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# Living on the edge: distribution of Dungeness crab *Cancer magister* in a recently deglaciated fjord

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ABSTRACT: Glacier Bay, Alaska, has supported a productive Dungeness crab fishery, although the area where the fishery occurred was small relative to the remainder of the Bay. We hypothesized that 1 or more abiotic limiting factors prevented crabs from surviving in the upper Bay. We tested this hypothesis by systematically sampling for relative abundance of Dungeness crabs from the mouth to the head of the Bay. We measured salinity, temperature and turbidity at each of the sampling sites and at permanent stations to characterize the habitat within and among years. We expected to find a completely truncated spatial distribution. Instead, we found that adult Dungeness crabs can survive in habitats heavily influenced by tidewater glaciers. There were significantly fewer crabs in the upper Bay and a sharp decrease in abundance around 40 km from the mouth of the Bay. The region of the Bay beyond 40 km from the mouth had a very low density of predominately adult male crabs. The narrow size frequency distribution and the lack of small crabs is consistent with poor survival in one of the pre-adult life stages in the upper Bay.

KEY WORDS: Dungeness crab · Recruitment · Post-settlement mortality · Fjord · Oceanography · Temperature · Salinity

## INTRODUCTION

Glacier Bay, a recently deglaciated fjord estuarine system with strong salinity, temperature and turbidity gradients, has supported a productive Dungeness crab *Cancer magister* fishery. Although the Bay is large (1255 km$^2$), the area where the fishery occurred until December 1999 (National Park Service 1999), was relatively small and was concentrated in the southern portion of the Bay (C. Soiseth National Park Service unpubl. data). Dungeness crab populations in Alaska are near the northern boundary of their range (Hart 1982), which is also approximately the northern limit for all members of the genus *Cancer* (MacKay 1943). Because there was no crab fishery effort in the upper Bay and we had not found Dungeness crabs during preliminary SCUBA transects in this area, we hypothesized that one or more limiting abiotic factors prevented crabs from surviving in the upper Bay. We tested this hypothesis by systematically sampling for relative abundance of Dungeness crabs from the mouth (south) to the head (north) of the Bay. We measured salinity, temperature and turbidity at each of the sampling sites to characterize changes in habitat from the lower to the upper Bay. The same water quality measurements were collected at permanent stations to characterize the habitat within and among years.

Glacier Bay has numerous tidewater glaciers and the marine waters in this deep fjord are cold (Pickard 1967). Cold water can affect Dungeness crabs at all stages of their life cycle. Cold water increases (1) the length of time females brood their eggs (Wild 1983, Shirley et al. 1987); (2) the duration of larval stages (Sulkin & McKeen 1989, 1996); (3) larval mortality (Reed 1969, Moloney et al. 1994); (4) adult mortality (Shirley et al. 1987); and (5) molt interval of juvenile crabs (Gutermuth & Armstrong 1989, Kondzela & Shirley 1993, Wainwright & Armstrong 1993). Cold water also decreases the metabolic rate of juvenile crabs (Gutermuth & Armstrong 1989) and changes the

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morphology of larvae (Shirley et al. 1987). Many of these effects are likely to decrease a population's growth rate, which could alter the response of populations to commercial fishing. Alaska's Dungeness crab fisheries in Kodiak, Cook Inlet and Prince William Sound have experienced long-term declines without significant rebounds (Orensanz et al. 1998).

Our initial hypothesis—that there would be no crabs in the upper Bay—was not supported; we found low numbers of apparently healthy adult crabs within 1 km of tidewater glaciers in the upper reaches of the Bay. As a result we tested for relationships between abiotic factors (temperature, salinity and turbidity) and distance from the mouth of the Bay to determine whether 1 or more of these factors might be limiting the survival of larval or juvenile Dungeness crabs. We also compared the age and sex composition of crabs in areas of high (lower Bay) and extremely low (upper Bay) densities.

## MATERIALS AND METHODS

**Study area.** We sampled for Dungeness crabs in Glacier Bay, Alaska at the northern end of SE Alaska (Fig. 1). Glacier Bay is a young, silled fjord system with high sedimentation rates of clay-silt particles from streams and tidewater glaciers (Cowan et al. 1988). In the last 220 yr, the glacial terminus has retreated 100 km from its maximum extent at the mouth of Glacier Bay. The sill at the mouth of the Bay is approximately 25 m deep, and there are numerous sills of varying depths throughout the Bay. Deep basins exist between these sills, and the maximum depth in Glacier Bay is approximately 450 m. The tides are mixed semidiurnal, with a maximum vertical range of 7.5 m. The primarily unconsolidated rocky coastline is highly convoluted, creating numerous small bays characterized by clay-silt bottoms that also commonly include sand, pebble, cobble, boulder and shell substrates.

**Crab sampling.** We sampled for Dungeness crabs with commercial crab pots (0.91 m in diameter and 0.36 m tall, with 5 cm wire mesh) modified to retain smaller crabs by closing the escape rings with webbing. The pots are not effective at sampling crabs with carapace widths less than 120 mm (unpubl. data). Pots were baited with cod, and bait jars filled with chopped herring and squid. A total of 468 pots were set at 52 sites from 14 to 23 August and 8 to 12 September 1999 (Fig. 1). Of the total pots, 460 were 'valid' pots, the other 8 were either lost, found open or were mistakenly not baited.

Three criteria were used to select sampling sites with comparable habitat: (1) slope less than 10°; (2) depth 10 m relative to mean lower low water (MLLW); and (3) habitat within 2 km of a stream mouth. Polygons that encompassed all 3 criteria were mapped in a geographic information system (GIS) environment using ArcView GIS (Environmental Systems Research Institute). Potential pot locations were selected along the 10 m bathymetry line at 150 m intervals in the polygons. The Beardslee Island archipelago (Fig. 1) in the lower Bay was eliminated from the analysis because there was no large cluster of islands in the upper Bay, which might have biased the upper and lower Bay comparisons.

