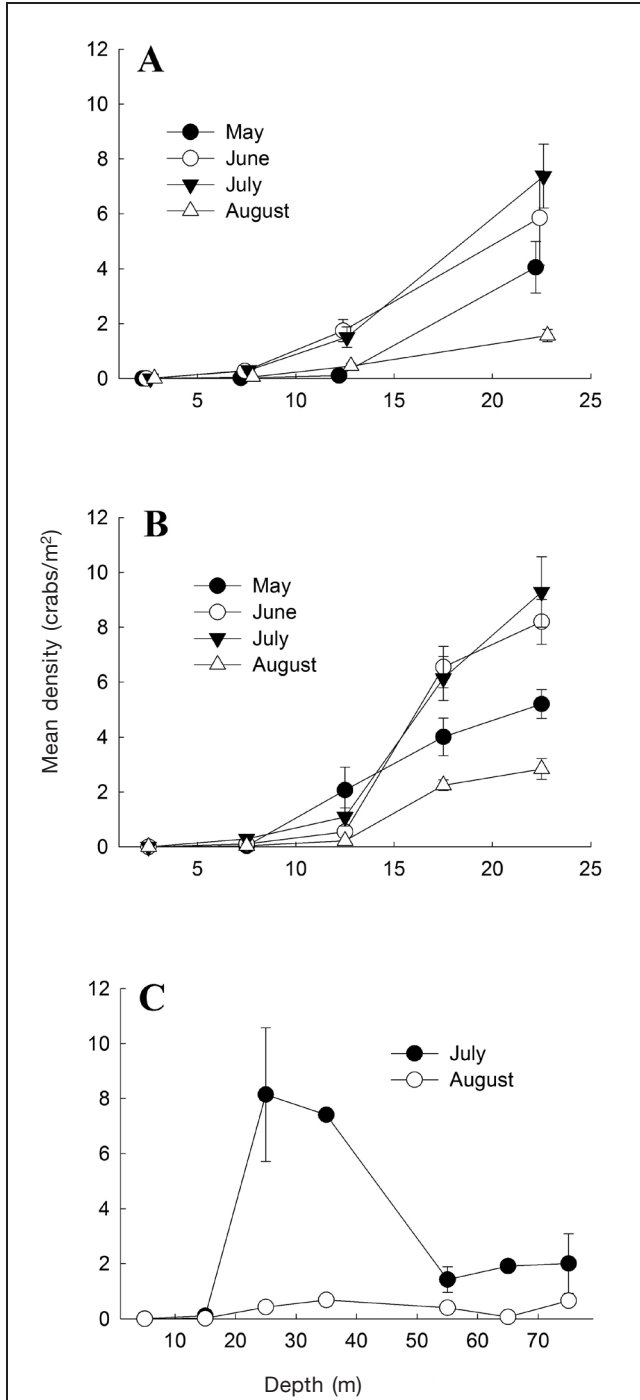
**Figure 2**

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*), plotted against depth, from scrape tows conducted during the months of May–August in 2010 around Kodiak Island, Alaska, at (**A**) Holiday Beach and (**B**) Pillar Creek Cove and (**C**) from beam trawl hauls conducted at Pillar Creek Cove in July and August 2010. Error bars indicate standard error of the mean. Note that the depth range for beam trawl hauls on the *x*-axis in panel C is different from the range in the panels that show depths of scrape tows.
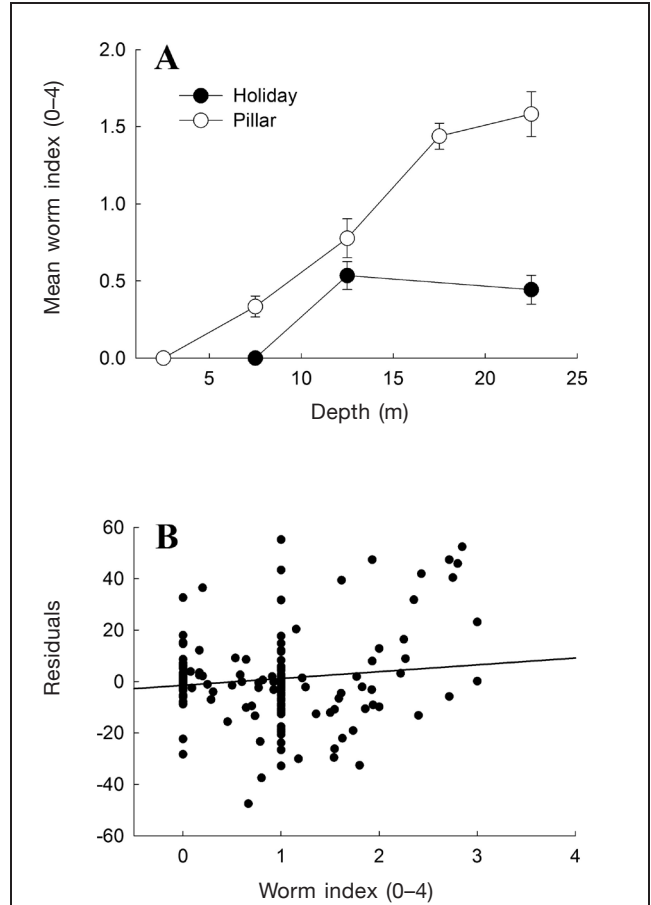


**Figure 3**

(**A**) Mean worm index scores (averaged over months), which provide a measure of relative abundance of worm tubes on a 5-point scale (0–4), plotted against depth for the sites at Holiday Beach and Pillar Creek Cove, Kodiak Island, Alaska, for surveys conducted in 2010. Error bars indicate standard error of the mean. (**B**) Residuals from generalized linear model analysis of crab density (without the worm index included as a covariate), plotted against worm index scores and indicating a positive relationship between crab and worm tube abundance after the confounding depth effect had been removed.

