

Development and Distribution of Dungeness Crab Larvae in Glacier Bay and Neighboring Straits in Southeastern Alaska: Implications for Larval Advection and Retention

Wongyu Park* and Thomas C. Shirley¹

Department of Marine Biotechnology, Soonchunhyang University, Asan 336-745, Korea; ¹Harte Research Institute, Texas A&M University-Corpus Christi, 6300 Ocean Drive, Unit #5869, Corpus Christi, TX 78412-5869, USA

Abstract: Development and distribution of larval Dungeness crab, *Cancer magister* Dana, 1852 were investigated in southeastern Alaska from late May to mid-September in 2004. Larvae were collected during daylight hours at three inner and two outer Glacier Bay stations at the two different depths in the water column, above and below the thermocline. Larval density decreased dramatically for three larval stages, zoeae I (ZI), zoeae IV, and zoeae V (ZV), but relatively little for zoeae II and zoeae III. ZI predominated at all stations in late May and were collected until late July. Larval stages progressed seasonally from ZI to ZV and density decreased from ZI through ZV. The densities of each zoeal stage at the inner and outer bay stations and at the shallow and deep depths were similar. The density of each larval stage above (shallow) and below (deep) the thermocline and between inner and outer bay stations were not significantly different. The occurrence of larval Dungeness crab is dramatically later than in other parts of the species range, in that larvae appear in abundance beginning in late May. The pattern of spatial distribution of larval stages for the inland waters of Alaska was also markedly different than the patterns reported for Dungeness crab larvae from other parts of the species range, in that the early and intermediate stages occurred within inland waters; from British Columbia to California these larval stages increase in abundance with distance offshore.

Keywords: larval development, larval distribution, thermocline, Dungeness crab, *Cancer magister*

INTRODUCTION

Estuarine crab larvae generally follow one of two patterns: 1) crab larvae emigrate from the estuaries soon after

hatching, undergo development in the coastal regions, and then immigrate to the estuaries; or, 2) crab larvae are retained and undergo development within the parental estuaries (Sandifer, 1975; Lambert and Epifanio, 1982; DiBacco et al., 2001). These patterns are controlled by vertical migratory behaviors, which allow larvae to utilize tidal current patterns to determine their horizontal position (Sandifer, 1975; DiBacco et al., 2001; Yannicelli et al., 2006). In Chesapeake Bay, Virginia, distribution of blue crab zoeae I (ZI) in the upper portion of the water column results in their seaward transport from the estuaries during ebb tides (Provenzano et al., 1983). Megalopae return to near coastal waters or estuaries during nocturnal flood tides after larval development offshore (Little and Epifanio, 1991; Epifanio, 1995).

Alternatively, some crab larvae are retained in estuaries throughout their larval development. All larval stages of *Lophopanopeus* spp. in San Diego Bay, California (DiBacco et al., 2001) and *Rhithropanopeus harrisi* (Gould, 1841) in Broadkill River, Delaware (Lambert and Epifanio, 1982) are found within the bays. Endogenous vertical migrations associated with diel tidal rhythms aid larval retention within the bay (Sandifer, 1975; Cronin and Forward, 1979). However, endogenous and exogenous rhythms of larvae are not location-specific, but species-specific: in Delaware Bay, *R. harrisi* larvae are retained in the bay, while *Uca* spp. are advected from the bay and return to the bay after development in the offshore coastal region (Lambert and Epifanio, 1982). In San Diego Bay, California, *Lophopanopeus* spp. zoeae are retained in the bay while *Pachygrapsus crassipes* Randall, 1839 emigrate to the coastal region and return to the bay after larval development (DiBacco et al., 2001).

Off the Pacific northwest coast, ZI of Dungeness crab, *Cancer magister* Dana, 1852 is found within tens of

*To whom correspondence should be addressed.
Tel: +82-10-5538-5923; Fax: +82-41-530-1638
E-mail: pwg09@hotmail.com

kilometers of shore while post ZI and megalopae are found progressively further offshore, and late intermolt stages of megalopae occur nearshore (Lough, 1976; Reilly, 1983; Jamieson et al., 1989). Estuarine run-off and upwelling move surface waters and presumably larvae offshore, approximately 30 km from the coast (Lough, 1976; Reilly, 1983). Internal waves associated with tides and surface winds may transport megalopae shoreward (McCounnaughey et al., 1994; Shanks, 1995; Miller and Shanks, 2004).