Rapid and accurate placement of pots was facilitated with an onboard GIS system which projected the research vessel's position in real-time on the ArcView layer which contained the potential pot locations. The research vessel's

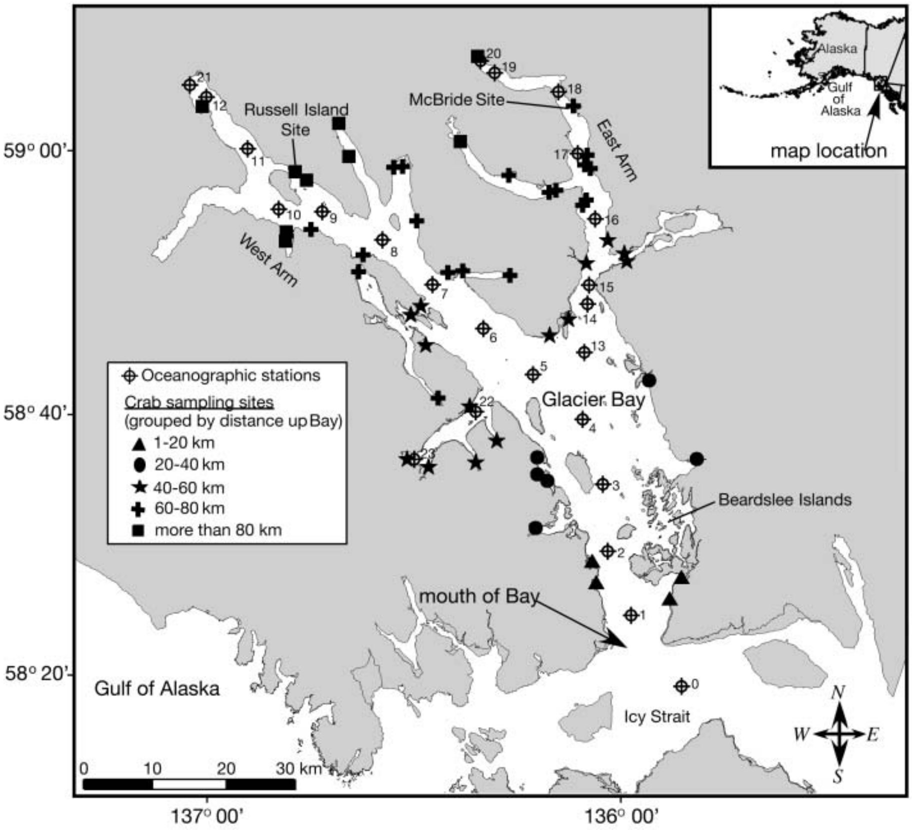

Fig. 1. Sampling sites and oceanographic stations, Glacier Bay, Alaska

position was continuously updated with custom software that integrated the data output from a global positioning system (Rockwell PLGR+) with the Arc View layer. Due to inaccuracy of the digital bathymetry layer, some of the target pot locations were not at 10 m depths; pot placement was adjusted on site to achieve the 10 m MLLW depth. The actual pot locations were recorded in an ArcView file.

Each day, 9 to 96 pots were set and left to soak for 24 h. As the pots were retrieved, all organisms were counted, identified to species (rarely to genus) and returned to the water. Dungeness crabs were measured and examined. Sex, carapace width, carapace condition and appendage damage were recorded for all crabs. Carapace width, immediately anterior to the 10th anterolateral spine, was measured to the nearest mm with vernier calipers (Shirley & Shirley 1988, Shirley et al. 1996).

The distance through water from the mouth of the Bay to each pot location was measured using an extension to ArcView[1]. Distributional differences in relative abundance were examined by plotting the number of crabs caught in each pot against the distance from the mouth of the Bay.

**Oceanographic sampling.** A Sea-Bird SBE-19 SEACAT profiling conductivity-temperature-depth (CTD) probe was used to measure temperature, salinity and optical backscatter (OBS) at each study site within 1 d of the pot sampling. Oceanographic data were also collected at permanent stations 2 to 5 times annually from August 1992 to July 2001 as part of a long-term monitoring program in Glacier Bay (Hooge & Hooge 2001). Oceanographic monitoring stations were located from Icy Strait, about 10 km outside of Glacier Bay (Fig. 1), and then mid-channel approximately 9.3 km apart, and extended into the heads of the 2 major fjords (Fig. 1). To allow for a comparison of nearshore and mid-channel oceanographic data, an oceanographic survey was conducted concurrent with the pot sampling in August 1999. Salinity, temperature and OBS data collected at each pot sampling site were compared to the samples collected at the nearest long-term oceanographic station with simple regression. The 2 sets of oceanographic data were compared at depth of the 2, 4 and 10 m. All statistical tests were conducted with StatView (SAS Institute).

To characterize the specific depths and seasons that were likely to be critical to the 3 life stages (adult, juvenile, and larval) of Dungeness crabs, we analyzed salinity, temperature and OBS data from oceanographic surveys that have been conducted since 1992. For adults, we used oceanographic data from 10 m depth. This was the depth at which we set the pots and the depth at which adult crabs were most abundant on dive transects (unpubl. data). Juvenile crabs are usually associated with the intertidal to upper subtidal zones (Reilly 1983, Orensanz & Gallucci 1988, Gunderson et al. 1990, Fernandez et al. 1993b, Armstrong et al. 1995); consequently, we analyzed oceanographic data from 0 m depths. The average tidal range in Glacier Bay is approximately 4 m. Therefore the portion of the water column a juvenile crab would encounter at 0 m depth (MLLW) would be the top 4 m of the water column. Similarly, a crab at 10 m (MLLW) would be exposed to the 4 m of the water column below 10 m. Thus, for our selected depths (0, 10 and 50 m) we averaged the temperatures from the appropriate 4 m segments. Since larvae migrate vertically, they most likely encounter conditions at these and deeper depths. To characterize the deeper water temperatures that larvae might encounter, we used data from 50 m depths (i.e. average of the 4 m below 50 m). Seasonal patterns by depth were compared by plotting temperature values from 4 oceanographic stations (Stns 0, 3, 7 and 19) (Fig. 1) by month. We also tested for temperature gradients from the lower to upper Bay (temperature vs distance from mouth of Bay) using linear regression at the 3 selected depths.

**Effects of temperature on mortality and growth.** Infrequent cold temperature events can cause mortality of adult crabs (Shirley et al. 1987). Juveniles apparently can tolerate temperatures down to 0°C (Kondzela & Shirley 1993). To test for potential effects of temperature on adult crab survival, we selected the coldest temperatures recorded at 0 and 10 m during any of the oceanographic surveys. These temperatures were plotted against the distance from the mouth of the Bay. We omitted 50 m from this analysis because the megalopae settle during the autumn and are not in the water column in the winter.