July, then decreased from July to August (Fig. 2, A and B). The density of age-0 Tanner crabs was strongly influenced by depth; crabs were generally absent from depths <8 m. At depths greater than 8 m, crab density rose with increasing depth. There was a significant interactive effect of depth and site; crabs were distributed more deeply at Pillar Creek Cove than at Holiday Beach (GLM depth×site: Wald $\chi^2$=8.01, df=3, $P$=0.045). The depth effect also varied among months, with a more uniform distribution across depths in August as overall density decreased (depth×month: Wald $\chi^2$=55.1, df=12, $P$<0.001). Crab density was generally higher at Pillar than at Holiday, although the magnitude of this dif-

ference varied somewhat between months (site×month: Wald $\chi 2$=12.9, df=3, *P*=0.005).

We conducted limited beam trawl sampling at Pillar during July and August, including depths beyond those attempted with the scrape (Fig. 2C). The depth distribution of crabs differed between July and August (Wald $\chi^2$=17.1, df=6, *P*=0.009). During July, crab density increased from the shallows to a peak at 25–35 m, declining farther offshore. By August, crab density was more uniform across depths as overall density decreased.

Worms tubes, principally those of *S. sibirica*, were generally more abundant at Pillar than at Holiday (Fig. 3A). At both sites, tubes were rare in the shallows but increased in abundance with depth. Therefore, the depth distribution of age-0 Tanner crabs mirrored the distribution of worm tubes. Abundance of worm tubes had a significant positive influence on crab density (Wald $\chi^2$=233.1, df=1, *P*<0.001). To graphically demonstrate this association, we performed a second GLM analysis, leaving out the worm covariate, and plotted the residuals against the worm index (Fig. 3B).

Crab densities were lower in 2011 than in 2010. With the addition of Womens and Kalsin sites in 2011, differences between study sites also became more evident (Fig. 4, A–D). Beyond the obvious difference in the overall abundance of crabs, perhaps most noticeable was the influence of site on depth distribution (Wald $\chi^2$=56.0, df=8, *P*<0.001). As in 2010, crab density at Holiday and Pillar consistently was highest at the greatest depth. In contrast, at Womens and Kalsin, crabs were found at shallower depths and more evenly distributed among depths. There was also an interactive effect wherein depth distribution differed among months (depth×month: Wald $\chi^2$=17.4, df=9, *P*=0.043). This effect was manifest as a "flattening" of the depth distribution curves, particularly during August at Holiday and Pillar—an effect similar to that observed during 2010.

Seasonal, or month to month, changes in crab density also differed among sites (month X site: Wald $\chi^2$=27.4, df=9, *P*=0.001). Most notable were changes in crab density subsequent to the end of settlement in July. Post-hoc comparisons indicated that mean crab density (crabs/m$^2$) declined from July to August at Holiday (July: 0.61 [standard error (SE) 0.18]; August: 0.26 [SE 0.09]; Wald $\chi^2$=59.0, df=3, *P*<0.001), as well as at Pillar (July: 0.66 [SE 0.25]; August: 0.15 [SE 0.07]; Wald $\chi^2$=62.4, df=3, *P*<0.001) and Kalsin (July: 0.34 [SE 0.07]; August: 0.20 [SE 0.05]; Wald $\chi^2$=12.8, df=3, *P*=0.005). In contrast, there was no decline in crab density from July to August at Womens (July: 0.11 [SE 0.02]; August: 0.12 [SE 0.02]; Wald $\chi^2$=4.6, df=1, *P*=0.201). There was no significant 3-way interactive effect of site, month, and depth on crab density (Wald $\chi^2$=25.4, df=18, *P*=0.115).