Water temperature affects embryo development rate and timing of crab larval hatching (Wild, 1980; Shirley et al., 1987). Development rates of embryos during the incubation period are inversely related to temperature: the duration of egg incubation at 15°C was 42 days while that at 5°C was 160 days (Shirley et al., 1987). Timing of larval hatching of Dungeness crabs along the west coast of North America encompasses a wide temperature range. Hatching occurs progressively later northward from California, where larval release occurs in December and January (Wild, 1980; Reilly, 1983), to Alaska where it occurs in late April and May to July (Shirley et al., 1987; Fisher, 2006).

Glacier Bay is located approximately 50 km west of Juneau, southeastern Alaska. Semi-diurnal tides result in approximately 4 m tide ranges and create tidal fronts throughout the bay; maximum tidal ranges are 7.5 m (Hooge and Hooge, 2002). Strong semi-diurnal tidal currents inside and outside of the bay may result in the

exchange of zooplankton and waters between the bay and adjacent straits (Hooge and Hooge, 2002; Cokelet et al., 2007).

We investigated the development and distribution Dungeness crab larvae to provide information about their early life history in southeastern Alaska. We examined the larval densities between shallow and deep depths during ebb and flood tides to investigate whether Dungeness crab larvae are advected from or retained within Glacier Bay. In addition, we provide information of the seasonal pattern of occurrence of Dungeness crab larvae in the study areas.

MATERIALS AND METHODS

Data collection

Zooplankton were collected at five stations inside and outside of Glacier Bay, fortnightly, from late May to mid-September 2004 (Fig. 1). Three stations located within Glacier Bay were defined as inner bay stations; two stations positioned near the mouth of the bay in the Icy Strait were defined as outer bay stations. All samples were collected during daylight hours from 0800 to 1800 hrs Alaska Standard Time. The sampling stations were located with a global positional system (GPS, GPSMAP 176, Garmin Inc.). Before plankton sampling, salinity and temperature were measured with a CTD (conductivity, temperature, and depth profiler, Sea-Bird SBE 19 Seacat) from the water

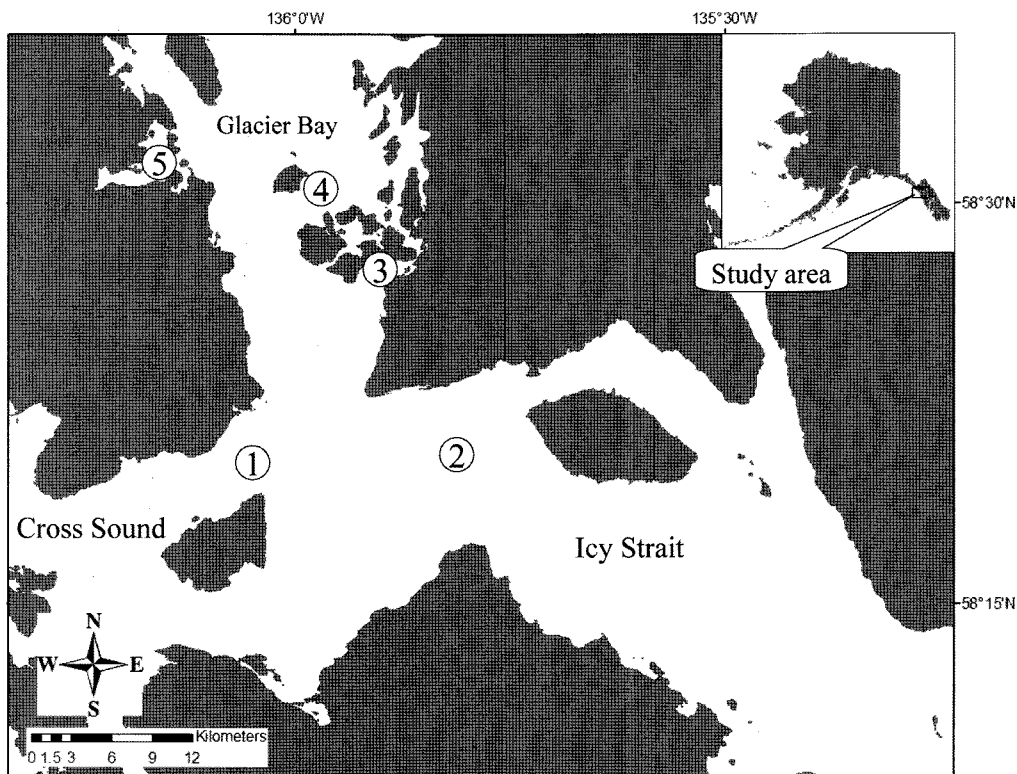


Fig. 1. Map of sampling stations. Zooplankton at stations 1 to 5 were collected fortnightly from late May to mid September 2004.