To estimate the effect of temperature on growth, we used an integrated growth model that combines a bent-line model for molt increment with a temperature-dependent model for inter-molt period (Wainwright & Armstrong 1993). The molt increment ($Z$) was calculated as:

$$Z = \mathrm{c} + \mathrm{d}X \quad (1)$$

where $X$ is pre-molt carapace width in mm, c = 1.3, and d = 0.23 (Wainwright & Armstrong 1993).

The inter-molt period ($Y$) was calculated as:

$$\log_e(Y) = (\mathrm{a} + \mathrm{b} \times X) - \log_e(T') \quad (2)$$

where $T'$ is temperature in °C – c, $X$ = pre-molt carapace width in mm, and a, b and c = 5.25, 0.017 and

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1.13, respectively. Wainwright (1993) estimated the constants (a, b, c) based on a laboratory study in southeastern Alaska (Kondzela & Shirley 1993).

The inter-molt period was calculated for 4 distances (10, 40, 70 and 100 km) from the mouth of the Bay. Temperature data (0 m depth) were pooled among years and a gradient from the mouth of the Bay to the heads of the fjords was calculated for each month using linear regression. For each location, temperature for each month was estimated from the linear regression. For months with non-significant gradients, we assigned the average temperature (all stations) for the month across all locations. The molt date for each molt stage, by location, was determined by calculating cumulative degree-days (Wainwright & Armstrong 1993). The growth rates were plotted against time starting at settlement, which we estimated to occur in September in Glacier Bay (G. Eckert pers. comm.). For comparison, growth rates for Dungeness crabs based on published temperatures from Grays Harbor, Washington, were plotted using June as the time of settlement (Gutermuth & Armstrong 1989). Only 5 consecutive months of temperature data were available from the Grays Harbor study, so the growth curves were limited to these months.

**Salinity.** Low salinity can have deleterious effects on any of the life stages of Dungeness crabs (Sugarman et al. 1983, Moloney et al. 1994). We examined salinity gradients within the Bay to determine whether salinity reached potentially lethal or debilitating levels. We plotted salinity gradients by distance from the mouth of the Bay for 2 oceanographic surveys that were representative of high summer freshwater input.

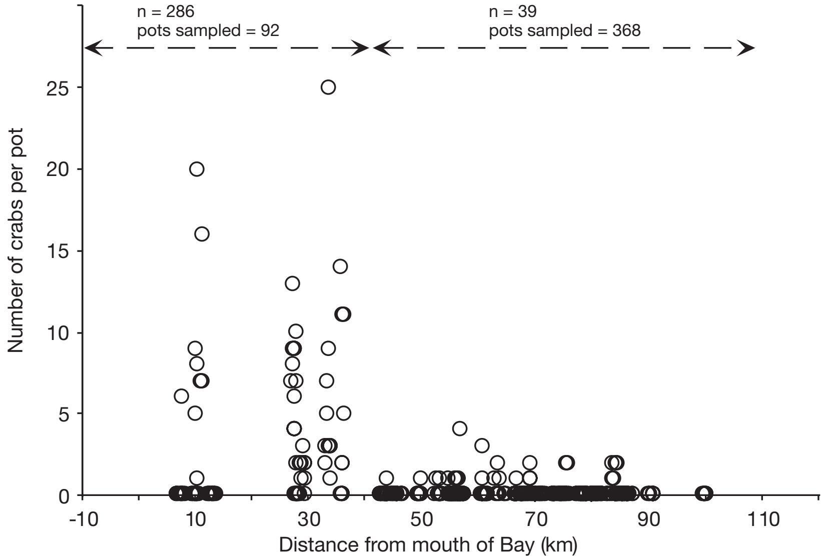

Fig. 2. *Cancer magister.* Relationship between the distance from the mouth of Glacier Bay and the number of individuals caught per pot; n: no. of crabs. Note: pots were not fished at or outside the mouth of the Bay

To reduce osmotic stress, adult crabs intermittently pump water across their gills at 23.2 ppt, and at 15.5 ppt they stop pumping altogether (Sugarman et al. 1983). Based on these threshold values, we selected 3 salinity ranges (<16, 16 to 23 and >23 ppt) and plotted the occurrence of these values by distance from the mouth of the Bay by month.

**Turbidity.** Most brachyuran crabs are negatively phototropic; they migrate vertically presumably using light intensity cues (Forward 1987). OBS was collected for 3 yr from 1999 to 2001. The OBS sensor used in the study has not been calibrated for the sediments found at the oceanographic stations along the length of Glacier Bay. Therefore, the OBS is reported in raw microvolts (mV). We hypothesized that high turbidity might interfere with the vertical migration of the larvae, so OBS values from the oceanographic surveys were plotted by month and distance from the mouth of the Bay.

## RESULTS

### Crab distribution

Dungeness crabs were captured much farther from the mouth of the Bay than we anticipated. Our original hypothesis that crabs were restricted from the upper Bay by an abiotic limiting factor was rejected. Instead of a complete absence, we found dramatically fewer crabs in the upper Bay (Fig. 2). Crabs were found as far-up Bay as Russell Island, 84 km from the mouth of the Bay, in the West Arm and at the mouth of McBride Inlet in the East Arm (Fig. 1). The Russell Island site is 9 km from Lamplugh Glacier and within 20 km of 3 other large, active tidewater glaciers (Grand Pacific, Margerie and Johns Hopkins Glaciers). The McBride site, 76 km from the mouth of the Bay, is 1 km from the face of McBride glacier. During the sampling at McBride, drifting ice and highly turbid glacial surface water characterized the area. Oceanographic Stn 9 was 6.5 km from the Russell Island sampling site and Oceanographic Stn 18 was 2.7 km from the McBride sampling site. The mean, minimum and maximum temperatures recorded at 10 m among years for Oceanographic Stns 9 and 18 were 6.4, 3.2 and 7.6°C, and 6.3, 3.6 and 7.7°C, respectively. The mean, minimum and maximum OBS measurements at Stns 9 and 18 were 19.2, 8.3 and 51.1 mV, and 22.2, 9.2 and 69.4 mV, respectively.