Results from beam trawl sampling (Fig. 5) indicate that, unlike in July 2010 when crabs were most dense at intermediate depths (25–35 m), crab density during 2011 was highest in the deepest tows (Wald $\chi^2$=17.0, df=4, *P*=0.002). Although crab density decreased from
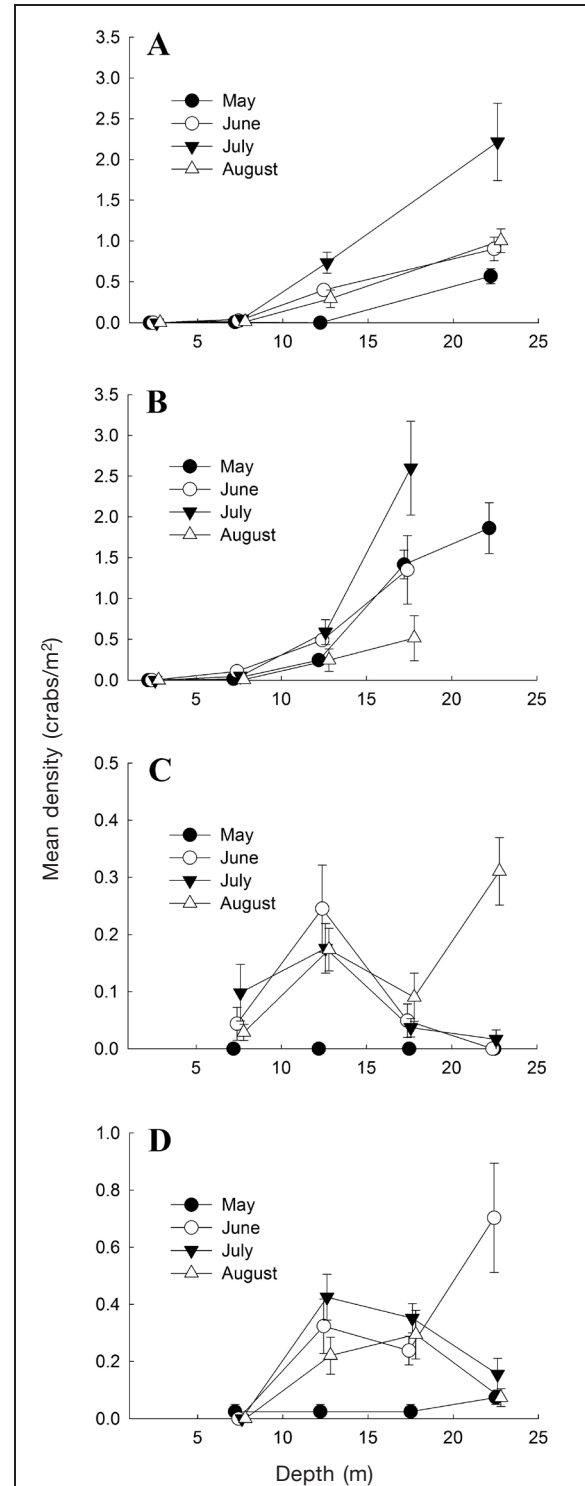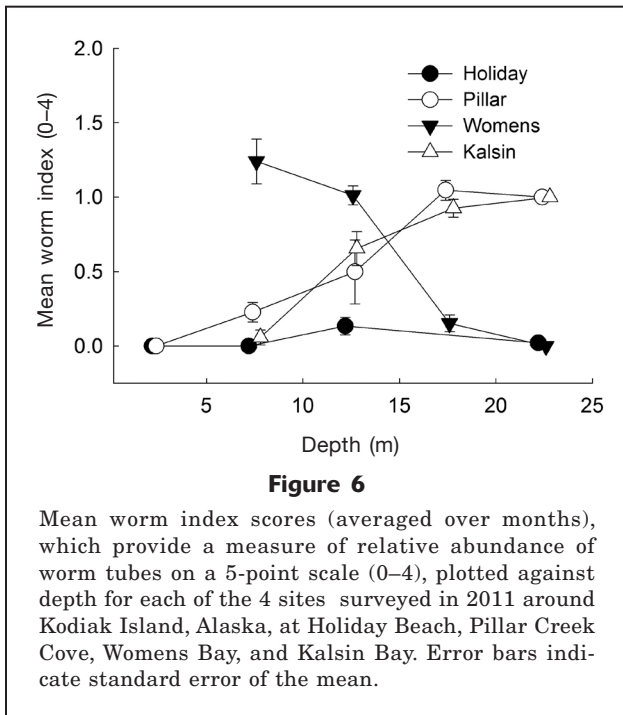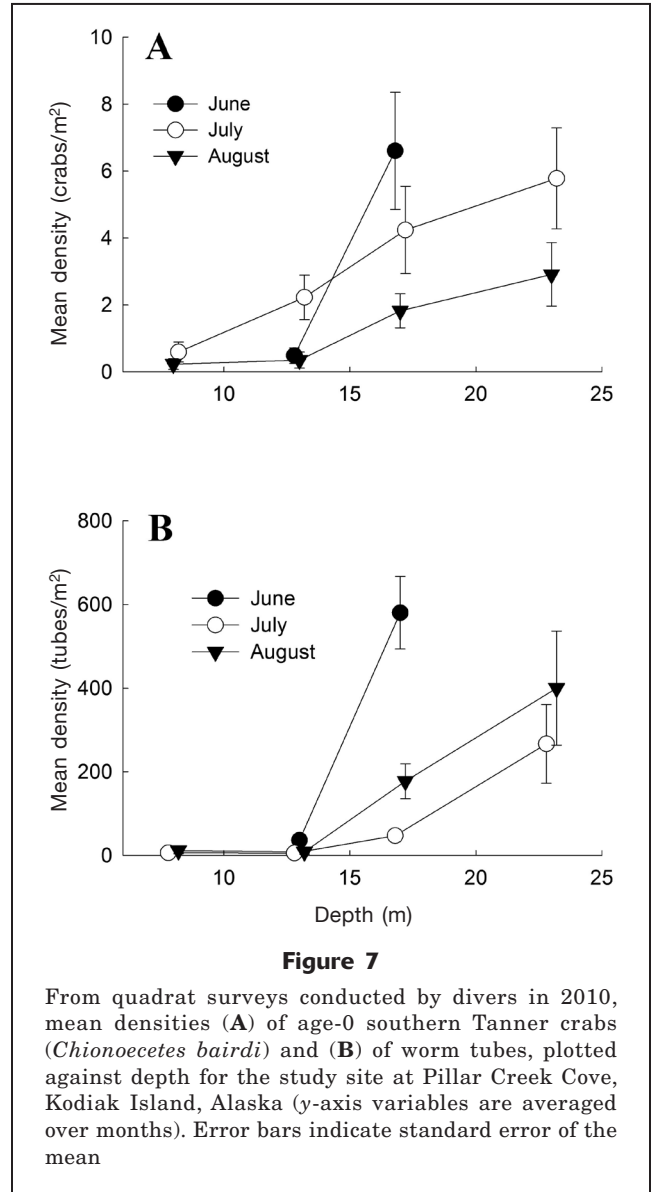


**Figure 4**

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*), plotted against depth, determined from scrape tows conducted at (**A**) Holiday Beach, (**B**) Pillar Creek Cove, (**C**) Womens Bay, and (**D**) Kalsin Bay around Kodiak Island, Alaska, in the months of May–August 2011. Error bars indicate standard error of the mean.