surface to within 10 m of the bottom. A multiple opening Tucker trawl (=NIO net) with 1 m² mouth opening and 500 µm mesh was deployed at two positions in the water column, above and below the thermocline, or the zone of greatest temperature change if a thermocline was not evident. General Oceanics model 2031 flowmeters were installed inside the nets to measure the water volume filtered. The Tucker trawl was released from a vessel slowly moving to windward against the current direction to generate an oblique angle of the path of the plankton net. The approximate Tucker trawl depth was estimated by multiplying the sine of the angle of the line by the length of line released. When the Tucker trawl approached the bottom, it was retrieved at a 45° angle. During the retrieval of the Tucker trawl, the first net was closed below the thermocline depth; the sample collected at that depth was regarded as a deep sample. The second net was opened simultaneously when the first, deep net was closed, and the tow continued to the surface. The sample collected by the second net was regarded as the shallow sample. Two replicate collections were made at each station. On 9 September, only surface water was sampled with the Tucker trawl for 5 minutes, twice at each sampling station, because no larvae were collected in late August. Samples collected were preserved in 5% buffered formalin on the boat and transported to the lab where *Dungeness* crab larvae were sorted, staged, and enumerated.

The sum of the densities of each larval stage during the entire sampling period divided by the sum of ZI density of all stations during the entire sampling period was regarded as the proportion of larvae surviving. The decrease in total number of larvae in the subsequent stages divided by the total number of larvae in the previous stage was defined as larval loss, the sum of potential larval advection and mortality. For this analysis, densities of each zoeal stage during the entire sampling period were summed.

Statistical analysis

The significance level used for all statistical analyses in our study was 0.05. The Kolmogorov-Smirnov test (hereafter K-S test) was used to test normality. If the p-value was higher than 0.05 in K-S test, the data were square-root transformed. After data transformation, the K-S test was used to test normality and the F-test to test equal variance. The differences in ZI density between shallow and deep depths during ebb and flood tides were analyzed with Analysis of Variance (ANOVA) after square root transformation. Tides at the sampling were estimated by the Tides and Currents for windows 2.1 (Nautical software Inc.). Larval densities of ZI on 27-28 May and 14 and 29 June were included in the analysis because ZI was predominant on these sampling times, but rare on other sampling dates. The K-S test was used to test for differences of densities of each larval stage between stations inside the bay and stations outside the bay and between larvae in the deep and shallow depths. All data were included in the analysis.

RESULTS

Distribution and density change of larvae: A total of 2,874 zoeae and 1 megalopa of *Dungeness* crab was collected during the sampling period. Larval density from one larval stage to the next decreased dramatically for three larval stages: ZI (66%), ZIV (77%), and ZV (99%) while it decreased relatively less for ZII (46%) and ZIII (37%) (Fig. 2). The densities of ZI at shallow and deep depths at all stations were not significantly different (Fig. 3; Table 1). Densities of ZI between shallow and deep depths during ebb (ANOVA, $F=0.289$, $df=16$, $p=0.598$) and flood (ANOVA, $F=0.055$, $df=10$, $p=0.819$) tides were similar. Larval density was highest on 27-28 May and ZI (92.4%) predominated; larval abundance gradually decreased

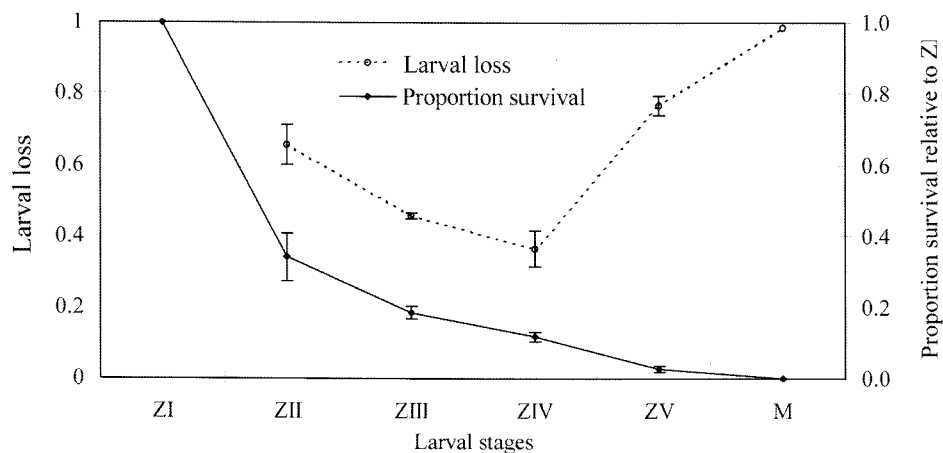


Fig. 2. Larval loss and the proportion of larvae surviving relative to zoeae I. Error bars indicate standard error between inner and outer Glacier Bay stations. Larval loss combines larval advection and mortality; larval survival indicates larvae remaining within the sampling area.