Based on the marked distributional changes in relative abundance (Fig. 2), we classified the portion of the Bay within 40 km of the

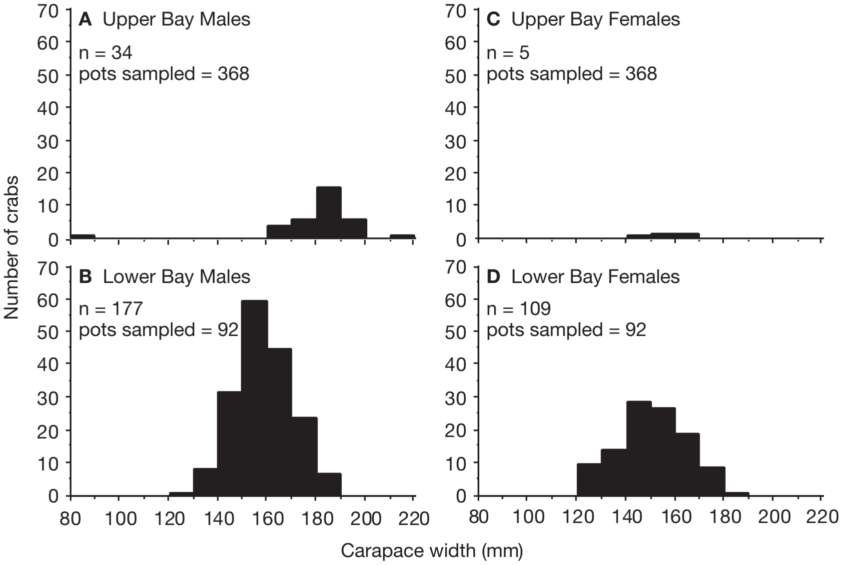

Fig. 3. *Cancer magister.* Size frequency distributions of (A) males in the upper Bay, (B) males in the lower Bay, (C) females in the upper Bay and (D) females in the lower Bay; n: no. of crabs

mouth of the Bay as the area of high crab abundance and the portion of the Bay farther than 40 km from the mouth as the area of low crab density. Subsequently, we refer to these 2 areas as the lower Bay and upper Bay, respectively.

Although we did not find a complete absence of crabs in the upper Bay, the number of crabs per pot declined markedly at distances greater than 40 km from the mouth of the Bay (Fig. 2). The mean number of crabs per pot was 32 times greater in the lower Bay (less than 40 km from the mouth) than the upper Bay (greater than 40 km from the mouth); in the lower bay, the catch per unit effort (CPUE) was 3.2 crabs pot$^{-1}$ (±4.8 SD, n = 92) and in the upper Bay the CPUE was 0.10 crabs pot$^{-1}$ (±0.42 SD, n = 368 pots).

### Size-sex composition of crabs in the upper versus lower Bay

The proportion of male crabs was significantly greater in the upper Bay than in the lower Bay ($\chi^2$ = 8.57, df = 1, p = 0.003). Male crabs in the upper Bay were significantly larger than male crabs in the lower Bay (paired *t*-test: $t = 8.50$, $p < 0.0001$) (Fig. 3A,B). The size of female crabs was not significantly different between the 2 areas (paired *t*-test: $t = 1.08$, p = 0.28); the sample size from the upper Bay was small and thus this test has low power (upper Bay: n = 5, 95% CI [150.11 to 163.09]; lower Bay: n = 109, 95% CI [147.58 to 152.61]) (Fig. 3C,D).

### Long-term oceanographic stations versus pot sampling stations

Temperatures declined from the mouth of the Bay to the heads of the fjords at 2, 4 and 10 m depths for both the pot sampling sites and the permanent long-term oceanographic stations (Fig. 4A,B,C). A similar pattern was observed for salinity by both sampling methods in shallow water (Fig. 4D,E,F). At deeper depths, however, salinity values were relatively consistent throughout the Bay (Fig. 4F). Oceanographic data collected at each pot sampling site were highly significantly correlated to measurements collected at the nearest long-term oceanographic stations (temperature: $r^2 = 0.53$, $p < 0.0001$; salinity: $r^2 = 0.75$, $p < 0.0001$; OBS: $r^2 = 0.13$, $p < 0.0001$). The high $r^2$ values for temperature and salinity allowed us to characterize the nearshore environment using data from the long-term oceanographic monitoring study. The $r^2$ for OBS was considerably lower, but because our primary interest in OBS was its potential effect on megalopae, the mid-channel oceanographic stations provided the best characterization of the larvae's pelagic habitat.

### Temperature

Mean water temperatures at 3 depths (0, 10 and 50 m) showed a strong seasonal cycle, with maximum temperatures in June through October, depending on depth, and minimum temperatures occurring in March (Fig. 5). From June to September at all 3 depths, there was a significant negative temperature gradient from the lower to upper Bay, with the steepest gradients at shallower depths (Fig. 6). During winter months, most of the gradients from lower to upper Bay did not have a significant slope.

The coldest temperatures occurred during 2 oceanographic surveys conducted in March 1996 and 1999. During both of these surveys, the temperatures at 0 m were lower than the temperatures at 10 m (Fig. 7); this mid-winter temperature maximum at depth is a pattern observed each winter throughout much of the Bay at the permanent oceanographic stations.

### Growth rate model

The predicted growth rates for crabs in the upper Bay were substantially less than the growth rates for