**Figure 5**

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*) from beam trawl hauls, by depth, conducted at Pillar Creek Cove, Kodiak Island, Alaska, in July and August 2011. Error bars indicate standard error of the mean.
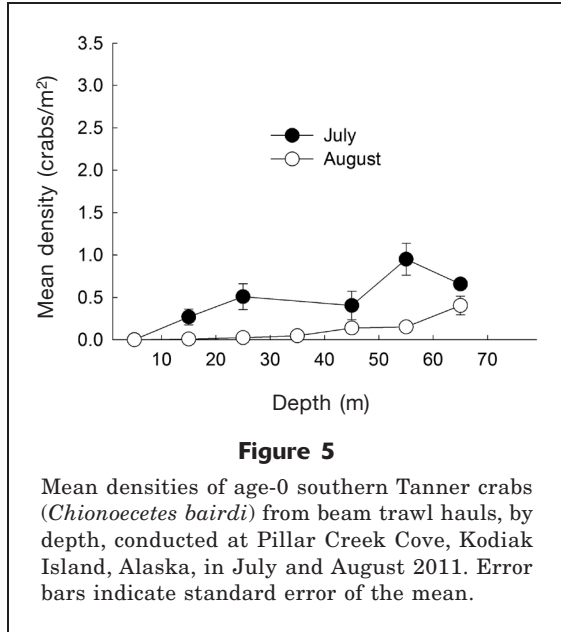
July to August (Wald $\chi^2$=23.4, df=1, $P$<0.001), the effect of depth on density was consistent across months (month×depth: Wald $\chi^2$=7.1, df=3, $P$=0.055).

At Holiday and Pillar, the depth distribution of polychaete worms in 2011 (Fig. 6) was similar to that observed in 2010 (Fig. 3), albeit, overall worm abundance was lower. Worms at Kalsin displayed a distribution similar to that of worms at Pillar, in distinct contrast to Womens, where worms were most abundant at the



**Figure 6**

Mean worm index scores (averaged over months), which provide a measure of relative abundance of worm tubes on a 5-point scale (0–4), plotted against depth for each of the 4 sites surveyed in 2011 around Kodiak Island, Alaska, at Holiday Beach, Pillar Creek Cove, Womens Bay, and Kalsin Bay. Error bars indicate standard error of the mean.



**Figure 7**

From quadrat surveys conducted by divers in 2010, mean densities (**A**) of age-0 southern Tanner crabs (*Chionoecetes bairdi*) and (**B**) of worm tubes, plotted against depth for the study site at Pillar Creek Cove, Kodiak Island, Alaska (*y*-axis variables are averaged over months). Error bars indicate standard error of the mean

shallowest depth and decreased in abundance as depth increased. On first examination, worm abundance might be construed as influencing the distribution of crabs at Womens because crabs also were more abundant in shallow water. However, worm abundance did not have a significant influence on crab abundance in the GLM (Wald $\chi^2$=3.0, df=1, $P$=0.083).

### Diver estimation of crab density

The quadrats used by divers to assess crab density during 2010 provided an examination of habitat associations on a micro scale (<1 m); the crab scrape, on the other hand, provided an examination at a larger scale (>10 m). Although there was a tendency for crab density from quadrats (Fig. 7A) to decline through the summer, this effect was not significant (Wald $\chi^2$=5.3,
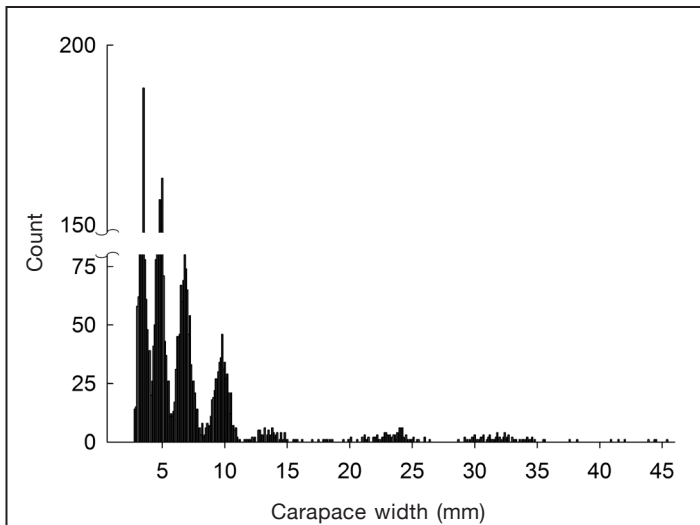
**Figure 8**

Cumulative size-frequency distribution of southern Tanner crabs (Chionoecetes bairdi) from all sites, months, and depths surveyed in 2010 and 2011 around Kodiak Island, Alaska. A tabulation of median size, size range, and molt increment for each molt stage is provided in Table 1.

df=2, *P*=0.070). As seen in the scrape data, crab density estimated by divers in quadrat surveys increased with depth (Wald $\chi^2$=12.8, df=3, *P*=0.005). This depth effect was consistent over months (month×depth: Wald $\chi^2$=3.5, df=4, *P*=0.474). Although crab density appeared to mirror the observed depth distribution of worm tubes (Fig. 7B), worms tubes were not a significant covariate in the GLM analysis (Wald $\chi^2$=0.9, df=1, *P*=0.354), indicating no association at this spatial scale.