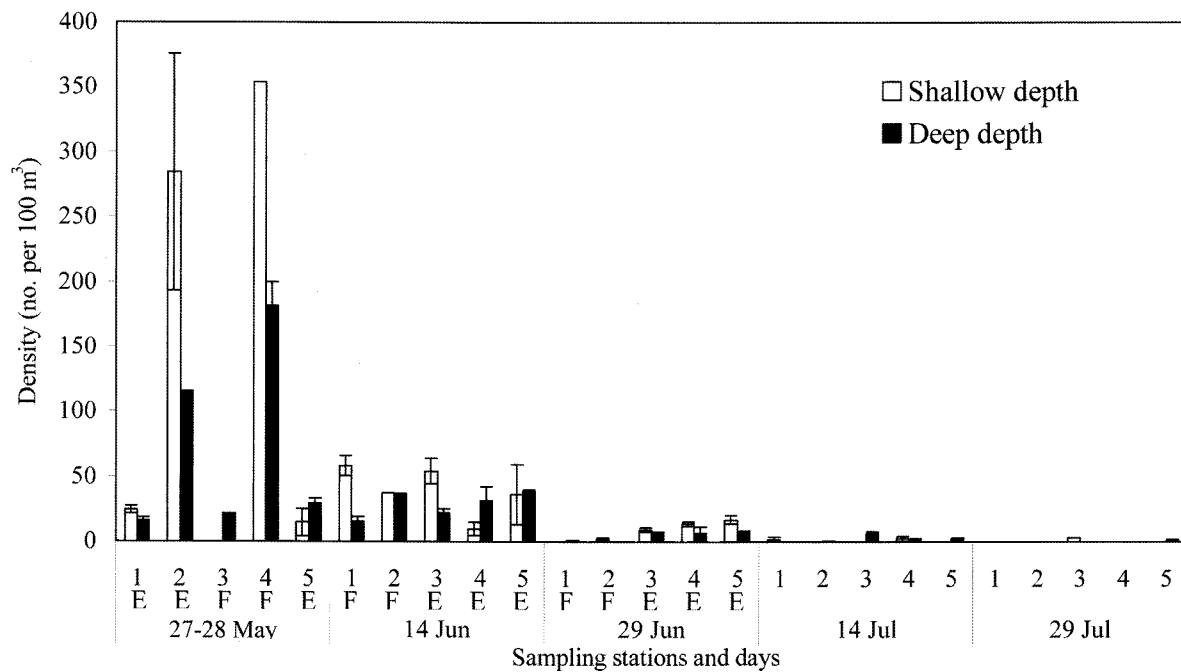


Fig. 3. Comparison of zoeae I density between shallow and deep depths. Zoeae I collected at inner and outer Glacier Bay stations in shallow and deep depths are compared. Error bars indicate standard errors of zoeae I densities between replicates at each station. No error bars indicate no replicate sampling (Deep depth, stations 3 and 4 on 27-28 May and station 2 on 14 June, 2004; shallow depth, station 4 on 27 May and station 2 on 14 June, 2004), or the same larval densities occurred at both depths. E and F indicate ebb and flood tides, respectively.

thereafter. Larval stages developed seasonally from ZI to the fifth zoeal stage (ZV); density decreased from ZI through ZV (Fig. 4). The densities of each zoeal stage in the inner and outer bay stations were similar (Fig. 4; Table 1). There was no significant difference in mean density of any larval stage above and below the thermocline (Fig. 5; Table 1).

Thermocline depths: Thermocline depths varied at each sampling station and date (Table 2). In general thermocline depths were deepest at station 2 while they were shallowest at station 3 and 5.