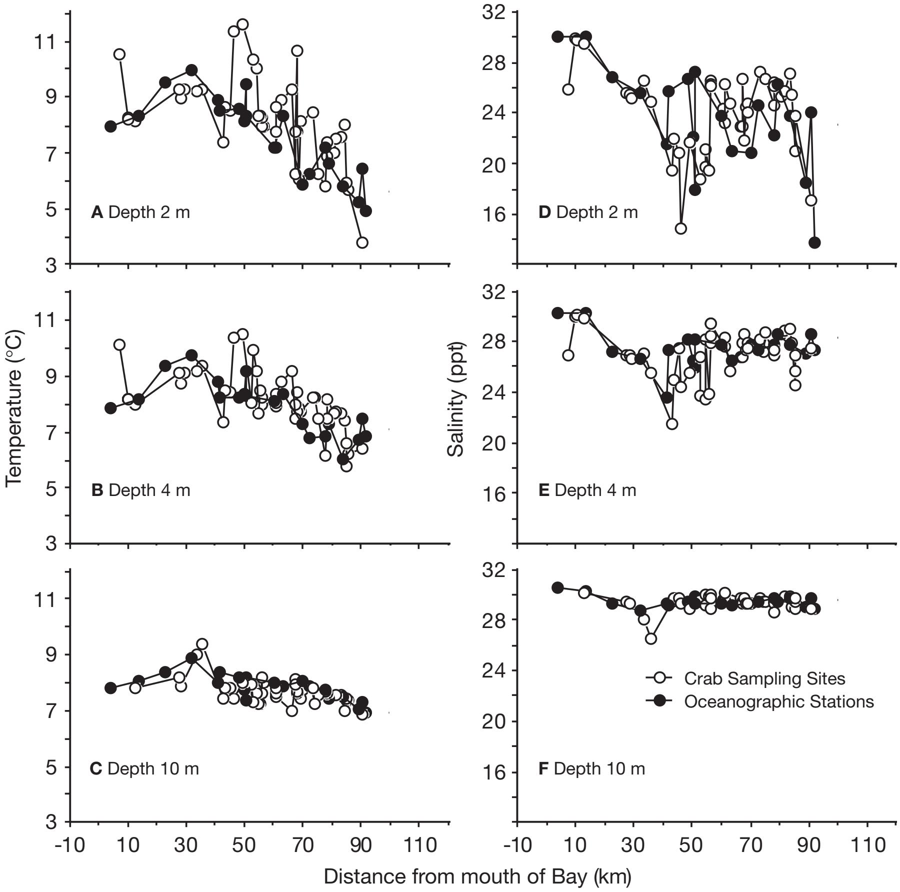

Fig. 4. (A, B, C) Temperature and (D, E, F) salinity data from 3 depths collected in August 1999, at both crab sampling sites and oceanographic stations from the mouth of the Bay to the head of the major fjords

crabs in the lower Bay. Both of these growth rates were less than the growth rates predicted from temperatures in Grays Harbor, Washington (Fig. 8). For example, according to this model, crabs in Grays Harbor (inner estuary) grow to 47 mm carapace width in 4.5 mo (Fig. 8), whereas a crab 40 km inside Glacier Bay would require 12.2 mo to reach the same size (Fig. 8). Crabs 100 km from the mouth of Glacier Bay would require 14.2 mo to reach 47 mm carapace width (Fig. 8).

### Salinity

In the upper Bay, the surface waters typically have substantially reduced salinities during summer months due to glacial run-off. Within the surface layer (2 to 4 m), salinity decreased with increasing distance from the mouth of the Bay (Fig. 9A,B). Salinities of less than 23 ppt occurred from May to November, and salinities of less than 15 ppt occurred from June to September (Fig. 10). From May to November, 40 % of the oceanographic casts in the upper Bay recorded salinities of less than 23 ppt, while only 13 % were found in the lower Bay. Salinities of less than 15 ppt were documented in 13 % of the upper Bay casts and none of the lower Bay casts (Fig. 10).

### Turbidity

High turbidity occurred in a seasonal pattern that paralleled the seasonal pattern of low salinity. All of the turbidity measurements >50 mV were greater than 40 km from the mouth of the Bay (Fig. 11).

## DISCUSSION

Contrary to our prediction, adult Dungeness crabs can survive in habitats heavily influenced by glaciers, where the water is cold and characterized by high sediment loads and low surface salinity. We expected to find no crabs in the low salinity, cold temperature and high turbidity of the upper Bay. Instead, we found an abrupt decrease in relative abundance approximately 40 km up-Bay from the mouth of Glacier Bay, where a very low density of predominately adult male crabs occurred, even near tidewater glaciers. The dramatic and abrupt decrease in relative abundance from the lower to upper Bay suggests that the threshold value of 1 or more limiting factors was exceeded, resulting in a reduced density of the population at one or more stages in the life cycle.

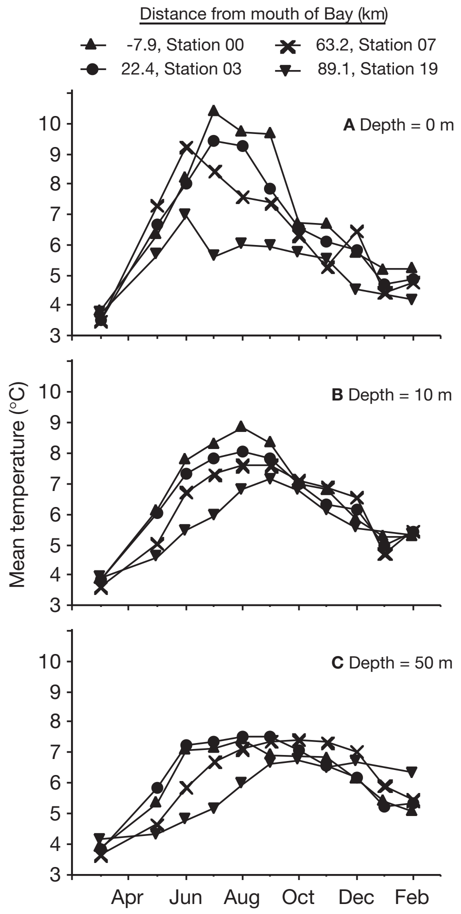

Fig. 5. Seasonal mean temperatures at 4 oceanographic stations and 3 depths of (A) 0, (B) 10 and (C) 50 m, respectively

The adult crabs inhabiting the upper Bay were large and appeared healthy, so individual crabs can survive in this environment. The crabs in the upper Bay were almost exclusively males and were significantly larger than those in the lower Bay. These size-sex differences are most likely explained by high commercial fishing mortality in the lower Bay since the commercial fishery targets large male crabs.

One possible explanation for the low crab density in the upper Bay is that one or more limiting factors completely prevent recruitment of young crabs and that adults immigrate into the upper Bay by walking from the lower Bay. However, if this were the primary mechanism, we would expect a gradual decline in abundance along the length of the Bay rather than the observed dramatic abundance transition (Fig. 2). One juvenile crab was captured up-Bay, demonstrating that some crabs recruit in the upper Bay.