**Table 1**

Medians and ranges of carapace widths (mm) for proposed molt stages of southern Tanner crabs (*Chionoecetes bairdi*) collected during 2010 and 2011 from all 4 sites that were surveyed around Kodiak Island, Alaska. Increment percentages indicate the relative increase in carapace width from one molt stage to the next.
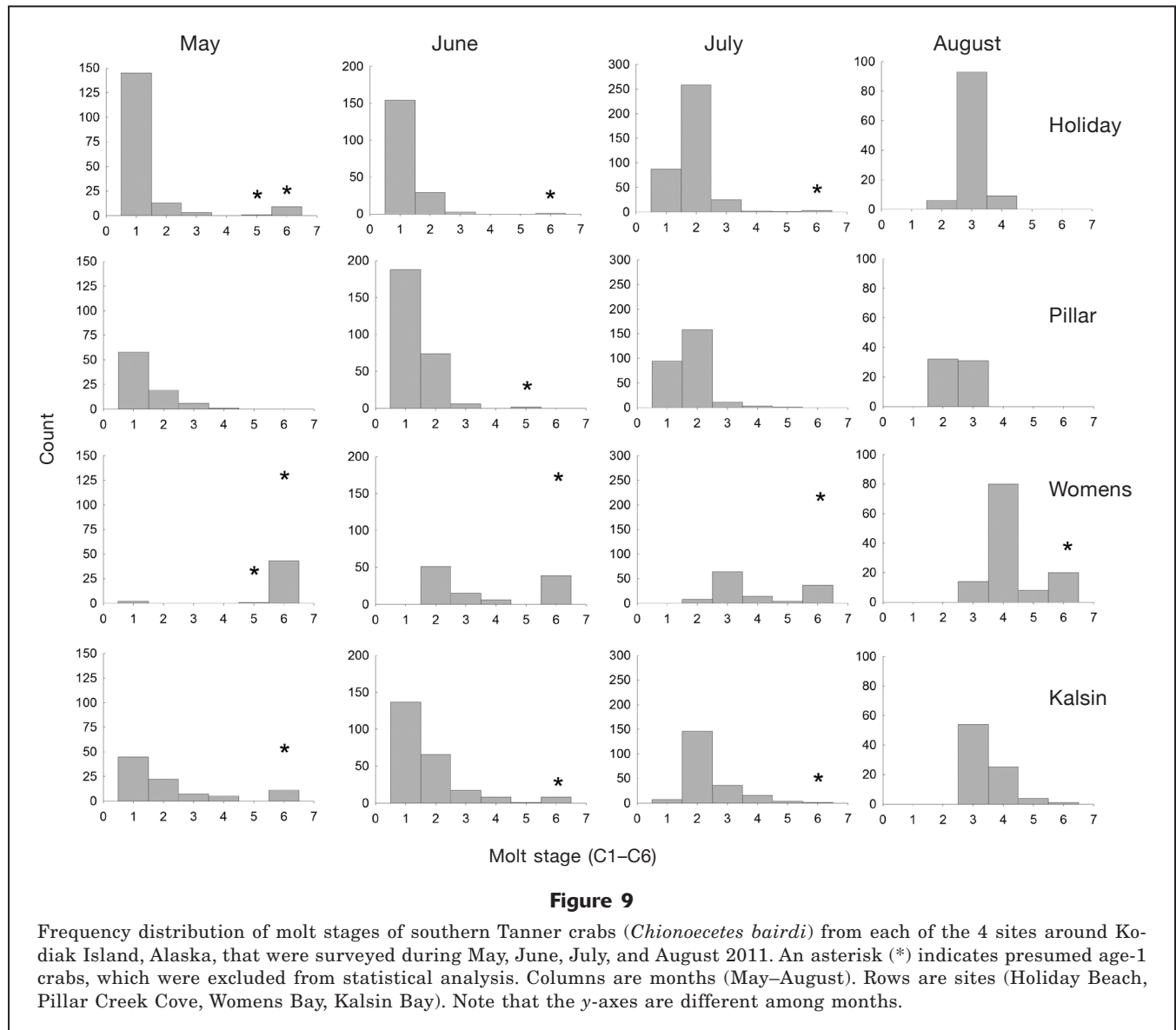
| Stage | Median (mm) | Range (mm) | Increment (%) |
|---|---|---|---|
| C1 | 3.4 | 2.6–4.1 | – |
| C2 | 4.8 | 4.2–5.6 | 41 |
| C3 | 6.8 | 5.7–8.2 | 42 |
| C4 | 9.7 | 8.3–11.3 | 43 |
| C5 | 13.4 | 11.4–15.2 | 38 |
| C6 | 17.8 | 15.3–20.1 | 32 |
| C7 | 23.4 | 20.4–26.6 | 31 |
| C8 | 31.8 | 28.5–35.6 | 36 |
| C9 | 42.0 | 37.3–45.7 | 32 |

### Age-0 crab molt intervals and size distributions

Cumulative size-frequency distributions (all sites and months) were examined initially for each year (2010 and 2011). However, because patterns were identical, we combined both years into a single distribution (Fig. 8; Table 1). Break points between peaks in the size-frequency distribution were taken to be boundaries between successive molt stages. Percent increase in size over the prior stage averaged 36.9%, within a range of 31–43% (Table 1). There was a trend for molt increments to decrease in later molt stages. Using this classification, we assigned individual crabs to stages, thereby allowing us to examine differences in population composition between months and study sites.

A comparison of the 4 study sites surveyed in August of 2010 revealed a significant difference in molt-stage frequencies ($\chi^2$=349.13, df=12, *P*<0.001). C4 instars were dominant at Womens and Kalsin, and C3 instars were dominant at Holiday and Pillar. Accordingly, the mean carapace widths of crabs at Womens (10.1 mm [SE 0.1]) and Kalsin (9.1 mm [SE 0.1]) were larger than those at Holiday (7.2 mm [SE 0.1]) and Pillar (7.0 mm [SE 0.1]; Kruskal-Wallis: *P*<0.001; multiple comparisons: *P*<0.05).