Table 1. Kolmogorov-Smirnov test (K-S test) results for the difference in densities of Dungeness crab larvae. Differences in the density of each larval stage above (shallow) and below (deep) the thermocline and between inner and outer bay stations were tested with K-S test. Stations located outside of Glacier Bay (1 and 2) were regarded as outer bay stations, while stations located inside of Glacier Bay (3, 4, and 5) were regarded as inner bay stations

	Difference of larval density between shallow and deep depths	Difference of larval density between inner and outer bay station
	p	p
ZI	0.999	0.202
ZII	0.979	0.972
ZIII	0.875	0.997
ZIV	0.324	0.944
ZV	0.199	0.900

DISCUSSION

Crab larvae may change their vertical location to enhance emigration on favorable tides (Sandifer, 1975; DiBacco et al., 2001). ZI of estuarine crabs that emigrate from hatching sites to coastal areas are concentrated at the surface of ebbing tides to emigrate to coastal areas (DiBacco et al., 2001; Yannicelli et al., 2006) while crab larvae that are retained are more abundant near the bottom than near the surface where net transport is upstream (Sandifer, 1973). Ovigerous females of *Callinectes sapidus*, Rathbun, 1896 release more than 90% of their larvae in a single ebb tide, favoring emigration of ZI (Provenzano et al., 1983). If the ZI of Dungeness crabs was advected after hatching from our study site to coastal areas for development, the ZI should have occurred at a favorable depth and tide. The lack of differences in ZI densities between shallow and deep depths during ebb and flood tides in our study area suggest that ZI in our study area did not follow a pattern of emigrating larvae.

However, the thermocline depth varied with sampling stations and times, and the use of only two sampling depths in our study may have been too coarse to identify the vertical distribution of ZI. Vertical migration of Dungeness crab larvae along their distribution range has been reported (Booth et al., 1985; Hobbs and Botsford, 1992; Park and Shirley, 2005). Zoeae I had strong vertical migration patterns at dawn and dusk at a site located near our