Another possibility is that crabs are recruiting into the upper Bay, but that extreme temperature or salinity events periodically kill most of the adult population in the upper Bay, leaving only a few survivors. In 1 study, 100% of adult female crabs (n = 8) died when they were held at 1.6°C for 35 d and 1 out of 8 died when held at 5.1°C for 48 d. No mortality occurred in the 10.1 and 14.8°C treatments (Shirley et al. 1987). The coldest temperatures that we have documented in our oceanographic surveys occurred during March, when the temperature was 3.1 to 3.6°C at 10 m depth in the upper Bay (Fig. 7). While these temperatures might cause some mortality, they probably are not extreme enough to kill the majority of the population. On the other hand, it is possible that colder temperature events have gone undetected, since only 3 February and 2 March oceanographic surveys have been conducted in Glacier Bay. Furthermore, we do not know the duration of cold temperature extremes in Glacier Bay.

Shallow estuaries like northern San Francisco Bay are characterized by dramatic seasonal changes in salinity near major freshwater input sources that can periodically kill entire benthic communities (Smith 1987, Nichols et al. 1990). Although deep fjord estuarine systems like Glacier Bay have large sources of freshwater input and the surface salinity can be greatly diluted, a normal-salinity refuge persists at depth (Figs. 4 & 9). Dungeness crabs can detect very small changes in salinity (Sugarman et al. 1983), and since adult crabs are highly mobile, it seems likely that adult

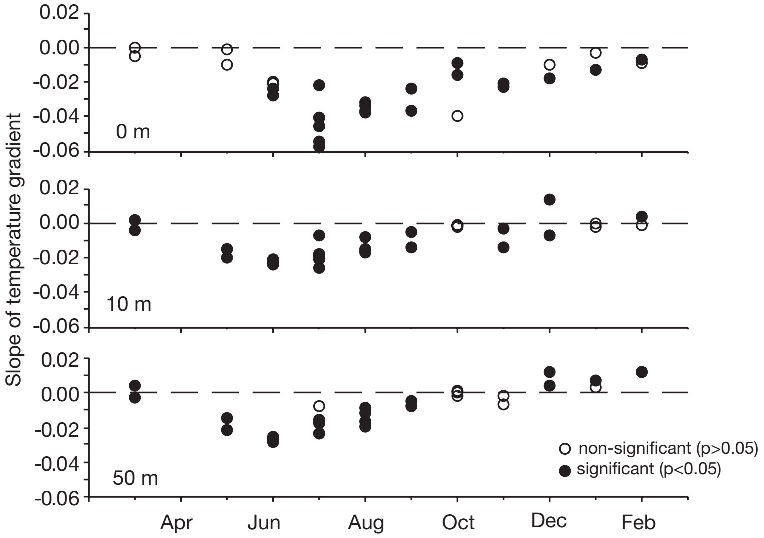

Fig. 6. Slope of the temperature gradient from the lower to upper Bay at 3 depths (0, 10 and 50 m) estimated with linear regression. Negative slopes represent conditions with colder temperatures in the upper part of the Bay. Each point represents data from an oceanographic survey conducted from 1992 to 2001

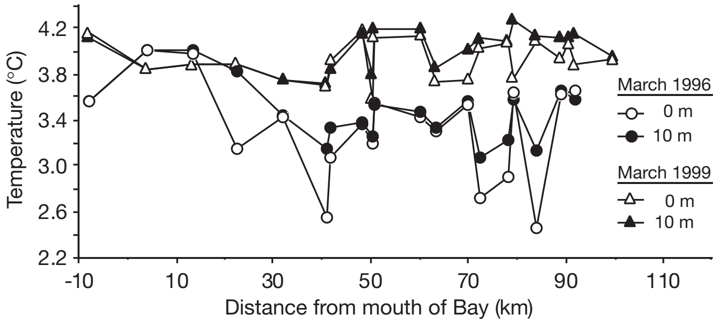

Fig. 7. Temperature data at 2 depths from the mouth to the head of Glacier Bay, collected during the 2 coldest oceanographic surveys, March 1996 and March 1999

crabs could escape physiologically stressful low-salinity surface water by moving into deeper water.

If the low density of crabs in the upper Bay were caused by high sustained adult mortality, we would expect to see a broad range of size classes and a rarity of very large individuals. The narrow size frequency distribution (Fig. 3) and the lack of small crabs in the upper Bay is consistent with poor survival in one of the pre-adult life stages. Recruitment could be episodic with an occasional successful cohort surviving. Alternatively, recruitment could be very low and continuous, combined with low adult mortality rates. Over time, several small cohorts would accumulate near the maximum carapace size, after which growth rates decline substantially (Wainwright & Armstrong 1993). In this scenario, the density of the young upper Bay cohorts would be so low that they would be unlikely to be caught in our pots. The shape of the size-frequency distribution, the mobility of adults, the restriction of low salinity to surface waters and the absence of lethally low temperatures all suggest that adult mortality is an unlikely explanation for the low density found in the upper Bay.

Low temperatures can substantially slow down the growth of juvenile crabs (Gutermuth & Armstrong 1989, Kondzela & Shirley 1993, Wainwright & Armstrong 1993). Growth models (Wainwright & Armstrong 1993) that were integrated with monthly temperatures from Glacier Bay predicted substantially slower growth for juvenile Dungeness crab in the upper Bay than in the lower Bay (Fig. 8). The greater length of time that Dungeness crabs are small would increase mortality because juvenile crabs are more vulnerable to predation (Reilly 1983, Orensanz & Gallucci 1988, Gunderson et al. 1990, Fernandez et al. 1993b, Armstrong et al. 1995) and to cannibalism (Fernandez et al. 1993a,b).

The lowest salinities in surface water occurred from June to September and were more frequent in the upper Bay (Fig. 10). Low salinities are likely to occur in September, when crab megalopae are settling. Dungeness crabs are hyperosmoregulators when the salinity is below 32 ppt (Sugarman et al. 1983, Brown & Terwilliger 1992). First instar juveniles are less able to osmoregulate than megalopae or adults (Brown & Terwilliger 1992). During the summer, juvenile crabs that recruited the previous autumn would still be constrained to shallow nearshore habitats because of their small size and thus, would be subjected to a second round of osmotic stress. Since osmoregulation requires ATP for active transport, osmotic stress probably translates into further reduced growth rates for juvenile crabs (Orensanz & Gallucci 1988). We believe that low salinity surface water is unlikely to have a large effect on adults because they are mobile and can retreat to high salinity refuges in deeper water. In contrast, juveniles would be exposed to significantly increased predation if they left the shallow habitat (Eggleston & Armstrong 1995). Thus, low surface salinities may have deleterious effects on juvenile crabs via 2 mechanisms: (1) juvenile