Examination of data from surveys conducted in 2011 revealed that differences between study sites in frequency distribution of molt stages were established relatively early in the late summer (Fig. 9). Differences in molt-stage composition between sites were evident in May ($\chi^2$=41.36, df=6, *P*<0.001). C1 instars dominated populations, although C2, C3, and even C4 instars were present at Kalsin and in lessening degrees at Pillar and Holiday (we did not include Womens in our analysis because only several C1 instars were encountered there). As a consequence, the mean carapace widths of crabs at Kalsin (4.5 mm [SE 0.2]) and Pillar (4.0 mm [SE 0.1]) were larger than the mean at Holiday (3.6 mm [SE 0.1]; Kruskal-Wallis: *P*<0.001; multiple comparisons: *P*<0.05). By June, crabs were present at Womens and were typically one stage further along than those at the other sites ($\chi^2$=184.89, df=9, *P*<0.001). Accordingly, the mean carapace width of crabs at Womens (5.7 mm [SE 0.2]) was larger than the means for crabs at Kalsin (4.2 mm [SE 0.1]) and Pillar (3.8 mm [SE 0.1]), where crabs in turn were larger than crabs at Holiday (3.5 mm [SE 0.1]; Kruskal-Wallis: *P*<0.001; multiple comparisons: *P*<0.05). Similarly, in July, C3 instars were prevalent at Womens, whereas C2 instars dominated the other sites ($\chi^2$=436.06, df=12, *P*<0.001). As a result, the order of mean carapace widths of crabs at the study sites was Womens > Kalsin > Holiday > Pillar, and all sites differed significantly from each other (Kruskal-Wallis: *P*<0.001; multiple comparisons: *P*<0.05). Lastly in August, C4 instars dominated at Womens, a mixture of C3 and C4 instars dominated at Kalsin, C3 instars were dominant at Holiday, and a

**Figure 9**

Frequency distribution of molt stages of southern Tanner crabs (*Chionoecetes bairdi*) from each of the 4 sites around Kodiak Island, Alaska, that were surveyed during May, June, July, and August 2011. An asterisk (*) indicates presumed age-1 crabs, which were excluded from statistical analysis. Columns are months (May–August). Rows are sites (Holiday Beach, Pillar Creek Cove, Womens Bay, Kalsin Bay). Note that the *y*-axes are different among months.

mixture of C2 and C3 instars were dominant at Pillar ($\chi^2$=291.00, df=12, $P$<0.001). As in July, the ranking of sites by mean carapace width was Womens > Kalsin > Holiday > Pillar, and all sites differed significantly from each other (Kruskal-Wallis: $P$<0.001; multiple comparisons: $P$<0.05). Molt-stage composition varied with the interaction of month, depth, and study site; however, there was no discernible pattern, and, therefore, we did not explore this interactive effect further.

Although the relative abundance of molt stages largely controlled differences in mean carapace width among sites, for crabs at given molt stages there were also small but significant differences between sites. Considering only C1 crabs, we found that there was no difference in mean carapace width between sites ($F_{[3,\ 928]}$=1.34, $P$=0.261). However, among C2 crabs, mean carapace width was greater at Womens (4.93 mm [SE 0.03]) than at Kalsin (4.82 mm [SE 0.02]) and Holiday (4.78 mm [SE 0.02]), where the means in turn were larger than the mean at Pillar (4.70 mm [SE 0.02]); Kruskal-Wallis: $P$<0.001; multiple comparisons: $P$<0.05). Among C3 instars, those at Womens (7.13 mm [SE 0.04]) and Kalsin (6.98 mm [SE 0.03]) had greater mean carapace widths than those at Holiday (6.67 mm [SE 0.03]), where the mean in turn was larger than the mean at Pillar (6.55 mm [SE 0.03]); Kruskal-Wallis: $P$<0.001; multiple comparisons: $P$<0.05). Lastly, among C4 instars, those at Womens (9.77 mm [SE 0.03]) and Kalsin (9.82 mm [SE 0.05]) again had greater mean carapace widths than those at Holiday (9.51 mm [SE 0.08]), where the mean was in turn greater than that at Pillar (9.08 mm [SE 0.09]); $F_{[3,\ 503]}$=26.6, $P$<0.001). Crabs in the C5 and C6 molt stages were too few in number to provide meaningful comparisons.

Mean daily seawater temperatures at 15 m (MLLW) for the period from 20 May through 22 August 2011, were 8.2°C, 8.1°C, 8.0°C and 7.7°C for Womens, Pillar, Holiday, and Kalsin, respectively. Mean daily seawater temperature increased though the season ($F_{[1, 375]}$=7475.21, $P$<0.001) and differed among sites ($F_{[3, 375]}$=31.95, $P$<0.001), with mean temperature at Womens and Pillar higher than that at Holiday and with mean temperature at Holiday higher than at Kalsin (Tukey's HSD: $P$<0.05).

## Discussion

Our results illuminate several aspects of the early life history and habitat use of recently settled Tanner crab. First, data indicate that settlement and metamorphosis by Tanner megalopae in the northwestern Gulf of Alaska begins in April and continue into July. We did not sample before May; therefore, our inference that settlement begins in April is based on the observation that in May nearly all age-0 Tanner crabs at our study sites were in the C1 molt stage, indicating that they had been on bottom for a relatively short period. By July, C1 instars were infrequent in scrape tows and were completely absent in August. This recruitment schedule resulted in increasing crabs densities from May to a peak in July, and it is consistent with the pattern of egg hatching (April–May) that has been reported for both primiparous and multiparous females (Stevens, 2003b; Swiney, 2008). Because the timing of settlement at our various sites was comparable and the 4 sites are separated by only tens of kilometers, we posit that larval sources for these sites were the same. Stevens (2003b) speculated that hatching of Tanner eggs in Chiniak Bay is synchronized with spring tides, which act to break down dominant costal circulation patterns and potentially result in greater larval retention within the Chiniak Bay system.

Depth had a strong influence on crab density, although this effect varied between embayments. At Pillar and Holiday, recently settled crabs were absent or scarce from scrape tows at depths <8 m, but they became more abundant with increasing depth out to 23 m. Trawl tows conducted during July 2010 at Pillar revealed that crab density was highest at depths of 30–35 m, decreasing farther offshore, at depths of 50–80 m. By August, densities had declined and there was no longer a maxima at intermediate depths. In contrast with densities at Pillar and Holiday, at Womens and Kalsin, crab density was generally highest at depths between 10 and 15 m, although there was variability among months. We did not conduct trawl sampling at either Womens or Kalsin and have no knowledge of what crab densities were at depths greater than those sampled by the scrape (25 m).