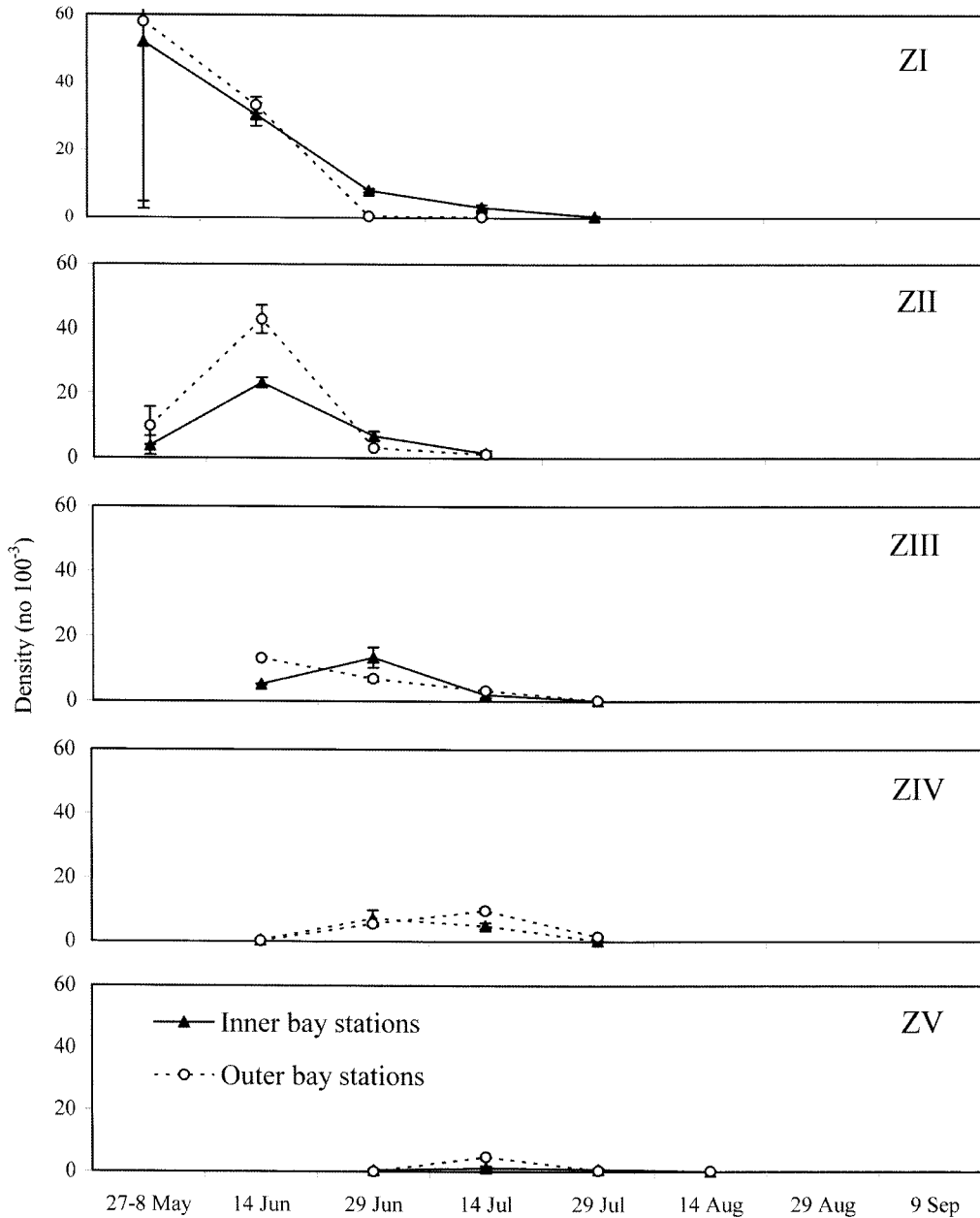


Fig. 4. Comparison and seasonal changes of mean larval density between inner and outer Glacier Bay stations, all sampling stations included. Fortnightly sampling dates near mouth and within Glacier Bay in 2004 were on 27-8 May, 14 Jun, 29 Jun, 14 Jul, 29 Jul, 14 Aug, 29 Aug, and 9 Sept. Vertical bars represent standard error of larval densities between stations.

sampling sites (Hobbs and Botsford, 1992; Park and Shirley, 2005).

The relatively higher decrease in density of ZI than the later zoeal stages may not be entirely a result of mortality, but instead may represent advection of larvae to other areas. In general, in estuaries from which larvae are advected, post-ZI are not found but megalopae are (Reilly, 1983; Epifanio, 1995; DiBacco et al., 2001). Advection of Dungeness crab larvae surely occurs within our study area, but the quantity or relative percentage of larvae that are advected is unknown. Although larval densities of post ZI in our study

area in May and June were relatively higher than those reported at the close study locations by Fisher (2006), the lack of late stage larvae during July and August in our study area supports the hypothesis that Dungeness crab larvae are advected. If larvae were retained within our study areas, a decreasing abundance of larvae corrected for larval mortality (which is usually very high) should occur throughout the sampling period.

Most studies of Dungeness crab larvae have reported that ZI occur near shore and post ZI are found progressively further offshore (Lough, 1976; Reilly, 1983). Late intermolt