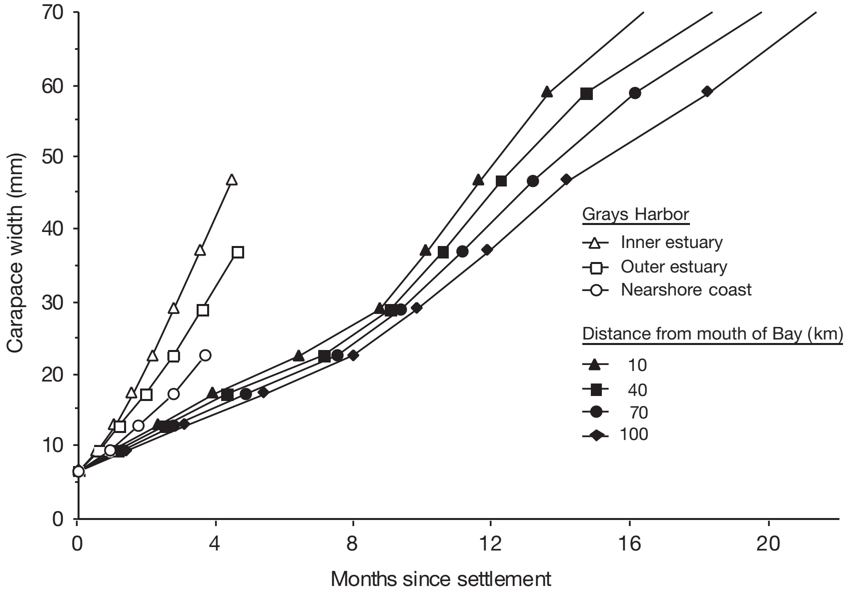

Fig. 8. *Cancer magister.* Predicted growth rate at 4 locations within Glacier Bay and 3 locations in Grays Harbor, WA; based on an integrated growth model that combines a bent-line model for molt interval with a temperature-dependent model for inter-molt interval (Wainwright & Armstrong 1993)

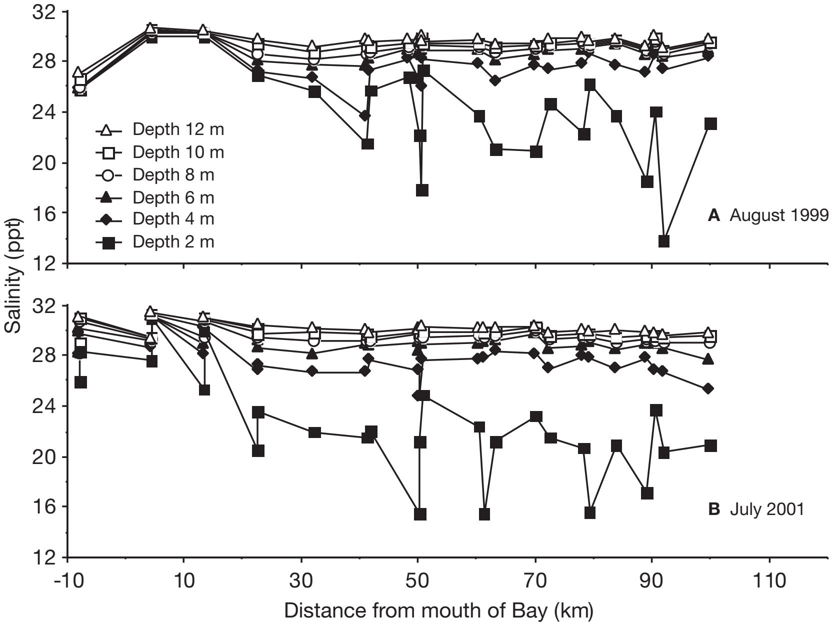

Fig. 9. Salinity gradients at 6 depths from the mouth to the head of Glacier Bay of major fjords during oceanographic surveys conducted during August 1999 and July 2001

crabs in the upper Bay may be subject to increased predation through extended time at small size; and (2) juvenile crabs may be forced into deeper, more hazardous depths to escape low salinities.

In SE Alaska, female crabs release larvae between May and June (Shirley et al. 1987, Swiney & Shirley 2002) and megalopae settle around September (G. Eckert pers. comm.). Little is known, however, about the movement, distribution or relative abundance of larvae in SE Alaska between hatching and settling. One possible model for the larval cycle of Dungeness crab in Glacier Bay is that larvae emigrate from Glacier Bay into the Gulf of Alaska and join a large meta-population of larvae, which is a common pattern among brachyuran crabs (Epifanio 1988, McConaugha 1988, Christy & Morgan 1998). Brachyuran megalopae enter estuaries from coastal waters by vertically migrating to the surface on flood tides (Epifanio 1988, McConaugha 1988, DeVries et al. 1994, Tankersley & Forward 1994, Lochmann et al. 1995, Rodriguez et al. 1997, Christy & Morgan 1998, Garrison 1999). In estuarine waters, Dungeness crab megalopae have been observed along tidal fronts in higher densities during flood than ebb tides (Eggleston et al. 1998). This suggests that Dungeness crabs may also return to estuaries by vertically migrating on flood tides. The northward flow of the Alaska Current creates a down-welling zone along the coast of SE Alaska that would probably concentrate larvae in nearshore waters (Jamieson & Armstrong 1991). According to this model, as the larvae mature into megalopae, they would vertically migrate toward the surface on flood tides to return to interior SE Alaska waters, including Glacier Bay.

A second possible model for the larval cycle is that larvae stay in Glacier Bay to mature. In Georgia Strait, off the NE end of Vancouver Island, where the bathymetry is similar to that of SE Alaska, megalopae appear to have behavioral adaptations that facilitate retention. Megalopae in Georgia Strait remain at 150 m during the daytime, a behavior that keeps them beneath the surface waters, where there is net offshore transport (Jamieson & Armstrong 1991).