We suspect that the difference in crab depth distribution between Pillar and Holiday, on one hand, and Womens and Kalsin, on the other, is primarily related to wave energy. Womens is the most protected of the study sites, with a narrow entrance and offshore islands that dissipate wave energy. Although not as protected as Womens, the Kalsin study site is located near the head of the Kalsin Bay and, as such, typically experiences lower wave action than the sites at Pillar and Holiday. Pillar and particularly Holiday are more exposed and frequently experience strong wave action from the Gulf of Alaska. Although bottom surge associated with wave action may directly affect crabs, by interfering with settlement, impeding foraging, or dislodging crabs from the bottom, we suspect that the influence of wave energy on sediment characteristics is also a primary factor.

Because of the inverse relationship between depth and wave-induced bottom scour, sites such as Pillar and Holiday are characterized by coarse sand in shallow water (depths <10 m), by fine sands or silty sands at depths of 10–25 m, and finally by an increasing contribution of mud at depths >25 m (Stoner et al., 2007). At Womens and Kalsin, as a result of lower wave energy, compared with that at other sites, finer silts and muddy sediments occur at shallower depths (senior author, personal observ.). For juvenile Tanner crabs, the ability to bury themselves in silty or muddy sediments is their first line of defense against predators. Similarly, juvenile flatfish use burial as a predation deterrent and preferentially choose sediment in which they can easily bury themselves (Stoner and Ottmar, 2003). Furthermore, fine sediments around Kodiak typically have higher organic content than coarse sediment (Stoner et al., 2007). Tanner crabs consume not only a variety of infaunal prey, including bivalves, polychaetes, and other crustaceans, but also detrital material (Jewett and Feder, 1983), which presumably occurs in higher concentrations in silty and muddy sediments than in coarser sediments. After the spring bloom, diatoms settle to the bottom and accumulate in low wave-energy areas. This flocculent material is readily observed on the surface of fine sediment in Womens Bay during late spring and summer months (Munk[4]).

Juvenile crabs and fishes often seek physically structured habitats. Juvenile red king crab and blue king crab (*Paralithodes platypus*) prefer highly structured habitats, which consist of pebbles, cobble, hydroids, macroalgae, shell material, etc., where they are less vulnerable to predators (Stoner, 2009; Pirtle and Stoner, 2010). Tanner crabs, like snow crabs, generally are thought to prefer sandy, silty, and muddy sediments—a preference that might be explained by their lack of spines that would, if present as in king crabs, inhibit them from rapidly burying themselves (senior author, personal observ.). However, in beam trawl hauls conducted during 2009, we observed that recently settled Tanner crabs were most common at depths of 15–30 m, the same depth range where *S. sibirica* is most abundant (Ryer et al., 2013). On the basis of this re-

lationship, we hypothesized that recently settled Tanner crabs were preferentially using the habitat created by *S. sibirica*. Juvenile flatfish, principally northern rock sole and Pacific halibut (*Hippoglossus stenolepis*), are also attracted to this type of habitat (Ryer et al., 2013). Although fish avoid areas where worms were so dense as to preclude burial, fish aggregate along the sparse and patchy edges of this habitat type (Ryer et al., 2013). In 2010, when both worm tubes and crabs were relatively abundant, there was a significant positive effect of worm abundance on crab density, after the effect of depth was factored out. However, during 2011, when both worms and crabs were less abundant, worm abundance had no effect on crab density. This difference in effects indicates that the habitat created by *S. sibirica* tubes has only a modest influence on distribution of age-0 Tanner crabs.

In a manner analogous to the refuge function of eelgrass (*Zostera marina* L.) (Wilson et al., 1987; Ryer, 1988), the physical structure of the worm tube habitat may provide age-0 Tanner crabs refuge from fish predators. Predation by Pacific cod (*Gadus macrocephalus*) is thought to regulate Tanner crab recruitment in the Gulf of Alaska and Bering Sea (Livingston, 1989). Juvenile Tanner crabs may also consume *S. sibirica* directly or the associated invertebrate species supported by the worm tube habitat (senior author, personal observ.). Alternatively, both species may be attracted to the same depth and sediment characteristics, possibly explaining their association. This interpretation is supported by results from our quadrat surveys, which were conducted by divers at a finer scale than that of the scrape tows and which indicated there was no relationship between crab density and worm tube density. Resolving the nature of this association could be addressed though controlled laboratory experimentation that might reveal whether age-0 Tanner crabs show an attraction for the structure provided by *S. sibirica* and whether an association reduces predation on age-0 Tanner crabs.

Growth in crustaceans is a function of molt increments, typically expressed as percent increase in size, and a function of the frequency with which those molts occur. Knowledge of the age distribution of a population can be important information in stock assessment. In practice, aging commercially harvested North Pacific crabs species relies upon imprecise estimates of the number of molts that occur during each year. Our data indicate that age-0 Tanner crab, around Kodiak Island, pass through between 3 and 5 molts from settlement through August. By May of the next year, crabs have gone through 6 or more molt stages. Although no other studies have documented growth during the first year for this species, Donaldson et al. (1981) reported a strong size mode at 18 mm (C6 instars) during May–June in Prince William Sound, northern Gulf of Alaska. Therefore, it appears that crabs in the northern Gulf of Alaska, including near Kodiak, typically go through roughly 6 molt stages in their first year. On the basis of various samples from areas in the Gulf of Alaska,

these authors concluded that Tanner crabs typically undergo 3 more molts in their second year and 2 molts in their third year, after which molting occurs annually. Donaldson et al. (1981) found that 50% of females were mature at 83 mm and 50% males were mature at 90 mm, indicating that age at maturity for this species is approximately 5 years for females and 7 years for males.