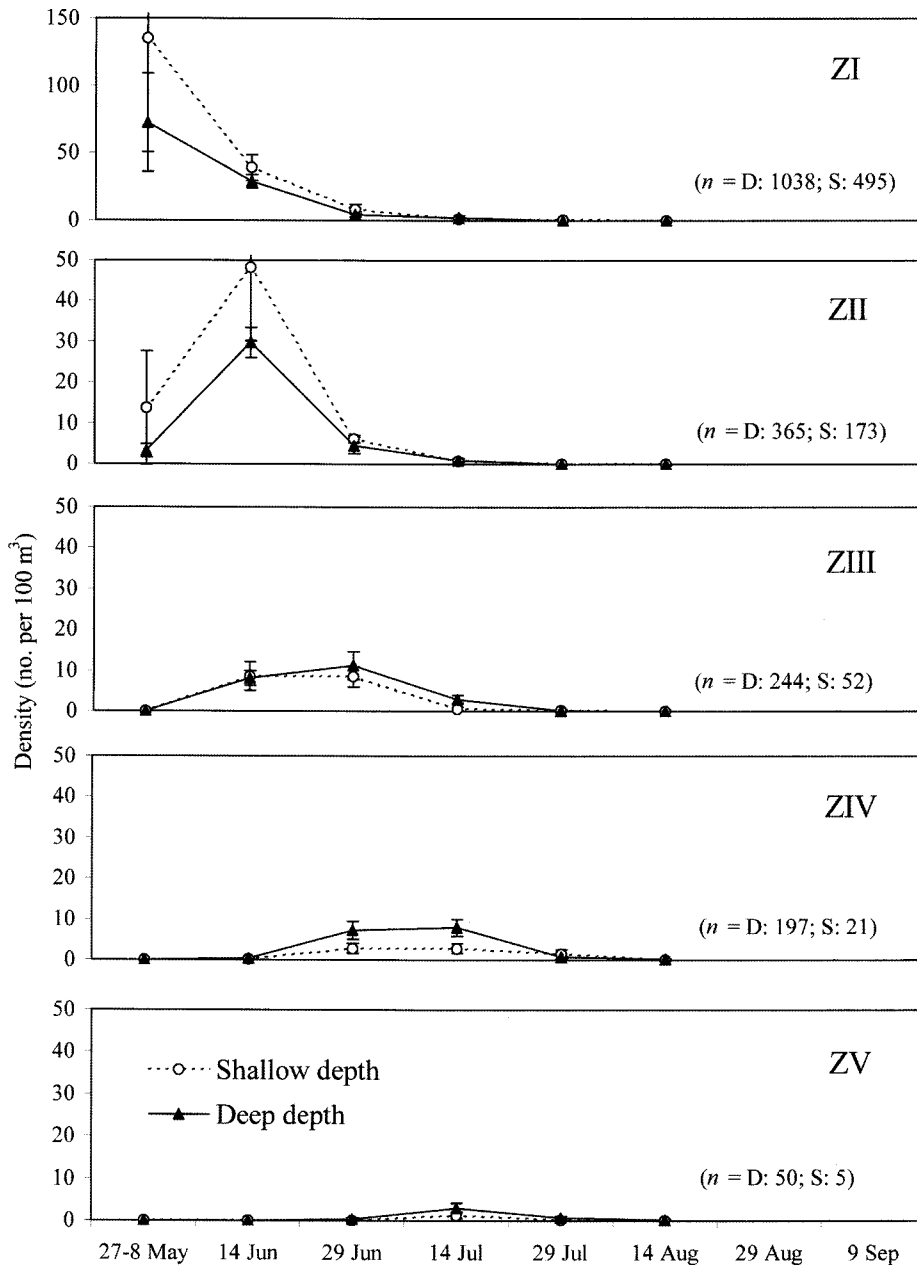


Fig. 5. Comparison of mean larval density of Dungeness crab between shallow and deep depths. Dungeness crab larvae were collected fortnightly near mouth and within Glacier Bay in 2004.

stage megalopae are predominant inshore (Hatfield, 1983; Eggleston and Armstrong, 1995; Miller and Shanks, 2004). In our study area, post ZI occurred at every station until mid-July. This represents a distinctly different pattern of larval distributions from the previous study that larvae were advected offshore for development (Lough, 1976; Reilly, 1983). If larvae had been advected offshore in southeast Alaska, larval abundance would have been higher offshore; however, larval densities off the coast of southeastern Alaska were low during all sampling months (Park, 2007).

The low densities of ZV and megalopae that we found may have resulted from different behaviors of those larval

stages in the water column and sampling biases. Zoeae V are photonegative and reside in the deep water nearer the bottom, while megalopae are highly surface-associated (Lough, 1976). In addition, ZV and megalopae are stronger swimmers and more readily avoid nets. Accordingly, ZV and megalopae could be less easily collected than ZI-ZIV by net tows. Sampling gear such as light traps may be more effective than nets for sampling megalopae. Within our sampling area, light traps collected large numbers of megalopae, while plankton tows mostly collected zoeae at the same area (Porter et al., 2008).

The decrease in densities of subsequent larval stages in

Table 2. Depths (m) of thermocline in Glacier Bay from May to September 2004. Thermocline was used to separate shallow water and deep water plankton tows collected biweekly in Glacier Bay and neighboring straits, from May to September, 2004. Depths in parentheses indicate bottom depths at the sampling stations. Asterisks indicate that the water column was not stratified, these depths were used to separate the sampling strata. Question marks note data were unavailable. On September 9, only surface water was sampled. F=Flood tide; E=Ebb tide (Depth in meters)

Sampling date	Station				
	1	2	3	4	5
May 27-8	*15 (92) E	17 (127) E	15 (54) F	10 (70) F	10 (67) E
June 14	*21 (84) F	33 (110) F	*11 (?) E	*15 (64) E	10 (44) E
June 29	*17 (84) F	20 (109) F	*13 (52) E	20 (67) E	14 (48) E
July 14	10 (78) F	20 (110) F	8 (53) F	16 (70) E	10 (50) F
July 29	10 (81) F	27 (110) F	15 (?) F	10 (70) E	8 (56) E
August 14	20 (80)	25 (106)	15 (52)	20 (68)	15 (47)
August 29	*13 (83)	25 (107)	5 (54)	5 (70)	10 (52)

*On September 9, only surface water was sampled.

our study may have been a result of natural mortality; conversely, the declines could have represented larval advection to other areas. The magnitude of Dungeness crab larvae that were advected or retained within the study sites is unknown. Our data support the contention that larvae incubated at different temperatures were mixed within our study area. Small numbers of all larval stages persisted within inland waters. Perhaps more importantly, the pattern of distribution of larval stages in southeastern Alaska, both spatially and temporally, was markedly different than the distributional pattern reported from other parts of the range of Dungeness crabs.

ACKNOWLEDGMENTS

We thank many University of Alaska Fairbanks graduate students who helped with sampling. This research was sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-12) and the Global Climate Change Grant (G/C03-01).