In both larval models, the larvae migrate vertically. In the first model, vertical migration facilitates movement into estuaries, and in the second model it facilitates remaining at a depth with neutral transport. Brachyuran species are negatively phototropic and

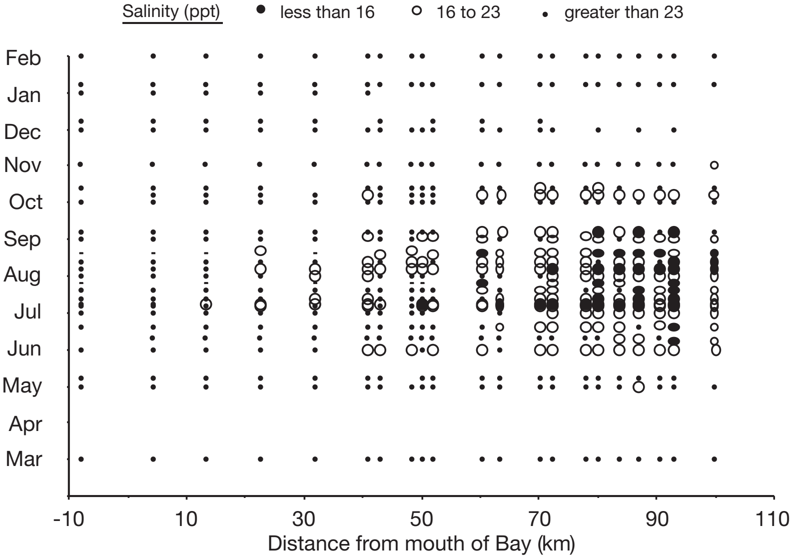

Fig. 10. Seasonal occurrence of 3 salinity range values (16, 16 to 23 and >23 ppt) from the mouth to the head of Glacier Bay. Each horizontal line of points represents an oceanographic survey conducted from 1992 to 2001

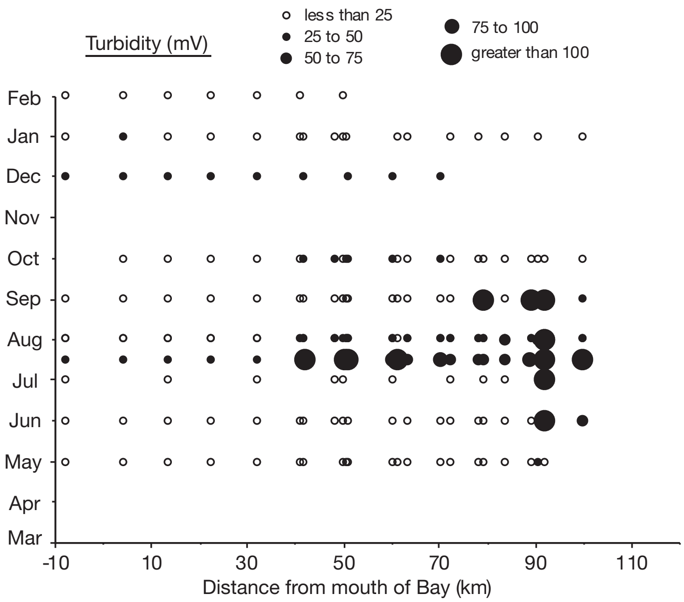

Fig. 11. Seasonal occurrence of maximum turbidity values from the mouth to the head of Glacier Bay. Each point represents the maximum turbidity value observed during a conductivity temperature depth (CTD) cast. Each horizontal line of points represents an oceanographic survey conducted from 1999 to 2001

probably use light threshold cues to descend during the day (Forward 1987). Since the upper Bay exhibits higher turbidity (Fig. 10), which reduces light penetration, megalopae (or larvae) may not descend as deep in the upper Bay. Jamieson et al. (1989) suggest that megalopae in turbid waters do not descend as deep during the day. Reduced vertical migration in the upper Bay could cause the larvae or megalopae to remain in a portion of the water column where net transport is toward the lower Bay. This effect would tend to reduce recruitment in the upper Bay.

Winds can create surface currents that can quickly transport megalopae over substantial distances (Ennis 1983, Hobbs et al. 1992, McConnaughey et al. 1992, Eggleston & Armstrong 1995). The adult crabs we see up-Bay might be the descendents of megalopae transported by a wind-event that coincided with a high concentration of megalopae in the lower Bay. This scenario would be similar to that observed along southern Vancouver Island in Juan de Fuca Strait, where surface currents normally prevent megalopae from moving into the Strait, but periodic wind events cause disruption of the surface current and megalopae are episodically transported into the Strait (Jamieson & Armstrong 1991).

If larvae are retained in Glacier Bay, the temperature and salinity conditions we observed could substantially decrease the proportion of larvae surviving to megalopae, especially in the upper Bay. Larval survival is affected by both temperature and salinity (Reed 1969, Sulkin & McKeen 1989, Moloney et al. 1994) and the summer water temperatures in upper and lower Glacier Bay are below the optimal temperatures for larval survival in this species. Individual-based simulation models predict that the proportion of larvae surviving to megalopae at temperatures below 10°C decreases approximately 20 % for each 1°C drop in temperature (Moloney et al. 1994). Salinity above 26 ppt has little effect. Below 26 ppt, however, the proportion of surviving larvae falls by 10 % for each ppt decrease in salinity. If larvae reside in the surface water when the salinity drops below 26 ppt, the survival would be further reduced. The additive effects of low salinity surface water and colder temperatures in the upper Bay could substantially reduce the survival of larvae.

In summary, we found that adult Dungeness crabs can survive in habitats heavily influenced by glaciers. The significantly fewer crabs in the upper Bay and the sharp abundance transition around 40 km up-Bay suggests that the threshold value of one or more limiting factors was exceeded, and the narrow size frequency distribution suggests the limiting factors are affecting one of the pre-adult life stages. The upper Bay appears to be a poor environment for both larvae and new recruits. The suspected slower growth for juvenile Dungeness crab in the upper Bay might increase the length of time that Dungeness crabs are small, which increases their exposure to predation (Reilly 1983, Orensanz & Gallucci 1988, Gunderson et al. 1990, Fernandez et al. 1993b, Armstrong et al. 1995) and to cannibalism (Fernandez et al. 1993a,b). When megalopae first settle in the intertidal and/or upper subtidal, they are likely to be exposed to low salinity surface water in early fall, which can cause osmotic stress and compound their slow growth. Because of slow growth, the young crabs are likely to still be in shallow water the following summer, when the seasonal low salinity surface water starts again. Whether Dungeness crab larvae mature in the Gulf of Alaska or stay in Glacier Bay, is a topic of future research. Maturation in the Gulf of Alaska seems more plausible, because the temperature and salinity conditions we observed should substantially decrease the proportion of larvae surviving to megalopae, especially in the upper Bay.

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