Variance in this age-growth schedule will result from differential growth rates between localities and years. Temperature plays an important role in modulating growth in crustaceans (Hartnoll, 1982). After 60 days, red king crab and blue king crab reared at 1.5°C were mostly still C1 instars, whereas those reared at 8°C for 60 days were mostly C3 instars (Stoner et al., 2010, 2013). This finding indicates that crabs settling into habitats with differing ambient temperatures may experience vastly different growth rates. Using published, temperature-dependent growth rates, Stevens (1990) estimated growth and years to maturity for red king crabs from areas with varying temperature regimes in Bristol Bay, Alaska. He concluded that growth varies greatly between areas, such that crabs recruiting to the pot fishery in the eastern Bering Sea in any given year may be derived from up to 4 or 5 year classes. This conclusion indicates that it would be advantageous for Tanner megalopae to preferentially settle in shallower water where temperatures are supportive of accelerated growth. Naturally, such an outcome would require that other factors, such as forage base and predation risk, do not compromise the enhanced growth for crabs settling in shallower water.

Data from out study indicate that growth rates differ among sites. During both 2010 and 2011, crabs from Womens were generally 1 molt stage larger by the end of August than crabs from Pillar and Holiday. There are several possible explanations for this observed size difference. Crabs may simply recruit earlier at Womens than at the other sites. However, this notion is not consistent with results from our May 2011 sampling which indicated that crabs at Womens may actually have recruited slightly later. Temperature may play a role. We did document minor differences in mean ambient bottom temperature (at a depth of 15 m MLLW) between sites; temperature was greatest at Womens. However, the difference in mean temperature between sites was only 0.5°C, and we are skeptical that this difference would result in the greater size observed for crabs at Womens. Age-0 Tanner crabs molt approximately once every 873 degree days in the laboratory, and a temperature shift of 0.5°C would only marginally increase the frequency of molting (Long et al., 2013b). Furthermore, temperature was lowest at Kalsin, yet crabs at Kalsin were closest in size to those at Womens and generally were larger than those at Pillar and Holiday. It is perhaps more important to note that bottom temperature at 15 m may not be representative of temperatures for an entire embayment. For example, at both Womens and Kalsin where high growth was seen, crabs tended to be found at shallower depths, where temperatures are expected to be higher.

The observed difference in molt-stage frequency between sites may be a product of differential emigration or mortality. If predation is size-dependent, and predators are largely consuming smaller crabs, the size-frequency distribution of crabs at Womens could be skewed toward larger crabs by heavy predation. If this size-selective postsettlement process was in fact occurring, we would expect crab numbers to decline rapidly as a result of predation. Settlement was largely complete by July, but Womens was the only site to experience no population decline from July to August, indicating that predation was low at that site. Alternatively, differential migration may offer an explanation, if it is a natural progression for Tanner crabs to settle in shallow water and then migrate to deeper water. Unlike the other sites, Womens has a narrow entrance with a sill that rises up to a depth of approximately 11 m. This narrow entrance could reduce offshore migration of juveniles in Womens Bay. However, there is no structural hindrance to offshore migration at Kalsin, where crabs were also relatively large. If anything, we suspect that the shallow sill at Womens may block the offshore migration of larger crabs in the fall, winter, or spring because Womens was the only site that retained an appreciable number of age-1 crabs.

Lastly, sites like Womens and Kalsin have finer sediments, which are likely to accumulate organic carbon and support a denser infaunal community than the other sites. Therefore, crabs may have more or better food there. Results of preliminary lipid and essential fatty acid analysis that we performed on crabs from our study sites (Copeman and Ryer[5]) indicate that crabs from Womens and Kalsin had higher levels of storage lipids and of diatom fatty acid markers than crabs from Pillar and Holiday. Overall higher levels of storage lipids and diatom-derived fatty acids have been associated with accelerated growth in larval Pacific cod (Copeman and Laurel, 2010) and juvenile red king crabs (Copeman et al., 2012).

We also observed that, for individual molt stages, crabs were larger at Womens and Kalsin than at Holiday and Pillar. In a review of crustacean growth, Hartnoll (1982) concluded that, for many species, increases in the quantity or quality of food not only decreased the intermolt period but also increased the molt increment. However, this effect of food availability on growth may vary ontogenetically. Among larger juvenile blue crabs, growth has been correlated with higher food density (Seitz et al., 2005), whereas, for smaller juveniles, this link has not been made (Long et al., 2011). In contrast, increases in temperature typically decrease both the intermolt period the molt increment, although Stoner et al. (2010) reported an increase in red king crab molt increments with increased temperature. A further understanding of the relative role of temperature versus food on growth of the Tanner crab will await controlled laboratory experiments that manipulate these parameters.

Whether juvenile Tanner crabs use habitats that are distinct from those occupied by adults remains unclear. The arguments presented here make the case that juveniles would fare better in shallow waters (depths <50 m). Further, we encountered few individuals larger than the C7 molt stage (carapace widths of 20–26 mm), indicating that crabs older than 2 or 3 years of age are found in different, perhaps, deeper habitats. In Glacier Bay, Alaska, Tanner crabs are segregated by ontogenetic stage; smaller, or juvenile, crabs are located at the heads of fjords, near glaciers, and adult, or larger crabs are more centrally located in fjords and in inlet areas (Nielsen et al., 2007). However, this segregation did not appear to be depth related, and the authors speculated that cannibalism, competition, predation, or differences in substrate preferences might be responsible. In Cook Inlet, Alaska, large individuals were found throughout the inlet, whereas juveniles with carapace widths <20 mm were concentrated in the inlet mouth at generally greater depths (Paul, 1982). This diversity of results indicates that the factors that control the distribution of age-0 crabs can vary between areas.

Although we do not yet know the full range of depths and habitats used by age-0 Tanner crabs, the settlement densities and patterns documented in this work indicate that relatively shallow waters (<50 m) may constitute an important habitat for Tanner crabs around Kodiak Island, particularly because temperatures in these shallow waters can be expected to speed growth and shorten the number of years before crabs recruit to the fishable or reproductive population.

## Acknowledgments

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