REFERENCES

- Booth J, Phillips A, and Jamieson GS (1985) Fine scale spatial distribution of *Cancer magister* megalopae and its relevance to sampling methodology. In: Proceedings of the symposium on Dungeness crab biology and management. University of Alaska, Sea Grant College Program Report 85-3, pp 273-286.
- Cokelet ED, Jenkins AJ, and Etherington LL (2007) A transport of Glacier Bay ocean currents measured by Acoustic Doppler Current Profiler (ADCP). In: Piatt JF, and Gende SM (eds), Proceedings of the fourth Glacier Bay science symposium, 2004. U.S. Geological Survey, information and technology report USGS/BRD/ITR-2007-5047, Washington DC pp 74-77.
- Cronin TW and Forward RB Jr (1979) Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. *Science* 205: 1020-1022.
- DiBacco C, Sutton D, and McConnico L (2001) Vertical migration behaviour and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. *Mar Ecol Prog Ser* 217: 191-206.
- Eggleston DB and Armstrong DA (1995) Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol Monogr* 65: 193-216.
- Epifanio CE (1995) Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid Atlantic states. *Bull Mar Sci* 57: 713-725.
- Fisher JL (2006) Seasonal timing and duration of brachyuran larvae in a high-latitude fjord. *Mar Ecol Prog Ser* 323: 213-222.
- GPSMAP 176 (2003) Garmin Inc. Olathe, KS.
- Hatfield SE (1983) Intermolt staging and distribution of Dungeness crab, *Cancer magister*, megalopae. In: Wild PW and Tasto RN (eds), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. *Cal. Fish Game Bull* 172: 85-96.
- Hobbs RC and Botsford LW (1992) Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab *Cancer magister*. *Mar Biol* 112: 417-428.
- Hooge PN and Hooge ER (2002) Fjord oceanographic patterns in Glacier Bay National Park. U.S. Geological Survey, Alaska Science Center, Gustavus, Alaska, pp1-148.
- Jamieson GS, Phillips A, and Hugget WS (1989) Effects of ocean variability on the abundance of Dungeness crab larvae. *Can Spec Publ Fish Aquat Sci* 108: 305-325.
- Lambert R and Epifanio CE (1982) A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. *Estuaries* 5: 182-188.
- Little KT and Epifanio CE (1991) Mechanism for re-invasion of an estuary by two species of brachyuran megalopae. *Mar Ecol Prog Ser* 68: 235-242.
- Lough RG (1976) Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. *Fish*

- Bull* 74: 353-375.
- McConnaughey RA, Armstrong DA, Hickey BM, and Gunderson DR (1994) Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. *Fish Oceanogr* 3: 22-38.
- Miller JA, and Shanks AL (2004) Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. *Mar Ecol Prog Ser* 271: 267-279.
- Park W (2007) Advection and retention of larval Dungeness crab *Cancer magister* in Glacier Bay and adjacent areas. PhD Dissertation. University of Alaska Fairbanks, Alaska, USA.
- Park W, and Shirley TC (2005) Diel vertical migration and seasonal timing of the larvae of three sympatric cancrid crabs, *Cancer* spp., in southeastern Alaska. *Estuaries* 28: 266-273.
- Porter SS, Eckert GL, Byron CJ, and Fisher JL (2008) Comparison of light traps and plankton tows for sampling brachyuran crab larvae in an Alaskan fjord. *J Crust Biol* 28: 175-179.
- Provenzano AJ, McConaughy JR, Philips KB, Johnson DF, and Clark J (1983) Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Est Coast Shelf Sci* 16: 489-499.
- Reilly PN (1983) Dynamics of the Dungeness crab, *Cancer magister*, larvae off central and northern California. In: Wild PW, and Tasto RN (eds), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. *Cal Fish Game Bull* 172: 57-84.
- Sandifer PA (1973) Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. *Chesapeake Sci* 14: 235-257.
- Sandifer PA (1975) The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. *Est Coast Shelf Sci* 3: 269-279.
- Shanks AL (1995) Oriented swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. *J Exp Mar Biol Ecol* 186: 1-16.
- Shirley SM, Shirley TC, and Rice SD (1987) Latitudinal variation in the Dungeness crab, *Cancer magister* zoeal morphology explained by incubation temperature. *Mar Biol* 95: 371-376.
- Tides and currents for Windows 2.1 (1993) Nautical software Inc. Denver, Colorado.
- Wild PW (1980) Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, *Cancer magister*. *CalCoFI Rep* 21: 115-120.
- Yannicelli B, Castro LR, Valle-Levinson A, Atkinson L, and Figueroa D (2006) Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: implications for transport. *J Plank Res* 28: 19-37.

[Received October 20, 2008; accepted December 4, 2008]